THE RESPONSE OF SOLITARY BEES TO LANDSCAPE CONFIGURATION WITH FOCUS ON BODY SIZE AND NEST-SITE PREFERENCE

Dissertation

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The response of solitary bees to landscape configuration with focus on body size and nest-site preference

Abstract: This thesis was motivated by the rapid decline of wild pollinators, which is partly driven by the still not well understood impact of landscape configuration. Solitary bees are wild pollinators living in semi-natural landscape elements. I asked how different types of solitary bees (differing in body size and nesting guild) interact with the landscape. I focussed on the effect of landscape fragmentation on the performance and the pollination potential of wild bees with a spatially-explicit individual-based model. Therefore I identified how behavioural traits of bees are affected by body size and defined allometric rules. With a model based on these rules I simulated spatial foraging behaviour in different landscapes for different bee types. I found that the combination of both nest habitat availability and foraging habitat availability determined the response of bees to landscape structure. An increase of nest habitat relative to foraging habitat in the landscape increases the number of brood cells that bees can build in one day and improves pollination. Nesting guild only affected habitat usage, while body size affected the behaviour and the performance of bees. The percentage of foraging habitat that was visited by bees, as a pollination proxy, was least affected by body size. An experimental case study for one bee type (*Osmia bicornis,* a cavity-nesting bee of intermediate size) confirmed that both nest habitat and foraging habitat had a significant effect on the response of bees to landscape structures. The case study additionally revealed a high impact of microsite conditions around the nest. The effect of landscape fragmentation was rather positive than negative and always low compared to other factors, both in the model and the case study. I found that landscape fragmentation improves foraging performance, by facilitating more available space for nesting sites in edge structures reducing local competition between bees. I suggest that for both conservation of bees and for stimulation of pollination services the focus should be on protecting nest sites at small scales in addition to maintaining abundant foraging resources in the landscape.

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"Wenn die Maurerbiene nach vielen vorgenommenen Besichtigungen, sich an einen tauglichen Ort zu Anlegung der Wohnung oder des Nestes, erwählet hat; so fängt Sie, und zwar ohne alle Hilfe, den Bau selbst an. Alle die verschiedenen Verrichtungen, wozu beij Aufführung eines Gebäudes so viele Hände erfordert werden, verrichtet sie allein. Sie ist Baumeister, Sandführer, Kalchlöcher, Mörtelrührer, Handlanger, und Maurer. Und alle diese mannigfaltigen Arbeiten verrichtet sie mit einer bewundernswürdigen Geschicklichkeit, und Geschwindigkeit!"

Jacob Christian Schäffer (1764) - Die Maurerbiene in einer Rede beschrieben.

"Aber welcher Fleiss gehört dazu, um so und so viel Zoll Gänge in den Boden zu graben und alle die Zellen mit Futter zu versehen und wie wenig Zeit ist dem Weibchen zu dieser Arbeit vergönnt?"

Otto Schmiedeknecht (1882) - Apidae Europaeae

"The honey-bee's great ambition is to be rich, to lay up great stores, to possess the sweet of every flower that blooms. She is more than provident. Enough will not satisfy her, she must have all she can get by hook or crook."

John Burroughs (1887) - Birds and Bees, Sharp Eyes and Other Papers

"Die einsam lebenden Sammelbienen tragen Blütenstaub und Honig ein, so daß die auskriechende Larve wörtlich im überfluß schwimmt."

Otto Schmiedeknecht (1907) - Die Hymenopteren Mitteleuropas

"Five per cent vision is better than no vision at all. Five per cent hearing is better than no hearing at all. Five per cent flight efficiency is better than no flight at all."

Richard Dawkins (1986) - The Blind Watchmaker

Summary

Solitary bees are wild pollinators that pollinate wild plants and provide pollination services to crops. They are often considered as alternative to honeybees for crop pollination.

Land-use effects on solitary bees were reviewed in chapter 1. Severe losses of these natural pollinators are for a major part driven by land-use changes and agricultural intensification. Habitat loss has reduced nesting and foraging resources in past and more recent times. Landscape fragmentation has altered the spatial configuration of the patch mosaic and bees may be forced to fly longer distances and cross inhospitable fields without foraging resources. Solitary bees are present in most landscapes, but their response to landscape composition and configuration is not well understood yet. Field studies show different effects of resource availability and contradicting effects of fragmentation. One reason is that solitary bees cannot be generalized as one group of pollinators, since they differ in nesting preferences and vary over a wide range of body sizes. The central question I aim to answer is therefore how solitary bees of different body size and different nesting preference interact with the landscape.

Solitary bees vary relatively much in body size (ranging from about 4 to 28 mm in body length), but the effect of body size on their foraging behaviour has never been thoroughly investigated and reviewed so far. I identified several body-size related (proxy-) traits that affect pollen collection: visual ability, flight velocity, foraging and homing range, pollen transport capacity and flower handling time (chapter 2). I reviewed the literature and was able to quantify these relationships. Small bees were restricted in visual ability (smaller eyes perceive less light and have less sharpness), flew slower and required more time to collect pollen from a single flower. Compared to large bees they had the advantage that they also required less pollen per brood cell and thus fewer flowers. Therefore, I expect that small bees interact differently with the landscape than large bees. Small bees also had a shorter foraging and homing distance, which may point to lower flight capabilities but may alternatively be a result of lower area requirements depending on landscape composition and configuration. Flower handling times were apart from body size also highly affected by the resource collected (pollen or nectar) and the plant species. Trait measurements were in general amply available for intermediate sized bees and I was able to provide new allometric relationships and to evaluate existing ones. However, the number of available measurements for small and large bees was often low. Hence, systematic studies over the complete range of body sizes are required to confirm how well the few data points contribute to the real functional relationship.

Up to date there are no simulation models that compare the performance of different solitary bees at the landscape level. Body-size related traits affect individual foraging behaviour. I therefore combined different traits and behavioural rules in a spatially-explicit individual-based simulation model, SOLBEE, which mimics the behaviour and movement of pollen-collecting solitary bees (chapter 3). With this data-based model I combined bee traits and landscape characteristics to study their interactions. The model landscape was a square kilometre in size and consisted of many patches with foraging habitat separated by inhospitable matrix. Each landscape had a certain amount of foraging habitat and fragmentation that could be controlled. The foraging habitat had patch attributes such as floral density and minimum patch size. Bees differed in size and nesting preference (bee types) and individuals in nest location. The model system was further characterized by a timeframe of a single foraging day in which bees forage and compete for pollen. To focus on the effect of landscape fragmentation and to compare the performance of bee types directly, I scaled bee numbers with available foraging resources and body size. During a model day these central place foragers displaced pollen from flowers (distributed over a mosaic of patches) to their nest. The main goal was to compare how bees perform in terms of fitness (brood cells) and

pollination services (number of flowers visited, percentage foraging habitat visitation and foraging distance) within a foraging day. A simulation can be summarized as follows. A population of bees of a certain type (body size, nesting preference) is distributed over nesting sites in a certain artificial landscape (characterized by foraging habitat availability and landscape fragmentation). Each bee, at each time step of the day can perform one of five behavioural types (forage flowers, fly to a neighbouring grid cell, fly around, fly back, nest reached). It was defined in rules what happens in each behavioural unit and under what conditions these behavioural units follow each other. Parameterization of the model input was mainly based on literature review (extended in appendix A) and the model's rule behaviour was tuned with a pattern oriented approach.

Before I could investigate my main research questions, I tested the model with four simulation experiments to investigate parameter effects and parameter sensitivity (chapter 4). I showed that the model produces realistic foraging behaviour progressively during the foraging day (simulation experiment 1). The responses overlapped well with values from the literature, which can be considered as a validation. However, model bees were found to be somewhat more efficient than real bees, yielding higher number of brood cells. I also used this first simulation experiment to choose the values for two important time budget parameters, foraging time (total length of the foraging day) and time spent at the nest (for non-foraging activities). It further showed that the model realistically mimics local depletion (more flower visits per time unit later on the day) and that realized foraging distances were much lower than given homing distances. The second experiment (simulation experiment 2) involved a global sensitivity analysis with more extreme parameter values within the biological range. It revealed that the response variables were affected by different dominant parameters. The number of brood cells and foraging habitat visitation were most affected by pollen per flower (i.e. flower size). The number of flowers visited and the mean distance flown were most affected by bee type (body size and nesting preference). All responses were affected by extreme differences in relative bee density. These extreme parameter values helped understanding the model, but were not further considered. I aimed to use common vegetation (not sunflowers with a large amount of pollen per flower) and natural rather than extreme bee densities for exploring my research questions. The simulation experiment also showed that the most uncertain parameters did not have relevant effects on the responses. The remaining two simulation experiments (simulation experiments 3 and 4) addressed the robustness of bee-related and landscape-related parameters against small (10%) parameter changes. Ten per cent change in parameter value always caused less than ten per cent change in the response. Hence, all parameters can be considered robust against small changes. The handling time per flower (bee-related parameters), the amount of pollen per flower and pollen limitation (landscape-related parameters) in these simulation experiments affected the responses most.

With a new simulation experiment I investigated how bees of different types (distinction between soil-nesting, wood-nesting, small, intermediate-sized and large bees) respond to different landscape composition and configuration (a gradient of foraging habitat availability and habitat fragmentation). The performance of bees was measured as the mean number of brood cells after a foraging day. Body size and nesting preference appeared to have more effect than landscape composition and configuration and are thus essential traits when studying landscape effects on bees. Since by definition bees were provided abundant pollen, time (one day) was more limiting than pollen. Time constraints limited large bees more than small bees and wood-nesting bees more than soil-nesting bees. Large bees need to collect a large amount of pollen for one brood cell (and need to visit a large number of flowers) which is apparently not compensated by low flower handling times and high flight velocities. The effect of landscape fragmentation (positive) and foraging habitat availability (negative) were most clear in the context of local nest density and the ratio of nest habitat to foraging habitat. The number of brood cells was lower when the local nest density was very high and when there was little nest habitat compared to foraging habitat (low ratio). This context of relative resource ratio also explained the difference between soil-nesting bees (high ratio) and wood-nesting bees (medium to low ratio due to their restriction to field edges for nesting). Pollinators can be maintained in agriculturally dominated landscapes by managing landscape elements that provide enough nesting substrates, increasing the relative availability of nesting sites compared to foraging habitat. Fragmentation works out positively (but weak) on bees, bringing nest habitat and foraging habitat closer together. Large bees hardly profit from their better flight capabilities. This perspective of the interaction between solitary bees and landscape structure opposes to studies that consider either foraging or nesting resources as most limiting for solitary bees. In single case studies one of both may be the limiting resource, but I conclude that their ratio is the broader perspective for comparing all landscapes.

The fact that bees face time restrictions rather than resource limitations has marked consequences for their pollination potential (chapter 6). I investigated three pollination proxies (number of flowers visited, foraging habitat visitation and foraging distance) with the same parameter variations as in chapter 5. The pollination measures showed partly opposite responses. In landscapes with the highest foraging habitat visitation (well pollinated) bees flew on average least far (low pollination distance). Large bees visited most flowers per individual and the number of flower visits were hardly affected by landscape composition and configuration. Foraging habitat visitation was low when wood-nesting bees had to cover a large area of foraging habitat without nesting resources. The relative availability of nest habitat to foraging habitat (ratio) illustrated this very clearly. A high ratio (good landscapes for bees) reduced flower visits and foraging distances and increased foraging habitat visitation. The preferred pollination measure is foraging habitat visitation. It reflected the fitness of the bees (chapter 5), but was at the same time hardly affected by the body size of bees. Small bees provide - in the sense of foraging habitat visitation - a similar contribution to pollination as large bees, despite lower foraging distances and fewer flower visits. I additionally showed that altered vegetation parameters lead to a very similar (and thus stable) pollinator response. The model result suggests that below a relative ratio of nest habitat to foraging habitat of 0.2, which is the case for fields larger than one hectare, pollination by solitary bees rapidly decreases.

The last research chapter (chapter 7) describes an experimental case study for an intermediate-sized cavity-nesting solitary bee (the red mason bee, *Osmia bicornis* L.) in a highly fragmented landscape, the urban region of Leipzig. In cooperation with colleagues I employed a citizen science approach to investigate landscape-level and local drivers behind the spatial distribution of this solitary bee. Volunteers hung trap nests at different locations and collected information on eight local, microsite conditions (such as sun exposure, attachment position and local flower availability). We derived 14 landscape factors from a digital GIS biotope data map (including nest habitat availability, foraging habitat availability and fragmentation measures such as mean shape index and number of patches). We analysed occurrence of *O. bicornis* in a trap nest (yes/no) and the number of brood cells per trap nest by a combination of machine learning and multiple (logistic) regression. The results indicate that the red mason bee is ubiquitous in urban area but has a higher probability to occupy a trap-nest when floral resources are nearby. Although we expected a balanced influence of landscape factors and microsite conditions, we found that hang location of the trap nest was most important (occupancy and number of brood cells), followed by sun exposure (occupancy only). Landscape configuration measures did not have a significant effect on the responses. The number of brood cells per trap nest was additionally higher when there were little alternative nesting resources around (concentration effect). Cities with many fine-scaled floral resources (such as private gardens but not parks) and an open housing structure with higher sun exposure between buildings provide a good environment for cavity-nesting bees such as *O. bicornis*. In places without suitable nesting opportunities, artificial nest can support the bees.

Synthesizing (chapter 8), I showed that body size of solitary bees affected how they interact with the landscape. Behavioural traits related to body size affected time budgets in different ways and gave small bees an advantage so that they could build on average more brood cells in the same amount of time. This difference in body size was prominent for the investigated pollination proxies as well, except for the proportion of foraging habitat that a bee community visits. The bee's nesting guild was affecting habitat use rather than behaviour, causing time budget restrictions for wood-nesting bees in field edges. Landscape fragmentation did only affect performance (model) weakly and habitat selection (case study) not significantly. Fragmentation enhances nest site opportunities and improves the relative ratio of nest habitat to foraging habitat. This ratio appeared to be a very useful landscape-level proxy for estimating bee fitness and pollination potential and a suitable bee-centred description of landscape composition and configuration. The model showed a strong positive response to this ratio (brood cells, foraging habitat visitation) and the case study a positive trend (brood cells). I recommend for the conservation of bees and pollination services that the ratio of nest habitat to foraging habitat should remain above 0.2 at the landscape level, translating in small fields (1 ha) with woody edge structures or field strips. This model results may extend from meadows to foraging resources in general, including crop fields. Implications for specific crops require additional simulations. I developed the model to study the effect of landscape structure, but it can also be used for the study of different vegetation (crop) mosaics, competition between different bee types and trade-offs in time budgets. The high realism of the model gives potential for further development and validation. Although all model parameters can be measured in the field it is accompanied by high efforts that may not be exerted and I give suggestions for priority setting. In this last chapter (chapter 8), I also discuss the knowledge gaps. This mainly concerns foraging behaviour and trait estimation for very small and very large bees for which clearly more data are needed to understand the mechanisms. Solitary bees are an important but little investigated group of pollinators, for which I provided an important contribution with this thesis.

General structure

Glossary

Wild bees	Wild bees are all bees that live in the wild, including eusocial bumblebees, several semi-social species and solitary bees.
Solitary bees	Bees that live solitary without the help of other individuals. Females of non-parasitic species collect pollen and nectar for their own offspring which they distribute over brood cells. Solitary bees are generally used in the context of a sub-set of wild bees, but some wild and solitary species are managed (domesticated) as well.
Native bees	In North America wild bees are mostly indicated as native bee. In contrast to Europe the imported, non-native honeybee (*Apis mellifera*) often lives in the wild.
Nesting guild	A collection of similar nesting preference and behaviour. Nesting guild is used interchangeably with the term nesting preference.
IBM	IBM stands for individual-based model. This kind of model simulates interacting individuals (or agents; ABM) with their behaviour often defined in rules. In ecological modelling IBMs are often applied when individuals with biological variability are involved.
Simulation model	Model results are produced by computer simulation and enables the use of many parameters and interactions between parameters. Ecological simulation models often include stochasticity to mimic biological processes.
Landscape structure	Landscape structure has two main components; landscape composition and landscape configuration
Loss of foraging habitat	Loss of foraging habitat means for solitary bees the loss of fields with flowering vegetation which offer pollen and nectar. Throughout this manuscript we used it as measure for landscape composition.
Habitat fragmentation	The subsequent loss of habitat patches leaves a mosaic of remaining habitat with patches of different size. Throughout this manuscript used it as measure for landscape configuration.

Contents

CHAPTER 1

Introduction: Wild bees and land use

View from the Brocken Mountain in Germany. Such a mosaic of large agricultural fields in diverse colours is highly valued by tourists. They especially like the yellow flowering oil seed rape. Contrary to common belief do such mass flowering crops hardly support wild bee communities. What requirements do wild bees have?

1.1. The ecological importance of solitary bees

1.1.1. Bees as pollinators

Bees are known for their ecological function as pollinators. Of all pollinators, including butterflies, flies, wasps, beetles, bats and birds, bees are considered the best pollinators. The honeybee (*Apis mellifera*) is the single-most important pollinator in the world (Aizen et al. 2009). However, the world counts about 20.000 wild bee species that are good pollinators as well (Michener 2000). Honeybees and other bees differ in their pollination effectiveness in different situations and often fulfil complementary pollination services to plants (Klein et al. 2003). Pollination is essential for many wild plants and human food crops. The rapid worldwide decline of honeybees and wild bees (Williams 2002, Committee on the Status of Pollinators in North America 2007) has alarmed conservationists and politicians to take action to reduce pollinator losses (Steffan-Dewenter et al. 2005).

Pollinators fulfil an important role in the stability of ecosystems. From the estimated 250.000 wild plant species, 90% are animal pollinated (Kearns et al. 1998). Pollination limitation can result in reproductive impairment in plant populations (Potts et al. 2010a) threatening wild plant diversity. Pollinators enhance primary production and carbon fixation and appropriate vegetation buffers erosion, climate change and water pollution (Kremen et al. 2007). The largest plant family, the *Compositae*, has most entomophilous (insect-pollinated) species (Linsley 1958) and accounts for about 10% of the plant species. Plants from another family with many pollinator-dependent species, the *Leguminosae*, are essential to the earth's biochemical cycle, because they fixate aerial nitrogen to the soil. Extinction or rarefaction of leguminous pollinators would be catastrophic (Rasmont 1995). Pollination limitation also reduces seed sets (Corbet et al. 1991). Reduced seed production of wild plants could threaten many animal species, especially birds, insects and small mammals that feed on seeds and fruits (Osborne et al. 1991, Williams 2002).

The most discussed topic concerning the pollination value of wild bees is the so-called "pollen robbing". Nectar-collecting bees transport pollen unintentionally at body parts that reach the stamens of the next flower. Pollen-collecting bees actively transport pollen to provision their offspring and thus remove the pollen from the system. Most solitary bees collect more pollen than nectar and constantly brush it to specialized structures on the body for optimal pollen transport (Thorp 1979). Solitary bees are therefore often considered as pollen-robbers with insignificant contribution to pollination (Westerkamp 1996). However, bees that forage for pollen are also contaminated with pollen at unintended places of their body (Westerkamp 1997). Many solitary bees are pollen specialists that make them loyal visitors of a certain plant. It has repeatedly been shown that pollen-collecting solitary bees often contact the stigmas of the flowers, in many cases even more than honeybees (Neff and Danforth 1991, Bosch 1994, Bosch and Blas 1994, Javorek et al. 2002, Klein et al. 2003). Even a small amount of pollen that is effectively deposited by solitary bees leads to fertilization (Schlindwein et al. 2005). Wild bees can even be better pollinators than honeybees (Kendall 1973, Gerling et al. 1989, Richards 1996, Klein et al. 2003), but there are also exceptions (Franzén and Larsson 2009).

A diverse fauna with different bee species is considered to be of value for pollination due to complementary effects of different species. Honeybees and bumblebees visit only a small percentage of all plant species and are sometimes not suitable as crop pollinators (Buchmann 1996, Steffan-Dewenter and Tscharntke 1999). Species diversity secures a better spatial and temporal variability of pollinator availabilty (Klein et al. 2003). Especially early flying wild bee species in temperate regions such as *Bombus*, *Andrena*, *Osmia*, *Anthophora* and *Megachile* are the better pollinators of early flowering fruits, since they can operate at lower temperatures than honeybees (Williams 1996, Williams 2002). When both honeybees and solitary bees visit a certain plant or crop, they may contribute differently to pollination. Solitary bees can be the more effective pollinators, but in contribution to pollination be trumped by honeybees due to their high abundance (Klein et al. 2003). Some crops are better pollinated when visited by both solitary bees and honeybees compared to one of the groups (Chagnon et al. 1993). Presence of solitary bees can even cause shifts in behaviour of honeybees improving pollination (Greenleaf and Kremen 2006b).

Pollination is a key driver in maintenance of biodiversity and ecosystem function. Sustainability of pollinators is a crucial part of any conservation plan (Willmer and Stone 2004). In agricultural areas, habitat management for maintaining wild pollinator populations in the landscape can be a cost effective way of securing crop pollination, especially when honeybees are decreasing (Corbet et al. 1991). Even the conservation of pollinators in urban areas is gaining scientific interest (Gaston et al. 2005, Matteson et al. 2008, Spiewok 2011) since pollination services are required in cities as well. While most honeybee colonies are located in the countryside to pollinate mass-flowering crops, wild bees are the main pollinators in cities and enhance important levels in the food chain of the urban ecosystem (Osborne et al. 1991).

1.1.2. Pollination as ecosystem service

Wild solitary-living bees gain commercial interest because they contribute to the pollination of crops (e.g. Aizen and Harder 2009, Julier and Roulston 2009). Wild bees actively increase crop yields and therefore add value to managed honeybees. For instance, wild bees increase yields of coffee (Klein et al. 2003), apple (Ladurner et al. 2004), tomato (Greenleaf and Kremen 2006a) and sunflower (Greenleaf and Kremen 2006b). A community of wild bees can provide pollination services equivalent to a colony of honeybees, given that the community of wild bees has a certain minimum species diversity (>20 species, Kremen et al. 2002) ensuring a sufficient community density during crop flowering. Crop production can profit in several ways from pollination, including an increase in seed number, seed quality, fruit production, fruit quality and uniformity in ripening (Kearns et al. 1998).

Recent studies have tried to capture the value of pollination services in numbers and conclude that the importance of pollination services in agriculturally dominated landscapes has long been underestimated. About 75% of the 115 leading global food crops profit from pollination and pollination is essential or highly important for 40% of the pollinated crops (Klein et al. 2007). In economic terms, the worldwide value of pollination was estimated at 153 billion Euros (Gallai et al. 2009) and more recently at almost 300 billion Euros, with its value still rising (Lautenbach et al. 2012). With a constant relative value of about 10% of the value of agricultural human food production (Lautenbach et al. 2012) is the demand for pollination services quite high and we need clearer picture at the supply side of pollination services (Lautenbach et al. 2012). There is a shortage of pollinators for crops in different parts of the world (Osborne et al. 1991, Richards 2001, Kremen et al. 2002). Although staple food production (e.g. wheat, rice, maize) is largely independent of insect pollination, a further pollinator decline at the global scale will result in a lower production of fruits, vegetables and stimulants crops (coffee, cacao) and hence a forced lower consumption at the world scale of these crops (Gallai et al. 2009). This will increase food prices even more (Kevan and Phillips 2001, Gallai et al. 2009) and lead to an impoverished diet (Klein et al. 2007), especially in a reduction in natural vitamin C sources (Kremen et al. 2007).

Stimulation of pollination services provided by wild bees as an ecosystem service receives increasingly attention in landscape management in parallel to efforts in reducing honeybee declines. The contribution of honeybees to crop pollination may have been overestimated (Breeze et al. 2011, Garibaldi et al. 2011) and protecting natural habitat near crop fields seems to be a key solution in providing natural pollination services (e.g. Kremen et al. 2004, Ricketts et al. 2008, Carvalheiro et al.

2010, Garibaldi et al. 2011). Managing land for ecosystem services has many advantages (Kremen and Ostfeld 2005). However, the concept can be misused in landscape management when cheaper alternative land use is sought (Winfree 2010), for instance when an insect pollinated crop is replaced by a wind pollinated crop (McCauley 2006).

There is a consensus on how honeybee colony losses can be reduced (vanEngelsdorp et al. 2009, Neumann and Carreck 2010), but defining how agriculturally dominated landscapes can be optimized for wild bees is more complex (Ricketts et al. 2008). This makes it difficult to estimate costs and profits for optimizing natural pollination services. Conservation of natural and semi-natural habitats is advantageous for pollination services, but little information exists about landscape management options that influence agricultural pollination (Klein et al. 2007). Therefore the effect of landscape structure on pollination services needs to be investigated.

1.1.3. Pollinator changes

Losses

Recent decline of honeybee colonies have stimulated studies to quantify the decline of wild bees and to identify threats. Severe losses of wild species are known for several decades, also concerning that in in different countries about 27% of the bee species are listed in Red Data Books (Steffan-Dewenter et al. 2005). There was even for a short period discussion about the existence of a pollinator crisis (Ghazoul 2005, Steffan-Dewenter et al. 2005). Today we have a more balanced view on declines and causes. Nevertheless, detailed loss rates will probably never be available due to the longer time scales involved.

The decline of honeybee colonies is a longer known phenomenon. The number of beekeepers declines (Potts et al. 2010b) due to the low profit of beekeeping nowadays. However, in the last decade unexpected honeybee colonies losses occurred increasingly more (vanEngelsdorp et al. 2010). Complete colonies die, invoked by multiple stressors; a phenomenon called Colony Collapse Disorder (CCD). While beekeepers from the USA report an alarming rate of about 30% colony loss per year, beekeepers from Europe report a rate varying from 2-52% (Neumann and Carreck 2010). Some scientists point at the parasite *Varroa destructor* as the main cause for the losses. Others ask why this parasitic mite has suddenly such a large impact (Watanabe 2008), because the largest expansion of this mite was in the 1980's and 1990's (Williams 2002). The weakness of honeybees can have many causes. It is known that honeybees suffer from nutritional stress (due to limited uncultivated area with foraging resources, Naug 2009). Furthermore, insecticides and herbicides are given as cause for weakened bees (vanEngelsdorp et al. 2010, Decourtye et al. 2011) while others did not find significant effects of single chemicals (Chauzat et al. 2009, Bernal et al. 2011). In contrast to honeybees wild bees do not suffer from *Varroa* mites, but they do face similar risks as well, such as from agrochemicals and nutritional stress (Gerling et al. 1989, Frankl et al. 2005, Potts et al. 2010a), which are discussed later within this section.

In many countries up to dozens of wild bee species have gone extinct already and many are rare or endangered (Banaszak 1995, Steffan-Dewenter et al. 2005) especially long-tongued bees and species with a specialized diet (Rasmont 1995, Biesmeijer et al. 2006). The clearest proof that species diversity of wild bees is declining almost everywhere at local scales (10 km plots) comes from the UK (52% of the plots) and the Netherlands (67% of the plots). These declines were shown to be linked to declines of wild plants (Biesmeijer et al. 2006). Traces of pollen removal were found in museum specimens of South African wild plants and suggested a sudden drop in pollinators after 1940 (Pauw and Hawkins 2011). Extensive losses of pollinator guilds have forced farmers to use honeybees for fruit and seed production (Cane and Tepedino 2001).

Along with declines of wild bee species, densities of wild bees have probably also declined. Direct proof is available for bumblebees. The abundance of several species declined with 96% in North

America (Cameron et al. 2011) and up to 90% in Denmark (Dupont et al. 2011). Abundances of single species on organic clover fields decreased even up to 100% and five of eight species are considered locally extinct (Dupont et al. 2011). Already in the early 19th century, it was observed that wild bees were locally declining (Child 1833). Direct proof of declining abundances of solitary bees is sparse. Books on wild bees from the end of the 19th and early 20th century suggest that many species were widely abundant in Germany (Schmiedeknecht 1882-1886, Friese 1922). In France, there was almost no roof without *Megachile parietina* (syn. *Chalicodoma muraria*) at the end of the 19th century (Fabre 1879). It was then even considered a pest, while nowadays it is a rare species in France (Rasmont et al. 2004). Similarly, this species was common in Germany in the 1920's, uncommon in the fifties (Westrich 1989) and now "critically endangered".

Increases in species richness and abundance of wild bees are recorded as well. For the Netherlands and the UK an increase in species richness was reported for up to 10% of the investigated plots (Biesmeijer et al. 2006). A major increase of bumblebee densities for a single species was reported from Denmark (Dupont et al. 2011). This was the result of declining densities and extinction of several other species of bumblebees. Increases in diversity and densities remain an exception. The 2010 target to reduce the rate of biodiversity loss has not been met, despite increasing political effort to protect biodiversity (Butchart et al. 2010). Shortage of wild bees was buffered by beekeeping for decades but now are honeybees at risk as well. We tend to loose important pollinators, which is only partly buffered by increased densities of the remaining species.

Losses of wild bees are partly attributable to climate change. Past climate changes have altered the landscape and the proportion of open area to forest and therewith affected foraging and nesting resources for bees (section 1.2). Climate change affects distribution of food plants and the spatial borders of the climatic zone of the species distribution. The changing climate had a moderate (but measurable) effect on the distribution of bees in the past 60 years (Franzén and Öckinger 2012) and is predicted to highly affect distribution ranges of bees in the upcoming 40 years (Roberts et al. 2011). Since most wild bee species are thermophile, they may benefit from the current global warming. However, supposed benefits for single species may not hold when interactions between species (such as host plants, pathogens and competitors) are considered (Settele et al. 2010). It remains an open question whether climate change will disrupt pollinator and plant mutualisms by phenology shifts (Gilman et al. 2012) or range shifts of bees and host plants can keep pace (Bartomeus et al. 2011). Despite clear effects of climate change on the distribution of bees, agriculture has an impact at least as high on the distribution and quality of foraging and nesting resources.

Agriculture as driver for pollinator loss

Agriculture is probably the largest threat for wild bees. Increased land-use for agriculture leads to loss of bee-habitats and habitat fragmentation and seems to be the most important driver of wild pollinator losses (Potts et al. 2010a). They are further discussed in section 1.2. Wild bees have been declining along with increasing agricultural intensification (Biesmeijer et al. 2006). The application of insecticides reduces species richness and abundances of bees (Kearns et al. 1998, Kovacs-Hostyanszki et al. 2011), but mechanistic effects of multiple pesticide exposure are widely unknown (Brittain and Potts 2011). Especially neonicotinoids (e.g. the insecticides imidacloprid and clothianidin) seem to harm bees. They negatively affect foraging behaviour of honeybees (Schneider et al. 2012), reduce homing ability and survival in honeybees (Henry et al. 2012) and reduce growth rate and reproduction of bumblebees colonies (Whitehorn et al. 2012). The effect of insecticides and herbicides reaches far beyond the crops to which they are applied. Neonicotinoids can be found in the soil, on untreated fields and on dandelions near crop field which are used by bees to forage (Krupke et al. 2012). Insecticides probably affect smaller bees most due to a high surface to volume ratio, while large-bodied bumblebees may be more tolerant (Kearns et al. 1998, Kovacs-Hostyanszki et al. 2011). Herbicides destroy nectar and pollen resources for bees and may have an even larger impact than insecticides (Kearns et al. 1998). Wild bees are also negatively affected by the use of fungicides (Huntzinger et al. 2008, Ladurner et al. 2008). There is thus an important trade-off between crop protection by agrochemicals and protection of pollination services.

Other agricultural practices endanger wild bees as well. Grazing results in removal of food sources for bees and destruction of underground nests (Kearns et al. 1998). Furthermore, fertilizer use reduces plant diversity and therefore nutritional diversity for bees (Kovacs-Hostyanszki et al. 2011). Harmful agricultural practices are not likely to decrease soon. Hence, we need other solutions to these threats. Futurists imagine a disease-resistant honeybee (resistance against *Varroa destructor*, virusses and fungi) by genetic engineering (Zakaib 2011), but this does not reduce any of the other threats. To protect wild bees in agriculturally dominated landscapes it may not suffice to conserve small strips of semi-natural habitats. We need to understand how wild bees interact with the landscape to improve landscape configuration and meet all needs of vital wild bee populations.

1.1.4. Solitary bees

Wild bees are represented by 20.000 species worldwide, 700 species in central Europe and 500 in Germany alone (Westrich 1989). Solitary bees are the largest sub-group of wild bees with about 14000 species worldwide (Neff 2008). They live solitary and have a wide range of different food preferences, nest preferences and behavioural traits. They differ considerably from eusocial and semi-social bees in foraging behaviour (e.g. Chagnon et al. 1993, Aizen and Feinsinger 1994, Klein et al. 2003). Communication between eusocial bees can lead to near-optimal foraging (Pyke 1983, Andrieu et al. 2009), while solitary bees do not communicate about foraging patches. Solitary bees forage alone and therefore deal with limited knowledge of resource locations and their quality. While eusocial bees spend a large part of their time foraging for nectar, solitary bees focus on the collection of pollen for their offspring (Linsley 1958).

Partial habitats

Habitat availability and habitat fragmentation are considered the most important landscape properties for the survival of wild bees. The availability of foraging resources strongly affect wild bees (Pawlikowski 1989, Gathmann et al. 1994, Banaszak 2000, Calabuig 2000, Steffan-Dewenter et al. 2001, Steffan-Dewenter and Tscharntke 2001, Steffan-Dewenter 2002). Foraging resources were measured as area with semi-natural habitat, flower diversity or flower coverage and had a positive effect on wild bee species richness or abundance at the landscape scale. Sometimes nest habitat may have been limiting (Gathmann et al. 1994, Gathmann and Tscharntke 2002, Potts and Elith 2006, Steffan-Dewenter and Schiele 2008). Foraging and nest habitats for bees are often referred to as being partial habitats. A small patch where bees nest does often not provide enough foraging resources, which forces bees to forage farther away. Hence, the total area requirement of the bees depends on the distance between the required resources (Westrich 1996). Although bees are good flyers, they will try to keep their activity area low and nest in the vicinity of their foraging resource. This gets more complicated by the fragmentation of habitat patches (Westrich 1996).

The effects of fragmentation at the landscape scale on wild bees are manifold, but their relative importance is not well studied. Fragmentation leads to isolation of habitat and reduced patch colonization (Tscharntke and Brandl 2004) and is believed to affect populations negatively (Fahrig 2003). Apart from reducing connectivity, fragmentation affects the structure of the matrix between the habitat patches that must be crossed. A higher proportion of matrix between patches often means increased disturbance

(Tscharntke and Brandl 2004) and the type of matrix affects the movement of pollinators (Tscharntke and Brandl 2004, Diekötter et al. 2007). The severity of such fragmentation effects is questioned. Bees are good flyers and able to cross the matrix. Although the matrix can act as a barrier for bees (Powell and Powell 1987), bees may easily survive in a network of patches that are available within their foraging range (Cane and Tepedino 2001). It remains to be investigated how much the fragmentation of resource patches affects movement and performance of wild (and solitary) bees at the landscape scale.

Nesting preference

The differences in nesting preference are important when fragmentation alters nest site availability. Nesting preference of solitary bees can be basically classified into two groups (O'Toole and Raw 1991). About three-fourths (Westrich 1996) of them are soil-nesting bees (also called mining, digging, ground-nesting, subterranean-nesting or fossorial-nesting bees). They prefer open, bare ground for excavation of deep holes. Soil nesting species favour dry, fine grained soils with low humus content (Klemm 1996). The other solitary bees, mainly mason bees and carpenter bees, stay above ground and nest in cavities (Willmer and Stone 2004). They nest in existing cavities (such as beetle burrows in wood, deserted snail shells, hollow plant stems and dead twigs and branches, or man-made cavities like nail holes and key holes) or in self-made cavities in trees, galls, cones and fruits (Linsley 1958, Cane 1991). In agriculturally dominated landscapes, the nesting substrates for cavity nesters are found at structures with scrubs and trees that provide dead wood. For simplification we call these bees "wood nesting" throughout the manuscript.

Body size

Solitary bees comprise a wide range of body sizes. Body size affects traits such as the bee's velocity or capacity for carrying pollen. These traits influence the response of bees to landscape structure (Banaszak 2000). Only few studies investigated body-size related effects on performance of wild bees in fragmented landscapes. Body size of wild bees was larger in more isolated habitat patches (Steffan-Dewenter and Tscharntke 1999). Oppositely, in a tropical forest, isolated patches were less visited by large solitary bees than by more mobile (but smaller) honeybees (Aizen and Feinsinger 1994). Other studies found no effect of bee size (Steffan-Dewenter and Tscharntke 2001, Lopez-Uribe et al. 2008). There is an on-going discussion about the effect of mobility on habitat selection. On the one hand, small bee species are expected to be more affected by landscapes fragmentation (Gathmann and Tscharntke 2002), because interpatch distance increases with fragmentation and many gaps have to be crossed. Bees with intermediate mobility may experience problems when they are mobile enough to leave a large patch, but not mobile enough to reach a distant foraging patches (Ewers and Didham 2006). On the other hand, all bees may be mobile enough to reach all required patches (Steffan-Dewenter and Tscharntke 2001). Models can help to understand bees perform in patchy landscapes. Because honeybees and bumblebees that span a much narrower range of body sizes, bee ecologists consider them inappropriate model species for studying the limits of foraging behaviour of over 14000 species of solitary bees (e.g. Neff 2008). Therefore, a review of how body size affects performance-related traits is essential for studying performance effects at the landscape scale.

1.2. Solitary bees in changing landscapes and the effect of fragmentation

1.2.1. Change of resource availability: a short history

The history of landscapes helps us understanding how bee communities may have responded to past land-use changes. Landscape history is quite different for different biogeographical regions in the world. In tropical areas, the rainforest is cut for agricultural land, leaving patches of land surrounded by forest. Solitary bees come from the forest to pollinate e.g. coffee and cacao (Klein et al. 2003, Gallai et al. 2009). In temperate regions in Europe, on which we focus in this section, forests were cleared a long time ago and most agriculturally dominated landscapes have no original forest left. Landscapes are modified and planted with selected tree species, scrubs and crops. At places where landscapes are less managed, natural processes dominate again. Such places are indicated as semi-natural habitats. In fact, it are man-made habitats that we protect today (Klemm 1996). Those habitats now serve as source of wild pollinators and pollination services.

Floral abundance is the best predictor for bee abundance (Kearns and Oliveras 2009) and landscape changes that affect floral abundance must have highly affected bee communities with marked changes over centuries. The relative suitability of landscapes for soil-nesting and wood-nesting bees must also have changed due to changes in nesting substrates. Further, centuries of fragmentation of landscapes also changed spatial resource distribution and distances between partial habitats (Westrich 1996).

Until 500 A.D.

After the last ice age, Europe turned slowly from a tundra with grasses, herbs and sea-buckthorn into a dense forest with beech and other deciduous trees until Europe was completely covered with forest in the Neolithic age from 10.000 B.C. on (Behre 2008). Bees were confined to a handful of open habitat types such as inland dunes, landslides and rock steppes. The most important open habitats must have been the floodplains of wild river systems, providing suitable nesting and foraging resources (Klemm 1996). In the dense forest, early-season bees must have found good foraging resources on early spring bloomers. There were enough different habitats providing opportunities for specialized bees that can deal with patchy distributed habitats (Klemm 1996). Since the end of the Neolithic age agricultural activities increased, forests were cut and open areas expanded. Humans started to change the landscape and created open and sun exposed sites improving the conditions for bees (Monsevičius 1995). From 4000 B.C. on several tree species disappeared by both human activities (disappearance of pine shortly B.C.) and natural events (large scale elm disease) and were replaced by grasses and herbs (Behre 2008). The Vikings spread plum trees in Europe and the Romans facilitated a wide spread of apple trees (Behre 2008), both very popular food sources among spring-flying bees. Although many of the changes were profitable for bees, the oldest know pollination deficits are from around 500 B.C. for fig and palm trees (Kevan and Phillips 2001). Specific wasp species from the remaining natural vegetation that needed to pollinate complete plantations were not abundant enough. The human impact on pollinator assemblages is as old as agriculture itself.

500-1500 A.D.

After the Roman occupation of Europe, fruit trees disappeared again and open areas turned in to forests again (Behre 2008). Around 700 A.D. a strong increase of grasses and herbs started (Behre 2008) which probably lead to increase of wild bees since most species are thermophile and living in open areas (Hampicke et al. 2005). Fruit trees became abundant in monastery gardens and vegetables were grow in private gardens. This period was the peak period for flax and poppy (Behre 2008). These changes have benefitted certain bee species and probably increased their abundance.

1500-1800 A.D.

From 1500 A.D. on large-scale changes took place over large areas parallel to human population growth. There was a strong increase of grasses and herbs, as a consequence of forest clearing. Grasses and herbs reached their peak in the eighteenth century accompanied by forest of young trees and disappearance of old trees and an energy crisis for the European human population (Behre 2008). On one hand did many bees profit from these open landscapes and high abundance of foraging resources in these grasslands. On the other hand did cavity-nesting bee species - nesting in old forests and old dead trees - probably decline. Agricultural changes also affected bees. Land-use intensity increased in this period with a strong increase in cereal fields and *Brassicaceae* (Brande 2007). Humans bred the first oilseed rape from cabbage, which was until 1900 one of the most important oil sources (Behre 2008). At the same time there was a clear decrease in *Campanulaceae* (Brande 2007), which were abundant in agriculturally used landscapes in the preceding period and an important food plant for multiple bee species. Another popular food source among wild bees, *Lotus* spec., did also increase (Brande 2007). We can therefore assume that clear shifts of species composition and abundance took place in bee communities.

1800-1900 A.D.

From 1800 A.D. on large scale reforestation with pine trees started and is still on-going (Behre 2008). This fast growing tree species - which got extinct before in large parts of Western Europe - was re-introduced to produce timber and to indulge the high demand for wood in a time of increased industrialization. The reforestation reduced open sunny areas with herbs (Behre 2008) which served as foraging resources for bees. Agricultural practices on the arable land also changed. The three-field system was improved and the year of set-aside used to grow clover for nitrogen fixation or left with species rich herb communities (Hampicke et al. 2005). This means that at least one third of the arable land could serve as foraging resource for generalist bee species. The growth of buckwheat increased especially on poor soils and served to feed honeybee colonies and game animals (Behre 2008) and soil improvement (green manure). Buckwheat is also for wild bees a good source of foraging resources. Newly introduced plants from the Americas such as potato and sunflower gained importance as crop in this period (Behre 2008). Especially sunflower is valued by many different bee species (Greenleaf and Kremen 2006b).

1900-1950 A.D.

Development of agriculture and changes speeded up in the first half of the twentieth century and lead to the first reports of changing distributions of native bees (Linsley 1958). Farmers optimized fruit tree management by increasing orchard sizes (Behre 2008). Such orchards (apple, pear, plum, cherry) mass flower in spring and probably enhanced bee densities of spring flying species regionally. There was an increase an animal husbandry for which a large amount of alfalfa fields were grown (Linsley 1958) and in some regions of Europe there was a large scale increase of grassland (van der Knaap et al. 2000). Large scale alfalfa growing was especially strong in the United States, but was also applied in Europe. Alfalfa is a food crop for legume specialized bees, especially valuable to some bumblebee species. The increase of grassland facilitated plants including *Campanulaceae*, *Cruciferae* and *Leguminosae* (van der Knaap et al. 2000). These species-rich grasslands were regularly mown (van der Knaap et al. 2000) giving a mosaic of fields with herbs flowering at different times. In many European regions farms were still small, surrounded by natural habitats and provided good conditions for wild bees including slopes, small gardens and wooden and clay buildings (Monsevičius 1995). Globalization processes lead to changing spatial timber distribution and enhanced suitable nesting sites for bees, resulted in noticeable range extensions of some bees species (Linsley 1958). Despite some local increase in nest-site availability, nest habitat was destroyed at large scales (Linsley 1958). Field margins and hedgerows were cleared along agricultural fields (Kearns et al. 1998) to increase the arable land, leaving wild bees no opportunity to nest. The increased foraging resources served only few specific species while nest site destruction affected whole bee communities. It can therefore be assumed that this period was already characterized by severe local losses of wild bees.

1950-2000 A.D.

From the fifties on a period commenced with even faster and larger scale changes. This agricultural revolution, driven by a fast growing human population and fuelled by the believe that everything is makeable and controllable, had as goal to increase the agricultural production on existing fields. New machines, new technologies and new chemicals made it possible to increase efficiency, improve nutrient balances, exterminate weeds that compete with crops for nutrients and exterminate pest insects that damage the crops. This was inevitably the dismissal of wild bees in agricultural regions as well. Habitats of wild bees got destructed in whole Europe from the Netherlands to Lithuania (e.g. Monsevičius 1995, Ruszkowski and Bilinski 1995, de Ruijter 2002). Nest sites disappeared by removal of remaining field margins, clearance of forest strips and bush areas and cutting of old solitary trees standing in the way. Foraging resources decimated by the reduction of areas with wild flowers and cultivation of wild meadows. Additionally did refugee areas for wild bees decline rapidly due to excessive land drainage (Jablonski and Kołtowski 1995, Monsevičius 1995, Ruszkowski and Bilinski 1995, de Ruijter 2002). Introduction of large monocultures and regionalization of crops led to further food impoverishment for bees and reduced buffer and refugee possibilities, likely causing shifts in local species distributions and divergence of bee community assemblies (Pawlikowski 1987, Jablonski and Kołtowski 1995, de Ruijter 2002, Tanács and Benedek 2010).

Another marked change in this period was the introduction of intensive (or industrial factory) animal farming. From now on did grasslands mainly serve milk and meat production. Large pasture areas without entomophilous plants with a high grazing intensity of milk cows dominated (Monsevičius 1995). Heathlands and species-rich grasslands (with foraging resources for bees) were redundant and were given up for more arable land (Kleijn and Raemakers 2008). Animal husbandry shifted from small-scale farms to large industrially managed stalls with high stocking densities of meat cattle. Legume fields (e.g. alfalfa as fodder-crops) were abandoned (Kleijn and Raemakers 2008) and made place for large maize fields (Behre 2008). Plant breeding efforts resulted in maize varieties that could grow in Europe in high densities and be applied as high efficiency fodder crop.

The introduction of artificial fertilizers led to impoverished vegetation (Kovacs-Hostyanszki et al. 2011) and the abandonment of crop rotation with green fertilizers (legumes). Active weed control with herbicides and accurate crop seed purification led to disappearance of most weeds in agricultural fields and hence of important bee forage. Winter corn and summer corn lost their accompanying herbs cornflower (*Centaurea cyanus*), wild mustard (*Sinapis arvense*) and wild radish (*Raphanus raphanistrum*) (Jablonski and Kołtowski 1995). Only some bee-attracting herbs such as thistle (*Cirsium arvense*) remained because they could not be overpowered (Hampicke et al. 2005). Wild plants were exterminated at larges scales in agricultural areas. Wild herbs from the *Campanulaceae*, *Cruciferaee*, *Lamiaceae* and *Fabaceae* (including *Trifolium*) rapidly decreased and locally disappeared (van der Knaap et al. 2000, Tanács and Benedek 2010). As a result species diversity in wild bee communities fell to one third of the original number in Poland in the period 1974-1983, a period less than ten years (Pawlikowski 1987).

The present

The last two decades there was an increase in environmental awareness which lead to a clear deceleration of harmful processes. New regulations prohibited large scale intoxication of whole agricultural areas with the most harmful and persistent chemicals, but the use of other toxic herbicides and insecticides is still daily practice. Hedgerows and field strips are spared to conserve remaining wildlife in agricultural areas. However, what was removed in the past cannot be removed again. Deceleration of destruction of semi-natural habitat elements is therefore inevitable, rather than an argument of good landscape management. Occasional restoration and creation of new field strips does not seem to restore the optimal pre-1900 conditions. A vast increase in organic farming with low chemical use and small crop fields also increases buffer effects against remaining harmful effects (Holzschuh et al. 2008).

The main problem that still seems to grow in present agricultural landscapes is the availability of foraging resources. In Europe agricultural areas are still replanted with trees for forest (Monsevičius 1995) and land is increasingly used for roads and buildings (Jablonski and Kołtowski 1995). Land use is continuously changing, affecting nesting and foraging habitats of wild bees (Lautenbach et al. 2011). Especially forest cover affects bee abundance and species diversity negatively (Winfree et al. 2007). Recent increases in oilseed rape as bioenergy crop (Behre 2008) may increase foraging resources at first sight. However, current crop varieties bloom for a very short time and they provide no resource diversity. When oilseed rape is grown instead of rotational set-aside fields, it may even mean a reduction in food on a larger time scale (Frankl et al. 2005).

Historical land-use changes have clearly changed resource availability for wild bees. At first human activities improved the landscape for wild bees, but later reduced and homogenised foraging resources and nesting opportunities (fig. 1.1). Land-use change has become a very strong pressure for solitary bees in the last century and the effect of changing land-use mosaics deserves more research. There seems to be a trade-off between an increase of crop area and conservation of semi-natural habitats that indirectly provide pollination services to these crops. Growing field sizes increase the need for (managed) pollinators. While some wild bee species still may benefit from the current changes, other species are still under pressure. Our pollinator heritage of past landscapes should be actively protected.

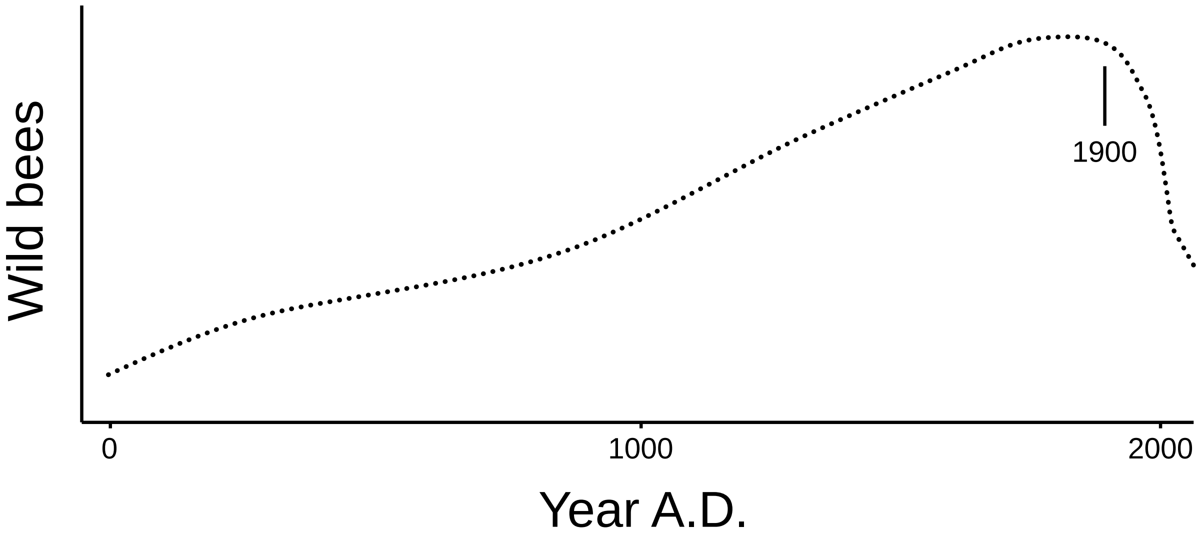

Figure 1.1. Land use by humans had a high impact on the number of wild bee species and the number of individuals over many centuries. This schematic representation focusses on West-Europe and is an attempt to follow the relative resource changes discussed in section 1.2.1 (relative changes following the time axis). We can only guess about the current position relative to the start of the graph.

1.2.2. Change of spatial resource distribution

The loss of nest habitat and foraging habitat (landscape composition) clearly negatively affected wild bee communities. But what effects on wild bees could changes in landscape configuration have? Wild bees cannot reproduce without a nest site or sufficient foraging resources to provide their brood with. Bees need these complementary habitats both and within a certain distance on relatively small scales (see also section 1.1.4). Often is nest habitat availability neglected and are wild bees absent despite abundant foraging resources (Westrich 1996). Fragments are often defined as vegetation patches, but the fragmentation of nesting locations should be considered as well. Further, dramatic loss of resources may overshadow subtle effect of fragmentation for pollinators. Bees live on resource islands in an unrewarding matrix (Cane 2001). Nest habitat such as hedgerows and field margins were destructed in the last century at large scales (Kearns et al. 1998), enabling larger field sizes. Nest and foraging habitat in fragmented landscapes are often spatially separated by roads and sprayed arable fields (Westrich 1996). Scale enlargement of crop fields does not only reduce nest sites, it also enlarges the distance between remaining nest habitat and foraging habitat and reduces food diversity within the foraging range of bees, probably affecting small bees with small foraging ranges most (Gathmann and Tscharntke 2002). Small scale field mosaics with small field sizes (< 16 ha) and maintenance of sufficient refugial habitat around the fields compensates for intensification (Pawlikowski 1987, Banaszak 1992, Banaszak 1996). E.g. cultivated orchards surrounded by other orchards have fewer bees than those surrounded by uncultivated land (Kearns et al. 1998).

Experimental studies found contrasting responses to fragmentation. Several studies found that bee communities responded negatively to landscape fragmentation expressed in a lower species diversity or abundance (Aizen and Feinsinger 1994, Steffan-Dewenter 2003). Other studies suggest that species diversity or abundance do not significantly change or even increase in response to fragmentation (Donaldson et al. 2002, Cane et al. 2006). The response of bees to fragmentation is poorly understood and it is doubtful that a general negative effect of fragmentation exists (Kearns et al. 1998, Cane 2001).

Effect of fragmentation depends on different factors. It depends on the landscape types, the bee types and the scale considered in the study. One can distinguish in forest fragmentation, fragmentation in agricultural areas and urban fragmentation. In terms of the distribution of foraging and nesting resources for bees they mean different things. In Europe bees were exposed to large scale forest fragmentation up to 1500 B.C. and long before, while this is a very actual threat in tropical regions. European bees now suffer mainly from fragmentation of open habitats with foraging resources in the agricultural landscape, drifting nest and food locations apart. Nest habitat often only remains in fragments between the fields. Further does the response of bees to fragmentation depend on the bee type roughly characterized by social status, nesting guild, food specialization and body size. Bee communities split in such groups, respond differently to habitat fragmentation (Cane 2001). The scale of investigation is essential too. At very small scales (metres) bees may hardly respond to fragmentation (Diekötter, et al. 2007). At very large scales (dozens to hundreds of kilometres), where landscape fragmentation leads to separation of meta-populations, genetic variation within bee populations often decreases. At this scale are oligolectic, polylectic and pioneer species affected differently by barrier and isolation effects that separate bee populations (Zayed et al. 2005, Exeler et al. 2008, Davis et al. 2010). Resource fragmentation of foraging and nesting resources for single bees that need to cope with different daily foraging distances occurs mainly within the patch mosaic of agricultural fields. It would therefore interesting to investigate fragmentation effects at this scale of one to several kilometres and to compare the performance of different bee types. We gave a short summary in section 1.1.4 of the mechanisms and bee traits that are important at this scale.

1.2.3. Urban areas

Urban areas consist of almost exclusively man-made habitats with a high disturbance rate. However, they may be good substitutes for destroyed natural habitats when they provide enough foraging and nest habitat for bees (Kearns et al. 1998). Cities provide favourable microclimatic conditions for wild bees and can harbour a high number of species (Saure 1996, Frankie et al. 2005). Wild bees require the right combination of specific foraging and nesting resources (Westrich 1996). Urbanization generally leads to native plant loss (Hahs et al. 2009), but cities also provide a range of successional stages at brownfield sites with a species-rich ruderal vegetation including Red Data Book listed bee-pollinated plant species (Saure 1996, Flügel 2005). Such sites have diverse vegetation and little disturbed seed banks (Tommasi et al. 2004, Flügel 2005). Exotic plants at sun-exposed sites in backyards, allotments, parks and even on balconies offer pollen and nectar throughout the whole season (Flügel 2005) but their value for bees is not known. Some believe that nectar and pollen are largely inaccessible to native pollinators or are not provided at all (Comba et al. 1999, Corbet et al. 2001, Tommasi et al. 2004), while others have shown that many ornamental exotic plants are used as forage (Barthell et al. 1998, Goulson et al. 2002, Frankie et al. 2005). The availability of nesting resources is also altered by urbanization. Many urban soils are probably too compacted to nest in (Matteson et al. 2008), but urban gardens have higher nest densities of bumblebees than a homogeneous countryside (Osborne et al. 2008). Cavity-nesting bees may fail to find enough nesting resources in urban green spaces and backyards due to frequent mowing and removal of dead stems (Matteson et al. 2008), but cities also provide a high diversity of compensating anthropogenic substrates suitable for cavity-nesting bees, such as wooden fences, barns and mortar brick walls (Saure 1996, Cane and Tepedino 2001). Cavity-nesting bees were for example more abundant in small urban habitat fragments than in natural vegetation, probably due to enhanced nesting opportunities (Cane et al. 2006).

In cities, patches with foraging and nesting resources are highly fragmented, which affects the spatial mosaic for bees (Cane and Tepedino 2001, Matteson et al. 2008). Effects of fragmentation on bees are contradicting (Kremen and Ricketts 2000, Cane 2001). The abundance of bees increased with habitat connectivity in an agricultural landscape (Steffan-Dewenter 2003), but elsewhere pollinator diversity was only predicted by vegetation cover and the same diversity was found for both small isolated and large patches (Donaldson et al. 2002). The effect of fragmentation and urbanization on bees are better understood when bees with a different nesting guild or diet breath are analysed as separate groups (Cane et al. 2006). Also traffic was thought to limit wild bee movement (Banaszak 1995), but recent experiments show that they cross busy motorways (Zurbuchen et al. 2010a). Roads probably do not separate nesting and foraging patches.

1.3. Bridging knowledge gaps

1.3.1. Motivation

Bees are important pollinators, but both honeybees and wild bees are rapidly declining. While honeybees are well studied, many questions about the role of the high variety of biological traits on the foraging behaviour of wild bees are still unanswered. The potential of wild bees, especially small species, for providing (complementary) pollination services may therefore be underestimated. One of the drivers for the decline of wild bees is land-use change that affects the field mosaic and the fragmentation of the landscape. In the literature, there is no general consensus about how wild bees respond to landscape configuration. Many authors underline the need for a better mechanistic understanding of the effect of landscape configuration on wild bees in order to estimate the importance of habitat loss and fragmentation, to estimate the effects of land use on pollination services and to support management decisions (Kearns et al. 1998, Cane and Tepedino 2001, Williams 2002, Tscharntke and Brandl 2004, Knight et al. 2009, Lonsdorf et al. 2009). Body size and nesting preference affect the response to landscape features and fragmentation, but up to date no systematic exploration exists. Review of body size related traits affecting foraging behaviour of solitary bees (excluding complex differences for difference in social status) can fill this basic knowledge gap. A spatially explicit modelling approach where solitary bees with different body size and nesting preference forage for resources and face different landscape configurations can improve our mechanistic understanding of their response.

1.3.2. Previous work on pollinator models with bees

Existing models with pollinators are of limited value for understanding the interaction between solitary bees and landscape configuration. Many models are based on the foraging behaviour of honeybees or bumblebees. They deal with optimal strategies and trade-offs based on nectar foraging (e.g. Pyke 1983, Pyke 1984) or provide different algorithms to search food (Ziarati et al. 2011) such as the bee algorithm (BA), artificial bee colony (ABC) and bee swarm optimization (BSO). In real systems, such eusocial bees perform only sub-optimal (Pyke 1984). Most models are too simplistic because they do not consider a constantly changing environment (resource depletion), do not distinguish between different types of costs and time budgets and do not deal with the imperfect knowledge about the environment and quality of patches (Pyke 1984). Even data-based approaches only include little biological detail (see for example Aronson and Givnish 1983, Harder and Wilson 1998). Although pollinators behave very different, "Honeybee", "flower visitor" and "pollinator" were long used as synonyms (Westerkamp 1991).

A few recent models included more realism. One model considered solitary foragers with limited memory rather than communicating eusocial bees (Thuijsman et al. 1995). Another study estimated field to field gene flow of crops by moving bumblebees based on experimental data (Cresswell 2010). A relatively detailed model exists on colonial food providers which included local competition and a spatial component (Dukas and Edelstein-Keshet 1998). Nevertheless, it did not include bee size and spatial configuration of patches. Further, it used honeybee-based data.

No model yet considered active pollen foraging as main driver of pollinator movement. Most of the models also lack comparison between different pollinators, partial habitats for nesting and foraging, differentiation between individuals, local competition and size of the pollinator. Solitary bees are mainly foraging for pollen to provide their brood cells with. Nectar replenishes during the day, while pollen depletes slowly, inducing strong local competition. Solitary bees fly out alone from the nest, forage at the closest suitable flower patch and return when they collected enough pollen and/or nectar. This typical behaviour of solitary bees that differs from eusocial bees was reason to develop a new model.

1.3.3. Approach and research questions

We basically follow three steps. First, we identify how body size affects foraging behaviour with a literature review (chapter 2). The largest section deals with a model. We develop a model that incorporates body-size related foraging rules at the landscape level (chapter 3), test it (chapter 4) and use it as tool for answering research questions (chapter 5 and 6). Finally, we perform an experimental case study with a single bee species to get a detailed understanding of how it interacts with a selected landscape (chapter 7).

Review (chapter 2)

A body size related framework for pollination behaviour is essential to close the knowledge gap about how solitary bees forage in different landscapes. Such a framework is helpful for modelling approaches where capabilities of bees in a spatial environment are of interest (Tscharntke and Brandl 2004, Lonsdorf et al. 2009). There is urgent need for understanding how wild bees forage to quantify their pollination potential. Hence, identifying body size related traits that affect pollination behaviour can be useful for a more mechanistic understanding of pollination patterns. We focus on pollen collection in the review. A major part of foraging activity of solitary wild bees consists of pollen foraging. Solitary bees spend more time on pollen collecting than nectar collecting (Danforth 1989b, Willmer and Stone 1989) and make more pollen-based than nectar-based flower visits (Hurd et al. 1980). We ask basic questions on foraging behaviour such as: How fast do bees fly? How far do bees fly? How much pollen do bees collect? How long does a bee visit a flower to collect pollen? Further, we aim to address for each trait the relative contribution of body size and other factors for differences between species.

Model (chapter 3-6)

We developed a model with biological detail to study the interaction of solitary bees with the landscape. We decided to use an individual-based, spatially-explicit simulation model to simulate naive solitary bees that forage for pollen in the landscape. Time could be more constraining than energy for wild bees (Westphal et al. 2006b) and we therefore focus on differences in daily performance. The individual-based model (IBM, or agent-based model ABM) is an established method for investigating competition in space and time. It allows the inclusion of multiple traits (related to size and nesting preference) that determine movement and decision rules, which create realistic depletion of pollen in space and time. Minimalistic approaches with the use of home range descriptions cannot account for local competition processes (Austin et al. 2004). IBMs with a high level of realism are often used in ecology and perceived as a welcome addition to the more theoretical approaches with a limited number of parameters. An earlier individual-based model successfully showed that individual body size differences of solitary bees can make a difference to fitness (Ulbrich and Seidelmann 2001). Modelling movement behaviour reveals the true value of habitat availability and fragmentation to a species, and can deliver insights that are useful for landscape planners and conservationists (Taylor et al. 1993).

We aim to quantify the effect of foraging habitat availability and fragmentation on the bee's performance and their relative importance. We also try to find indicators for optimal pollination services at the landscape scale. At the development stage, we ask what foraging rules are required to simulate foraging behaviour with body-size related traits. At the test stage, we ask whether the model produces realistic foraging patterns in time and how well the response variables overlap with real systems. We also ask which parameters are most influential within biological parameter ranges and how sensitive parameters are against small changes. In the application stage we simulate different landscapes with a gradient of foraging habitat availability and habitat fragmentation. We focus on the following questions:

What are optimal conditions for wild bees in fragmented landscapes? How well are pollination services provided in fragmented landscapes and what is a good measure? Do different bee types (differing in body size and nesting preference) respond differently habitat availability and fragmentation?

Case study (chapter 7)

We performed a case study parallel to the modelling approach (i.e. it does not serve to provide data for the model). The aim was to study how an intermediate-sized cavity-nesting bee, the red mason bee, copes with a fragmented landscape and to provide an additional perspective (to the model) of how bees respond to a resource mosaic. The red mason bee, *Osmia bicornis* syn. *rufa* L., is common to urban areas in Europe, along with other solitary bee species such as *Anthophora plumipes*, *Andrena flavipes*, *Andrena fulva*, *Nomada fucata* and *Melecta albifrons* (Banaszak 1995, Flügel 2005) and a suitable species for studying urban distribution patterns with standardized trap nests. The use of a single species has the advantage that landscape structure effects are not cancelled out by taxonomical differences (Cane et al. 2006). Solitary bees such as *O. bicornis* visit several times more flowers per day than honeybees (Teppner 1996) and require spring flowering plants in high quantities. *O. bicornis* prefers small cavities and clay and loam as building material (Flügel 2005). Urban features affect *Hymenoptera* assemblages in trap-nests, probably by affecting the biotic and abiotic microsite conditions (Zanette et al. 2005). The study region is Leipzig and as most urban regions an example of a highly fragmented landscape. *O. bicornis* is a common species in the study region.

Our leading questions were: Does *O. bicornis* build nests in every part of the city? Do urban areas provide enough foraging resources (pollen and nectar-rich flowers) and nesting resources (hollow tubes) and is the number of brood cells that *O. bicornis* builds affected by it? How do microsite attributes around the nest (abiotic conditions and nest site quality) affect nest distribution and number of brood cells? Does any measure of fragmentation affect *O. bicornis*?

CHAPTER 2

Identifying body size constraints for pollen collecting solitary bees

Bees of different size collect pollen and nectar on the same flower (*Arnica montana*). How do these bees differ in foraging behaviour?

This review aims to set up a body-size related framework of pollination with relevant bee traits. We review the available data for these body size related traits in order to identify ecological relationships. We review the effect of body size on vision, flying (and foraging distances), pollen collection (including transport capacity and handling time of flowers) and other foraging behaviour that may relate to body size (such as choice of flower size and time of day of foraging).

2.1. Body size of bees

2.1.1. The size of bees

Most parts of the world harbour a rich bee fauna with a wide range of body sizes. Body lengths of wild bees normally vary between 4 mm and 28 mm (Michener 2000). In some parts of the world body sizes of bees can be more extreme. The smallest solitary bee is probably *Ceratina parvula* which measures 3 mm (Friese 1922, Michener 2000). Social colony building bees from the genus *Trigona* in the tropics can even be as small as 2 mm (Friese 1922) and the smallest bees (genus Quasihesma) live in Australia and measure 1.8 mm (Exley 1980). The largest solitary bee of the world, *Chalicodoma pluto* (*Megachile pluto*), lives in Indonesia and measures 39 mm. It was long presumed extinct, because it was not seen since the last record of 1859, until it was re-discovered in 1981 (Messer 1984). Some other very large bees with a body length of 30 mm from the genus *Anthidium* can be found in Turkmenistan (Friese 1931). Such extremes in body size have never been included in studies related to bee size since they are biogeographical oddities. The most frequently observed and studied solitary bees are cavity-nesting bees of intermediate size (10 to 14 mm), mainly of the genera *Osmia* and *Megachile*, due to their commercial value as crop pollinators.

There are no obvious size categories, since bees occupy the entire continuum of body lengths from 4 to 28 mm. The large number of studies that speak in terms of "small" and "large" bees demonstrate a certain need for it, but there is no consensus about their use (table 2.1) and promote misinterpretation of results. We advocate for fixed terms for the whole range instead of "small" and "large" being relative terms for the data presented. We give a suggestion in table 2.1 with five size classes (four thresholds that are easy to recall: 6-10-12-16) including "very small" and "very large" (e.g. Hoehn et al. 2008). In practice, body size is not often measured (different alternatives are discussed in appendix A.3) and is in data analysis often added at a later stage by using literature-based body sizes for species. In this case body size classes may help to identify new patterns in the data and to formulate new hypotheses. In cases where accurately measured body sizes are available, it is always a bad idea to use size classes in regression analysis (Irwin and McClelland 2003, Royston et al. 2006). However, even on a continuous scale can fixed size definitions for "small" and "large" bees (as well as "very small" and "very large") help to reduce miscommunication.

Table 2.1. Size classes and thresholds for classifying wild bees by size (body length) according to different studies. Size classes can vary from two to five groups and are given here in body lengths. We calculated the thresholds from (Hoehn et al. 2008) and (Cane et al. 2006) from intertegular span (see section 2.1.2) and those from (Winfree et al. 2007) from dry mass.

Study	"very small"	"small"	"medium"	"large"	"very large"
Chagnon et al. 1993		< 10 mm	> 10 mm		
Dafni and Kevan 1995		< 10 mm	10-15 mm	> 15 mm	
Cane et al. 2006		< 5 mm		> 5 mm	
Albrecht et al. 2007		< 12 mm		> 12 mm	
Winfree et al. 2007		< 6 mm	6-10 mm	> 9/10 mm	
Stout 2000		< 15 mm	15-20 mm	> 20 mm	
Schweiger et al. 2005	< 8.5 mm	< 12.5 mm	12.5-15.5 mm	> 15.5 mm	
Hoehn et al. 2008	< 5.5 mm	< 7 mm	7-9 mm	> 9 mm	> 16 mm
Our suggestion	< 6 mm	< 10 mm	10-12 mm	> 12 mm	> 16 mm

2.1.2. Body size measures and interchangeability

Two widely used body size measures are dry body mass and intertegular span (i.e. the shortest linear distance between the two wing tegulae across the thoracic dorsum, short "it-span") which have a power relationship (fig. 2.1.A and table A.1.1 in appendix A) over a wide range of body sizes and bee families (Cane 1987). Bees in the field are measured in fresh mass, which seems linearly correlated with dry mass (fig. 2.1.B). Despite being based on a large number of bee and wasp individuals (277) and a correlation coefficient of 0.98 (Danforth 1989a), the extent of the relation is quite small (from 1 to 60 mg fresh mass). Solitary bees may show a slightly different relationship than the *Hymenoptera* as a whole, but the extrapolation is problematic: fresh masses of solitary bees are often higher than extrapolated here (e.g. Maddocks and Paulus 1987, Pasquet et al. 2008).

We use body length as the main unit for body size in this review. Body length is intuitive for anyone working with bees, well documented for most species and the more basic, linear dimension. In order to compare studies we needed a conversion measure for dry mass and it-span. The appendices of Müller et al. (2006) provide data to correlate dry mass with body length (fig. 2.1C). The study from Cane (1987) provided dry mass for several species without their body length. We therefore considered the general body size range from different literature sources (appendix A.2) to represent each species. We used the arithmetic mean of the known range for males and females separately when given and otherwise at the species level and occasionally at the subgenus level. The mean at the species level enabled us to correlate dry mass with body length for the species measured by Cane in addition to the relationship obtained from Müller et al., extending a larger range of body sizes (fig. 2.1.C). There is a good agreement between both datasets and the difference may represent a deviance caused by the few large species or a difference between males and females. The fits (power coefficients 0.31, 0.33 and 0.31 for combined and both separate fits respectively) are close to isometric scaling (0.33) for a linear body dimension (length, it-span) with a volumetric dimension (mass). Note that the dry body mass of solitary bees spans one order of magnitude as required for ecological scaling studies.

The similar fit in figures 2.1.A and C suggests a linear relationship between length and it-span. We used the it-span data from Cane with the species-specific body length, which correlate nicely (fig. 2.1.D). Additionally we used the It-span data from the appendices of (Greenleaf et al. 2007) and corresponding species-specific body length which show almost the same relationship (fig. 2.1.D). Note that the outliers in figure 2.1.D are a result of using literature values for mean body length. One of the outliers (*Megachile flavipes*, 16 mm) was one of the few "size by subgenus" and may be 10 mm instead (Alfken 1933), strengthening the fit. The other outlier (*Xylocopa violacea*, 21.5 mm) is a case in which we used twice the same x-value for two different y-values (the other *X. violacea* lies close to the regression line).

In the following sections we either calculated body length from dry mass or it-span when given in the study or we used the species (or female) specific body length from independent literature references. All statistical fits, transformed correlations and inverse functions are given in appendix A.1 and the original data points in appendix A.2. In all cases we used simple linear regression models (untransformed or log-transformed data), since it is our goal to give a basic description of the observed pattern. In following sections data were often gathered with such different methods that standardized experiments are required to verify the patterns. The analysis of different body size measures was completed with data on thorax length (Jander and Jander 2002) which also correlated well with body length (appendix A.1 and A.2). Thorax length has been used as fixed linear dimension for dried specimens similar to it-span (e.g. Aizen and Feinsinger 1994).

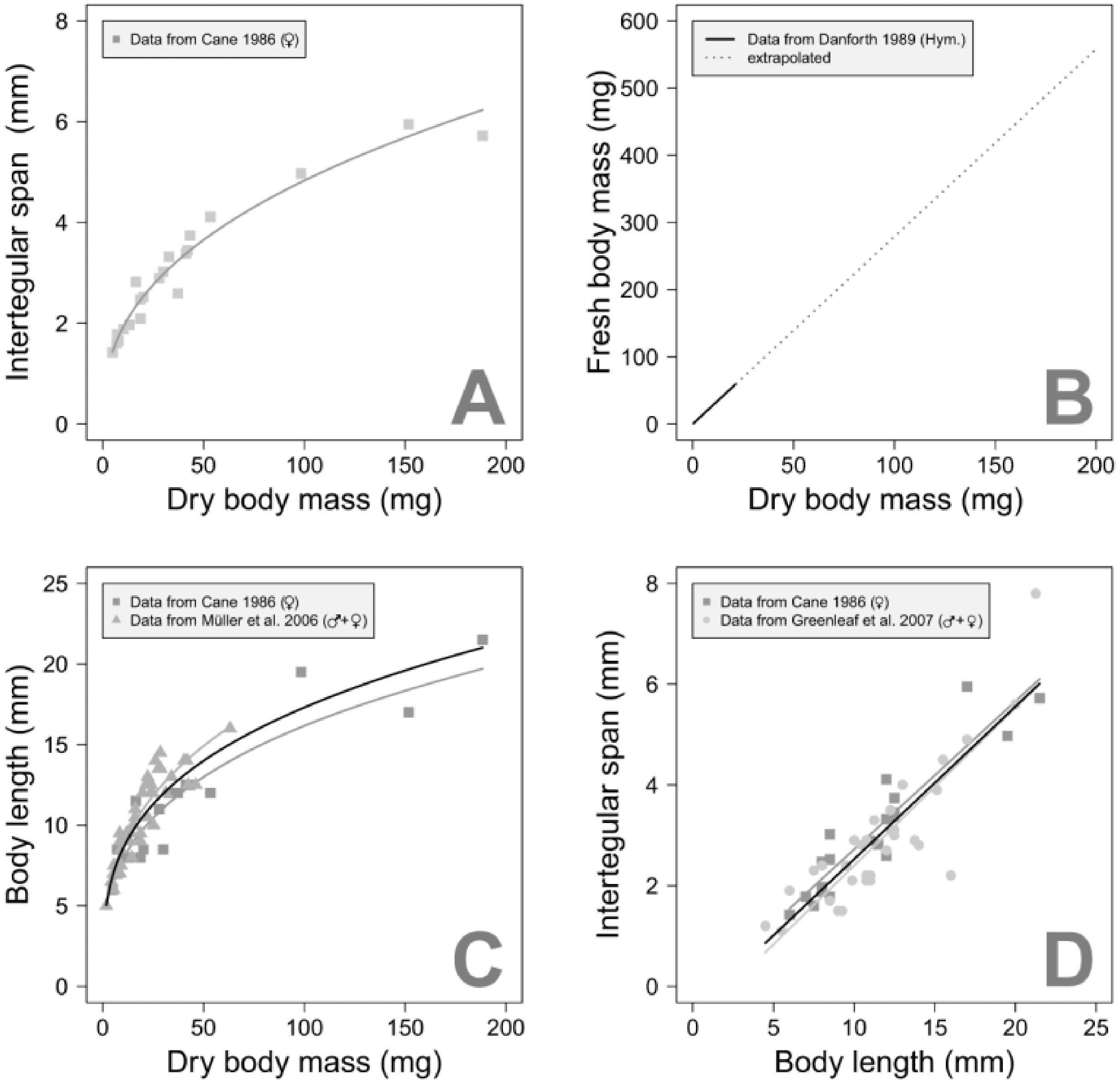

Figure 2.1: Correlations between the most commonly used body size measures for bees. The grey lines present the regression fit of the according dataset. Black lines represent the combined regression line over multiple datasets. Lines begin and end with outer data points. We log-transformed data before fitting when necessary to meet the criterion of normally distributed data.

2.2. Bee flight

2.2.1. Vision

Vision is probably the most important component of the bee's perception of foraging resources at most scales (Chittka and Spaethe 2007). The role of odometry is limited and at the landscape scale and is overruled by vision for honeybees (Vladusich et al. 2005) and probably for solitary bees as well (Guédot et al. 2007). Pollen collecting bees even ignore scent cues of nectar rewards at small scales (Stout et al. 1998). Vision is the main component of distance and size recognition of patches (Spaethe et al. 2001) and flowers (Chittka and Raine 2006). Better vision is an advantage for recognizing patches and flowers from larger distances and improves gap crossing abilities (Ewers and Didham 2006). How perception distance scales with body size would therefore help to understand how bees respond to landscape fragmentation. Within small mammals perceptual distance scales linear with body size (Mech and Zollner 2002). For bees there is no study that has measured perceptual distance directly so that we need to look at proxy traits in the bee's compound eyes, which are well studied and govern visual abilities.

The bee's two compound eyes give a "panoramic, pointillistic presentation of the surrounding world" (Srinivasan 2009). The sharpness of the image depends on multiple eye properties and the resolution of the compound eye does not double as eye size doubles, as it is the case for lens eyes (Jander and Jander 2002). The compound eye, build up from many facets or ommatidia (receptor unit with own lens), scales naturally with body size, but relative eye shape may strongly differ between taxonomical groups (see e.g. drawings in Friese 1922). Eye size (length and width) and shape can influence properties of ommatidia, such as number, size and angle between them (interommatidial angle) and affect light perception and image sharpness (Land 1997).

Light perception and image sharpness

The allometric scaling of eyes of bees of different genera (*Apidae*, *Megachilidae*, *Andrenidae*, *Halictidae*) is well studied (Jander and Jander 2002), and similar studies are known for ants (Zollikofer et al. 1995, Moser et al. 2004). Both length and width of the eye scale isometrically with body size (fig. 2.2.A). Larger bees also have more facets per eye (fig. 2.2.B), increasing image resolution (number of image points) linear with body length. The relation deviates from an isometric scaling with eye surface, hinting to a trade-off in eye structure. Image quality is also affected by the amount of light received per facet, the diffraction of light on the rhabdom (light sensitive unit) and the acceptance angle ($\Delta\rho$) of the ommatidium (see Land 1997, for an illustrated explanation of eye parameters), which can be approximated by facet diameter. Facet diameter (average, largest and smallest; representing variation within the compound eye) increases with body length (fig. 2.2.C, only mean diameter shown, Jander and Jander 2002). Even more important for image sharpness is the contrast perception between two receptor units and is determined by the interommatidial angle ($\Delta\phi$). The interommatidial angle decreases with body size and levels off for the largest species (fig. 2.2.D, Jander and Jander 2002). Hence, intermediate sized bees perceive more contrast detail than smaller bees (smaller $\Delta\phi$) and large bees only moderately more contrast detail than intermediate sized bees. Visual acuity is directly related to the interommatidial angle and computed as $1/(2\Delta\phi)$ (Land 1997). It implies for larger species that they can see smaller objects than small bees, or the same object from a larger distance that small bees.

Within a compound eye there is a another trade-off, balancing light perception and resolution, which becomes increasingly more important for small bees. A larger facet diameter means more light per receptor unit, but also more blurring of the signal due to a larger acceptance angle, which may explain why lens diameter levels off (fig. 2.2.C). The spherical shape of the eyes required for wide view of the environment increases the interommatidial angles and reduces the visual acuity. Packing more ommatidia together on the sphere (large bees) reduce interommatidial angles (figs. 2.2.B and 2.2.D). Small bees have a reduction in both and need to compromise. The so-called eye parameter measures this compromise between visual resolution and light sensitivity and is calculated as the mean lens diameter multiplied with mean interommatidial angle. Eye parameter increases slightly for smaller species (fig. 2.2.E) which means that their eye structure is adapted to light sensitivity and not to sharpness (Jander and Jander 2002).

The main deviation from a normal body size relationship for eye characteristics was found for nocturnal bees. Nocturnal bees have larger eyes (fig. 2.2.A) and larger facet diameters (fig. 2.2.C) in comparison to species of similar size. The allometric relationships are similar, but have a larger intercept (Jander and Jander 2002). Nocturnal bees have especially large eye parameter (fig. 2.2.E), trading off sharpness in favour of light perception more than any other bee type. In addition have nocturnal bees wider rhabdoms (photoreceptor that records the incoming photons), which highly increase light sensitivity (Land 1997). Nocturnal species face low light conditions and a low amount of available photons has to be distributed over a large number of ommatidia (instead of being combined within one large lens in the vertebrate eye) in the most efficient way. Land (1997) estimated that diurnal insects receive $4 \cdot 10^7$ photons per receptor per second in sunlight, $4 \cdot 10^4$ in room light, 40 in moonlight and 0.004 in starlight (1 photon every 4 minutes). Also in dim light conditions bees heavily rely on visual cues for foraging (Baird et al. 2011).

Bees have trichromatic color perception similar to mammals with sensitivity peaks at the wavelengths 340 (UV), 463 (blue) and 530 (green) nm (Srinivasan 2009). Different bees species use colours for many different activities such as specialized orientation mechanisms and nest localization (Guédot et al. 2007) and taxonomical differences in wavelength sensitivity can be expected. Body size may affect wavelength sensitivity since small bees cannot probe all flowers due to a short proboscis and are therefore restricted to flat and open flowers that are less often coloured blue and UV blue (Peitsch et al. 1992). There is however no indication that different species have a different wavelength sensitivity and the similarity between bees of different taxonomical groups was higher than expected (Peitsch et al. 1992). The only known exceptions are some tropical species that have adapted receptors with a higher UV wavelength sensitivity to forage better in dense tropical forests (Peitsch et al. 1992).

The scaling of physical eye properties with body size, here shown for solitary bees only (figs. 2.2.A-E), is similar to original publication which included eusocial species as well (Jander and Jander 2002). Differences in perception between solitary and eusocial species must mainly be sought in differences in pattern and shape recognition (Campan and Lehrer 2002).

Consequences for the perception of foraging resources

Since large bees can see better it is likely that they also have a larger perception distance and recognize foraging resources from farther away. Most research on perception distance and object size has been performed with honeybees and cannot be directly related to body size. Honeybees are e.g. able to estimate the size of objects irrespective of its distance (Horridge et al. 1992), while recognition of the colour of an object depends on object size and distance (Chittka and Raine 2006). For recognizing flowers from farther away, bees probably perceive a patch of flowers as single object because the signals merge (Wertlen et al. 2008). The contrast pattern of flowers against the background depends on the size of the flowers and the contrast in colour (e.g. Macuda et al. 2001, Spaethe et al. 2001, Spaethe and Chittka 2003, Chittka and Raine 2006).

We expect that recognition distances change with body size according to visual abilities. The only experiment that we know of found no evidence that patch recognition is related to body size (Stout 2000). We remark that their bees were in the range of 12 to 25 mm body length, but that bees in the range of 5 to 12 mm have the largest differences in visual ability (contrast detail, fig. 2.2.D). In general we can state that the largest bees can see best and that with a decrease in body size restrictions and trade-offs get stronger (i.e. steeper decrease in interommatidial angle and increase in eye parameter, figs 2.2.D and 2.2.E). Small bees have a strongly reduced visual resolution, which they seem to compensate by flying more erratically (Jander and Jander 2002). Large bees fly more in straight lines and have a better flight guidance due to better visual acuity (Land 1997). However, the better visual ability may conflict with other body size related traits. Larger bees also have a higher velocity which reduces image sharpness (Land 1997). Large bees indeed trade-off speed and foraging precision depending on task (Chittka et al. 2003). Large bees can see better than small bees at equal speed, but probably not when they also fly faster, unless they also have faster processing capacities. Processing capacity is probably linked to eusociality in bees rather than body size (Campan and Lehrer 2002).

In conclusion, there is no direct proof that large bees can see in general better than small bees; neither at the flower and patch level, nor at the landscape level. There are trade-offs in the compound eye, which favour large bees. The advantage is in practice probably very minimal, since each bee species has optimized eye traits. To which account the specific trade-offs have disadvantages at different spatial scales remains to be investigated.

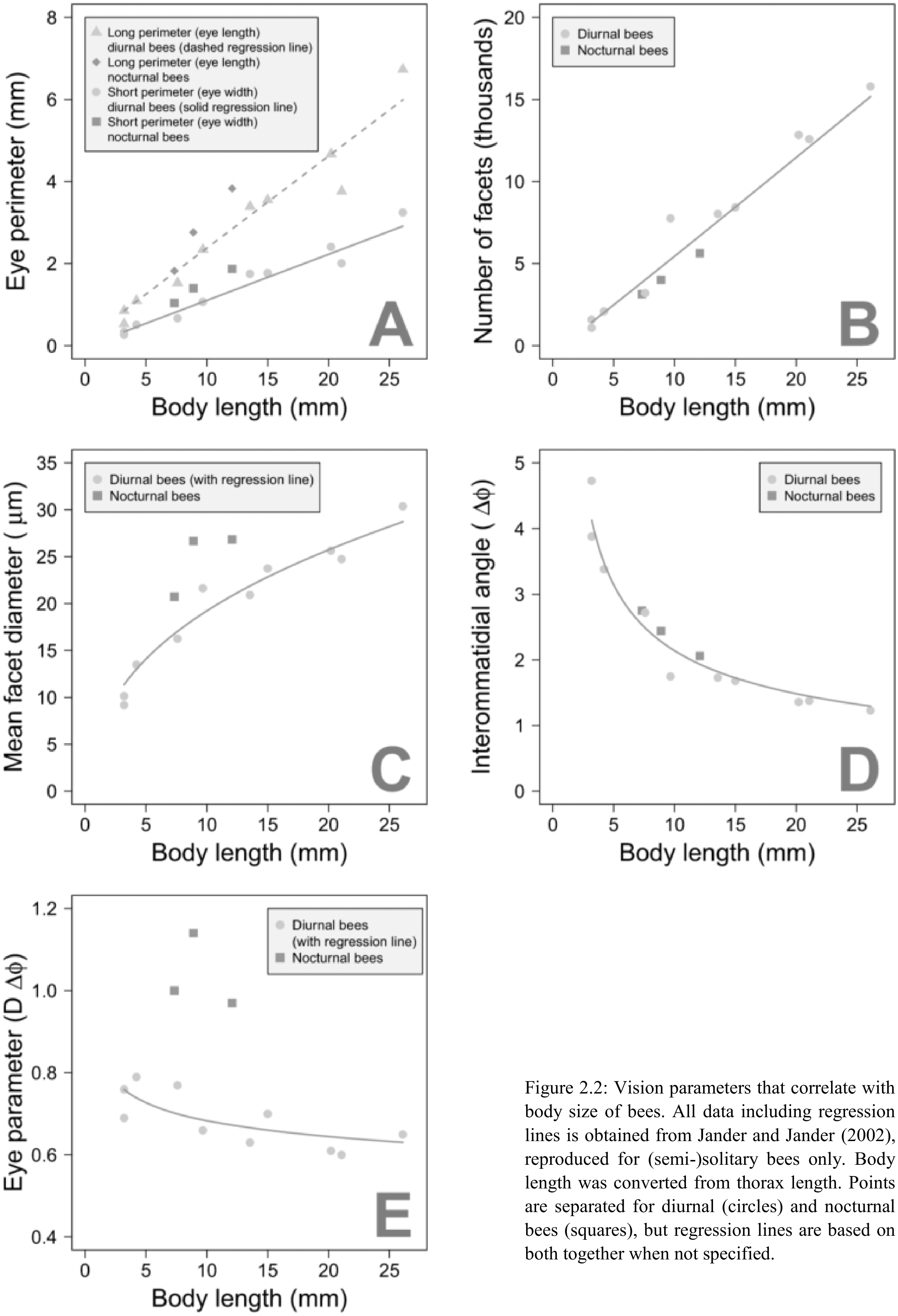

Figure 2.2: Vision parameters that correlate with body size of bees. All data including regression lines is obtained from Jander and Jander (2002), reproduced for (semi-)solitary bees only. Body length was converted from thorax length. Points are separated for diurnal (circles) and nocturnal bees (squares), but regression lines are based on both together when not specified.

2.2.2. Flying

Velocity

Bees are central place foragers that fly at different speed modes for their activities (Nachtigall et al. 1995). They fly at high velocity from their nest to a distant flower patch, fly with a medium velocity between flowers and inflorescences from which they collect nectar and pollen and fly at low velocities for finding the nest entrance or hovering. It is clear that larger species can fly faster than small species (Dafni and Kevan 1995), but measurements on insect flight speeds are in general not well documented (most represented by a single model species for insects, *Apis mellifera*) and lack standardization (Dean 2003).We collected published data on velocities of different bee species (eusocial and solitary) and distinguished between three different speed modes. We interpreted velocity measurements as follows: orientation flights around the nest as "low velocity", flights between flowers or flight experiments mimicking flower foraging as "medium velocity" and measurements at any larger scale (such as between patches and maximum velocity indications) as "high velocity". We fitted regression lines through the origin and included other *Hymenoptera* as well to get enough points for a reliable fit (table A.1.2. in appendix A). The velocity of *Hymenoptera* (all three speed modes) seems to increase linearly with body length (fig. 2.3). Note that the high velocity mode extends the range of body lengths that exists in solitary bees (body lengths up to 50 mm rather than 25 mm). We found no indication that wasps, eusocial bees and solitary bees differ in their velocities (fig. 2.3).

The measurements of Stone et al. (1995) and Kunze and Chittka (1996) were clearly lower than others (fig. 2.3, were considered outliers and excluded from the regression) for all seven values. However, the relative difference between the three speed modes in the former study was very similar to the relative difference of the estimated slopes in figure 2.3 (i.e. the medium velocity measured by Stone et al. has a relative value of 0.53 between high (1.0) and low (0.0) velocity, while the slope of the regression line of the medium velocity has a relative value of 0.58 compared the slopes of both other regression lines). This could mean means that the measurements of the different speed modes in both studies are reliable , but may have been performed under exceptional conditions causing their consistent shift to a lower value.

Non-standardized measurements of insect velocities in the field are highly affected by wind speed (Dean 2003). Wind speeds can change the ground speed by −17 and +15% for honeybees (Wenner 1963) and by −13 and +3% for bumblebees (Riley et al. 1999). Bees can reduce the effect of wind by flying low to the ground (up to 90% at 10 cm, Nachtigall 1992, Nachtigall 1994, Riley et al. 1999) and the effect of wind may be limited. Large pollen loads can slow honeybees down up to 25% (Barron and Srinivasan 2006). Bees of the same species can also have different velocities because they differ in gender and age (Dean 2003) or have differences in knowledge of the environment (Collett 2000). Some differences in velocity can be attributed to environmental conditions such as temperature, solar radiation and humidity (Dean 2003). Additional measurement error is introduced by the distance over which is measured, which is known to influence the estimation of velocity, especially when distances get very short (Pyke 1983, Collett 2000).

The linear relationship between velocity and body length may be inaccurate. For a group of wild orchid bees velocity scaled linearly with body mass instead of body length (Combes and Dudley 2009, original data were not provided). Also for locusts does flight speed scale linearly with body mass (Fischer and Kutsch 2000). For body length this would mean an exponential increase for velocity with increasing size (see also fig. 2.1.C with switched axes). The presented data (fig. 2.3) does not support an exponential increase of velocity with body length, especially not for the high speed mode. However, over a much larger range of body sizes (insects, birds and mammals) velocity scales with exponent 0.17 with body mass (Bejan and Marden 2006), suggesting a relatively lower velocity with body length

(0.17 < 0.33). We also note that Combes et al. (2009) found that 20% of the variability in velocity was explained by body mass, which may be higher for a linear fit with body length instead.

Flight parameters

Do flight parameters also scale linearly with body length? The wide range of velocities of bees has more consequences than their displacement ability alone. To start with, velocity affects the air viscosity that is experienced. Small organisms, including bees, experience the air like a fluid in which they rather swim than fly. The smallest wasps (such as fig wasps) are even not able to fly actively in wind (Compton et al. 2000). Reynolds numbers (measure of relative contribution of viscous forces in the air) for *Hymenoptera* vary roughly from 100 to 5,000 (Danforth 1989a). The Reynolds number decreases with velocity and body size and below a value of 10,000 viscous forces get dominant, heavily affecting the aerodynamic performance (Ellington 1991). Flight parameters such as wing shape, muscle mass and metabolic power may therefore scale differently with body size than velocity.

Wing length and wing area increase with body size between species (Darveau et al. 2005, small to intermediate sized bees) and within species (Roberts et al. 2004, large solitary bees). The scaling exponents are slightly larger than for isometric scaling (i.e. when wing length scales linearly with body with body length), suggesting a change in shape. The wings of larger bees are indeed more elongate and narrow (Danforth 1989a). The pterostigma (a heavy sclerotized spot bordered by wing veins, functioning as a concentration of mass on the wing and important for regulation of flight) is relatively larger for small species (scaling exponents smaller that for isometric scaling, small to intermediate sized *Hymenoptera*, Danforth 1989a). This may counterbalance for their wider and shorter wing shape or be an adaptation to higher viscosity of the air (Danforth 1989a). Allometric relations in wing shape were stronger within a taxonomic group than for all wasps and bees together, indicating that wing shape is also adapted to specialized flight behaviour (Danforth 1989a).

Flight muscle mass increases isometrically with body mass between species (Dillon and Dudley 2004, intermediate sized bees) and less strongly (power 0.62) within species (Roberts et al. 2004, large solitary bees, thoracic mass as proxy for muscle mass). In the latter case the relatively smaller muscle mass for larger individuals was compensated by a higher flight muscle efficiency (Roberts et al. 2004). In contrast, wingbeat frequency of bees decreases with about power 0.30 with body mass (Dillon and Dudley 2004, Darveau et al. 2005), suggesting a linear decrease with body length of bees and near-linear with wing length (Danforth 1989a).

Metabolic or mass-specific power is the energy for an individual required to lift its own weight and differs between speed modes. Within species the relationship is U-shaped (from low to high velocities) as well for honeybees as for other animals such as birds and bats (Ellington 1991, Nachtigall et al. 1995). Bees need to adjust their nectar (energy) intake rate according to the power required (Hocking 1953). The mass-specific power at intermediate velocities increases with body mass for *Hymenoptera* similar as for all animals together, but with a low scaling exponent (<0.20, Ellington 1991). This means that insect flight muscles can function at very high speeds compared to their body size (Hocking 1953) which enables complex flight behaviour such as hovering (Ellington 1991). Similar power exponents have been found for large bees between species (Dillon and Dudley 2004) and within species (Roberts et al. 2004). The mass specific power that is relatively higher for small species seems to enable higher wingbeat frequencies (Dillon and Dudley 2004).

In conclusion, some of the parameters compensate each other and there are indications that small and large bees face different challenges in the air. Altered wing properties may compensate for higher viscosity for small bees and mass specific power is linked to hovering abilities. It was long assumed that large bees were also oxygen limited, since diffusion respiration becomes more difficult with increasing size (Hocking 1953), but recent experiments show that for flight metabolic rate the wing form and kinetics are more limiting than oxygen supply (Darveau et al. 2005).

Compared to other flying animals do bees have relatively small wings for their body size and it was long believed that such small wings could not make an animal fly with such a high air resistance (Magnan 1934), also known as the "bumblebee paradox". Recent studies have showed how the aerodynamics of bee wings work and hold them in the air (Altshuler et al. 2005, Bomphrey et al. 2009). At the same time, it was found that honeybees and bumblebees do not use the most efficient aerodynamic flight possible. Honeybee flight may be adapted as a specialization for carrying large loads or it may be a physiological limit of the flight muscles (Altshuler et al. 2005). The even larger bumblebees have unlinked wing strokes, resulting in further loss of efficiency. This may be an adaptation to manoeuvre more accurately between flowers. It is also likely that bumblebees have such a wide thorax that the wing roots are separated and can only operate independently (Bomphrey et al. 2009). This may mean that large bees fly differently than small bees.

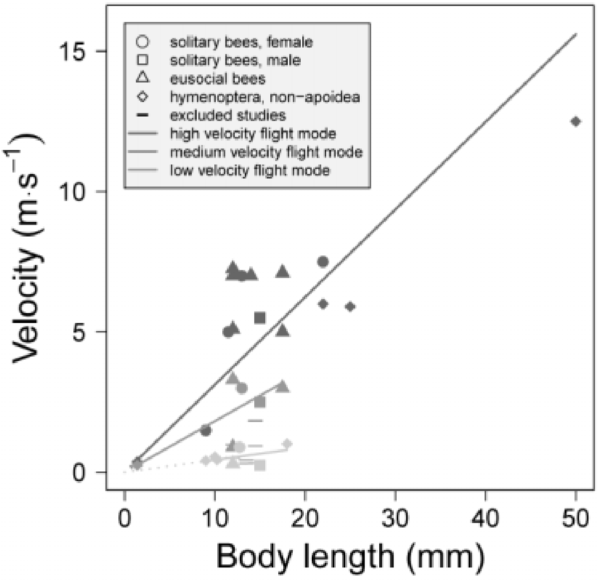

Figure 2.3: Three velocity modes (low, medium, high) in relation to the body size of bees. The dotted lines are extrapolations beyond the data.

2.2.3. Distance range

Homing distance and foraging distance

The distance a bee flies and forages away from the nest is a good and widely used proxy for flight capability. Studies mainly differentiate between homing distance and foraging distance. Homing distance is the maximum distance from which a bee can find its nest and was first published for a solitary bee more than a century ago (Fabre 1879). Homing distance differs for individuals of the same species, indicating that some bees have been further from the nest in their life than other bees (Gathmann and Tscharntke 2002). Despite differences between individuals, the distance at which 50% of the individuals are able to return (as well as 90%) can be considered as a species trait and relates to body size (Greenleaf et al. 2007). The foraging distance on a normal day is much more variable than a homing distance. The foraging distance from the nest to a flower patch varies within a day and between days. Solitary bees visit patches of many different distances from the nest due to lack of communication with other bees (in contrast to honeybees) about optimal flower locations. Although the mean distance from the nest on a regular foraging day may be too variable to be a species trait, it is probably a good local estimate of the area that is certainly visited around the nest and pollinated. Foraging range includes inbound and outbound flights from the nest to the resource and varies with the spatial and temporal availability of resources in the landscape (Guédot et al. 2009). Maximum foraging range is sometimes confusingly equalled with maximum homing distance. The maximum homing distance is given by an individual that has flown very far and has a wide knowledge of the environment. It may even be that this individual has come from far away searching for a nest. Maximum homing distance does thus lie far beyond everyday foraging activity of a species.

We found three papers (Gathmann and Tscharntke 2002, Greenleaf et al. 2007, Zurbuchen et al. 2010b) that reviewed the literature on homing experiments and direct foraging experiments (merely translocation experiments, feeder training, mark–recapture, pollen analysis, nest–forager association and harmonic radar) including many solitary bee species. We combined these studies and performed a power fit (on natural log-transformed body length and distance) for separate sets and combined sets (figs. 2.4.A and 2.4.B).

Homing distance increases exponentially with body length (fig. 2.4.A). Both the original regression given by Greenleaf et al. (including eusocial species) and the newly fitted relationship (excluding eusocial species) deviate from the other studies. The data collected by Zurbuchen et al. show a moderate exponential increase, as well as the combined data from solitary bees form both reviews taken together (fig. 2.4.A). When we include eusocial bees from both reviews ("all bees"), the homing distance increases somewhat more strongly with body size. It is generally assumed that eusocial bees have larger foraging (and homing) ranges than solitary bees, because they are forced to collect relative larger amounts of pollen and nectar to maintain the colony (e.g. Westphal et al. 2006a, Guédot et al. 2009). A similar result was found for social stingless bees (*Meliponini*): in the body size range from 6 to 12 mm the maximum distance from the nest (estimation by mark-recapture) increased from 500 to 2500 m (Araújo et al. 2004), which is somewhat higher than for solitary bees. Solitary wasps show very similar homing distance - body size relationships (Wesserling and Tscharntke 1995), despite the use of different resources.

The data from Greenleaf et al. suggest a two- to three-fold larger homing distance for 15 mm large bees compared to the other regressions. For very large bees of 25 mm long this deviation is even larger. We think that some outliers cause or induce the steep increase, which disappears when we merge the data with those from Zurbuchen et al. We think that the equation from Greenleaf et al. overestimates homing distance, especially for large species (both eusocial and solitary). The outliers may also relate to inclusion of some tropical species with extremely scattered food sources (increasing foraging and homing distances) as may occur in tropical rainforests (O'Toole and Raw 1991).

Normal foraging distance seems to increase almost linearly (exponent close to 1) with body length. Again most lines show a very moderate increase (solitary bees reviewed by Gathmann et al. and by Zurbuchen et al., solitary bees combined (two reviews), all bees combined (three reviews)). Also here the equation given by Greenleaf et al. shows a much steeper increase with body size. In this case it can be explained by the fact that only data from eusocial bees were used (which may have much larger foraging ranges). We also have to note that Greenleaf et al. had no bee with a body size over 15 mm and the other two only one bee each, which is not a good precondition for fitting attempts for the suggested body size range.

Figures 2.4.A and 2.4.B show different scaling with body size with exponents above 1 and below 1 respectively (table A.1.4 in appendix A). This means that the homing distance increases with body size proportionally more for larger bees and the foraging distance increases proportionally less for large bees. Another experiment also suggested that the increase in foraging distance levels off with body size (Steffan-Dewenter and Tscharntke 1999), confirming the pattern. Homing distance and foraging distance may be governed by different processes, but it is questionable that these processes cause opposite allometric rules for such similar flight proxies. We would rather question the consistency of the data (review of data collected over decades with multiple methods) and propose study with enough species at both ends of the body size range.

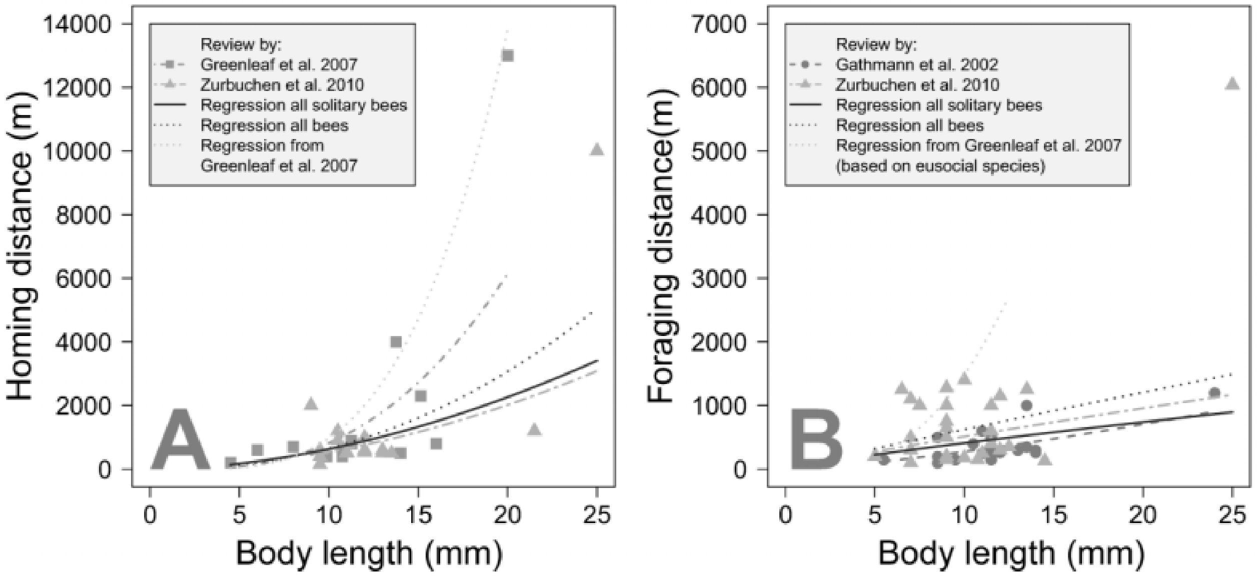

Figure 2.4: The homing distance (A) and foraging distance (B) of solitary bees in relation to body size. Note that eusocial species are not represented by a point here but were included in " regression all bees" and "regression from Greenleaf et al."

2.2.4. Foraging activity and flight distance

How does a body size related value for foraging distance or homing distance translate into the wide variation in foraging distances during the day? Foraging distance seems to be much smaller than homing distance (compare fig. 2.4.A and 2.4.B). The review by Greenleaf did not only considered (near) maximum homing distance but also a "typical homing distance", defined as the distance at which 50% of the bees are able to return to their nests (table A.1.4 in appendix A, homing distance 50%). It would fall between the other curves in figure 2.4.B and may represent typical foraging. We may thus be able to link homing probability with foraging data.

Classically, binary observation data (returned and not returned) are used to estimate a homing ability curve for a single species. Homing ability does decrease with release distance from the nest and was in the case of Gathmann and Tscharntke (2002) fitted with a sigmoid logit function. With such a curve one can estimate for a certain species at which point 50% of the bees were able to return and the point where only 10% of the bees were able to return (i.e. 90% of the bees have not been foraging beyond this distance). These two points for multiple species yielded two allometric rules (Greenleaf et al. 2007). Since we can now calculate these two points for a bee of any size (50% return and 10% return), we can also try to reconstruct a curve for homing ability for one species based on these points and compare it with foraging data.

The sigmoid curve for homing ability as used by Gathmann and Tscharntke (2002) cannot be used as a reliable estimate, since it estimates that when bees are released 1 m from the nest, up to 30% of the bees do not return (Gathmann and Tscharntke 2002). Abrol and Kapil present their homing data in a different way (Abrol and Kapil 1994). They were able to make informative histograms for each species on the percentage of returning bees, due to a high number of replicates (about 90 individuals per species released over a wide range of distances). These histograms make clear that within a certain distance of the nest, bees always return and that after this distance percentages rapidly decline. The distance at which bees always return also seems to increase with body size (Abrol and Kapil 1994). Foraging activity at given distances from the nest is also commonly presented in histograms and show similar patterns as for homing data (Pasquet et al. 2008, Zurbuchen et al. 2010b). Small distances from the nest will be visited by all bees (0 return), intermediate distances by most bees later on the day (that also visited close flower patches) and some bees (10%) forage farther away (probably by the end of the day) and in exceptional cases (1%) a bee flies even much farther. Both homing and foraging can be displayed as a histogram depending in a similar way on distance from the nest and both describe a kind of progressive knowledge of the environment. Homing (distance) describes the progressive knowledge during a lifetime and foraging (distance) the progressive foraging activity of bees during the day.

To investigate whether we can use the predicted homing distance from the allometric rules from Greenleaf et al. to describe foraging activity for certain species, we use the histogram data of a small, medium and large species (Pasquet et al. 2008, Zurbuchen et al. 2010b). We calculated the typical (r50) and far (r90) homing distance (distance beyond which 50% and 90% of the bees were not able to return at release respectively) for these three species:

$$\mathrm{r50} = 10^{(-1.643 + 3.242 \times \log_{10} \text{it-span}))} \quad (1)$$

$$\mathrm{r90} = 10^{(-1.363 + 3.366 \times \log_{10} \text{it-span}))} \quad (2)$$

(Greenleaf et al. 2007), where it-span can be replaced by $y = -0.504 + 0.303x$ (figure 2.1 and table A.1.1 in appendix A) to predict them from body length.

We use a Michaelis–Menten saturation curve to describe a return probability curve. With this curve we could solve the equation with two parameters (r50 and r90) for a bee of a certain size. Since a Michaelis–Menten curve normally goes through the origin and we preferred to have a range of x values (close to the nest) for which a bee would be able to return (minimal knowledge of the environment) we shifted the curve, based on the two known points on this curve (r50 and r90):

$$\mathrm{shift} = 1.125 \times \mathrm{r50} - 0.125 \times \mathrm{r90} \quad (3)$$

(See also equation 5 where 50% and 90% return probability share the same shift value, resulting in (3))
The saturation constant Km changes accordingly:

$$\mathrm{Km} = \mathrm{r50} - \mathrm{shift} \quad (4)$$

The return or homing probability is than described by a Michaelis–Menten curve:

$$\mathrm{P}_{\mathrm{return}} = \frac{dist - \mathrm{shift}}{\mathrm{Km} + dist - \mathrm{shift}} \quad (5)$$

where *dist* is the distance from the nest.

The response can be interpreted in different ways. It can be the probability that an individual has reached the distance beyond which it has no knowledge of the environment (direct interpretation of homing distance). Inverting the y-axis it could represent the proportion of bees reaching that distance at one of their foraging flights. This is what we did to compare homing probability with foraging histograms (fig. 2.5).

One would expect that for bees of all sizes the observed foraging distances are lower than the predicted homing distance curves, but that the foraging histogram has a similar shape. The knowledge of the environment (given by the homing curve) should be somewhat larger than the foraging activity and this curve should be shifted somewhat to the right relative to the foraging histogram, exactly as it is the case for medium sized bees (fig. 2.5.B). For large bees the predicted curve is shifted more to the right than we would expect and for small bees too much to the left. This could indicate a wrong power fit on the log transformed It-span and distance data by Greenleaf et al. When an outlier affects the slope at the end in a log-log regression (steeper regression line) this is exactly what you would get: too low values for small bees and too high values for large bees. Also a deviance in prediction may be caused by converting It-span (fitted data in Greenleaf et al.) to body length, or we may have selected non-representative species (fig. 2.4.A shows large deviations between species).

The shape of the curve (inverted and shifted Michaelis-Menten saturation curve) seems to be chosen plausibly. A range of distances from the nest is both well foraged by bees and not considered as unknown space, after which a steep decline takes place. An asymmetrical sigmoid-curve could be an alternative, but we could not fit it with only two known points. Sometimes a Lévy distribution is suggested for foraging distances (including honeybees and bumblebees, Reynolds 2009, Reynolds et al. 2009). This also fits with the sharp decrease for larger distances from the nest, but would also mean no foraging activity very close to the nest. This is plausible for bumblebees and honeybees that tend to fly further for larger mass-flowering patches (Dramstad et al. 2003, Westphal et al. 2006a). Large bees such as bumblebees have higher metabolic rates and reach a higher efficiency at larger scales by ignoring low-resource patches (Westphal et al. 2006a). Also the large solitary bee *Xylocopa flavorufa* (fig. 2.5.C) did have only two flights (of the same individual) recorded below 100 m, although distance between nest and flowers was less than 20 metres (Pasquet et al. 2008). However, a colony of bumblebees in the middle of a clover field was foraging mainly within 20 m of the nest (Brian 1954, cited in Heinrich 1976).

Whatever the exact relationship between distance from the nest and foraging activity is, it is clear that most solitary bees prefer to forage close to the nest (Neff and Danforth 1991, Zurbuchen et al. 2010a) and that bee abundance suddenly drops at a certain distance and that there are only few long distance occurrences (Artz and Waddington 2006, Kohler et al. 2008, Van Rossum 2009). An important factor is probably the spatial distribution of flower patches, determining the distance between these patches and the nest and between patches. During the day near patches get depleted and bees fly progressively farther away from their nest, but only few individuals will fly very far (Zurbuchen et al. 2010b). Also important is landscape-level flower availability (Banaszak 2000, Lopez-Uribe et al. 2008, Wolf and Moritz 2008). Distribution of mass crops in the landscape therefore also alters the actual foraging range of bees (e.g.Wojtoski et al. 1995).

The distance from which bees can return to the nest at release is widely discussed. Fabre (1879) already recorded an extremely large homing distance of 4000 metres for the 14-18 mm large bee *Megachile parietina* (*Chalicodoma muraria*). Most intermediate sized bees forage far below 4000 metres, and 90% of the bees does not know the environment beyond 2000 metres (fig. 2.5.B, note that this is a 12 mm large bee). However, still few bees (5%) will return home when released at 4000 metres (fig. 2.5.B). The proportion of bees that know the environment beyond 4000 meters is even higher for a 14-18 mm large bee. The picture is somewhat different for small bees. The 8-9 mm large bee *Rhophites trispinosus* was able to return to the nest when it was released 1000 meters away (F. Burger, pers. comm.) and the 7 mm large bee *Lasioglossum fulvicorne* foraged up to 1250 distance (Beil et al. 2008). When the homing probability curve for a small bee (fig. 2.5.A) would be plotted in the same proportion to the foraging data as for an intermediate sized bee, the above facts would be met. This indicates again that the estimation by the regression model from Greenleaf is unsuitable for small species.

Expansion ranges (yearly dispersal ranges) may be larger than either homing and foraging distance (Steffan-Dewenter and Schiele 2008), but are fairly unknown for most bee species. Several intermediate sized bees expand about 5 to 9.5 km per year (Frommer 2008) and large bees about 16 km (Pando et al. 2011). At the individual level the differences may be as large as in homing distance. Most bees prefer to nest in the vicinity of the old nest (Free and Williams 1970, Ivanov 2006), some drift farther away (Bosch and Kemp 2005) and in other cases bees may be prepared to search unlimited distances for a nest site (till they die), since they cannot reproduce without it.

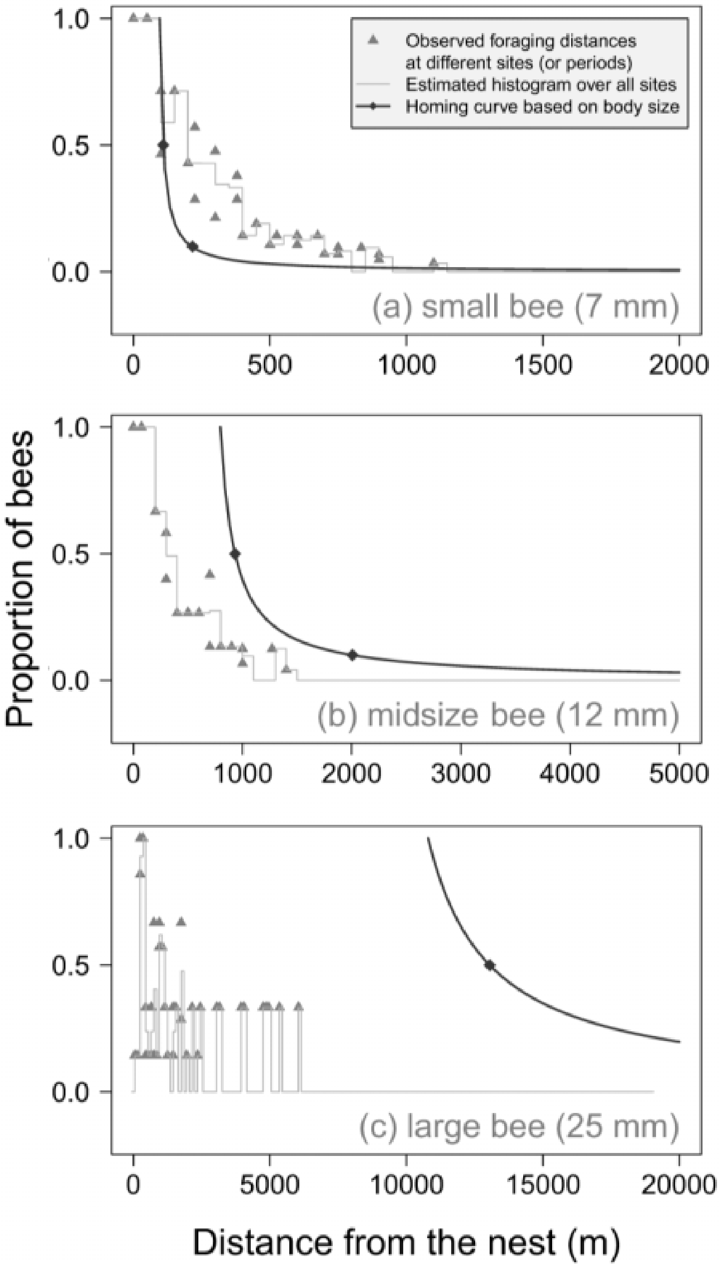

Figure 2.5: Comparison between estimated homing distance curves and real foraging data. Homing curves are fitted through two body size related points calculated with the regressions given in Greenleaf et al. Foraging distances are either based on proportion of bees foraging at a certain distance from the nest (a, b; Zurbuchen et al.) or on proportion of flights landing at a certain distance from the nest (c, Pasquet et al., data normalized to 1.0).

2.3. Flower visitation

2.3.1. Pollen transport capacity

Bees transport pollen on their body as resource for their offspring. External pollen transport is commonest, but some bee genera use nectar or oils to agglutinate the pollen and some even transport pollen by ingestion (Neff 2008). We focus here on external pollen transport. Although bees have specialized structures that affect pollen load (scopae, corbiculae and specialized hairs, see e.g. Friese 1922, O'Toole and Raw 1991, Westerkamp 1996), larger pollinators clearly can carry a larger amount of pollen (Griffin et al. 2009). Surface area increases overproportionally with body length, so larger bees should carry relatively more pollen. We collected data from the literature mainly at the level of brood cell provisions which is a proxy for the amount of pollen that bees collect per foraging trip. We review number of pollen grains (per brood cell and foraging trip) and pollen volume (per brood cell only).

Brood cell provision in pollen grains and provision per foraging trip

Both brood cell provisions and provision capacity per foraging trip are mostly measured as number of pollen grains, but data on pollen provisioning for bees is not abundant (fig. 2.6.A). The variance in number of pollen grains per brood cell for species of similar size is so high that a pattern across bee size is absent. The number of pollen grains transported per flight shows a similar pattern, but with values about four to ten times smaller (fig. 2.6.A). This suggests that a bee needs four to ten foraging trips to provision a brood cell, which seems indeed to be the case (Franzén and Larsson 2007).

The number of pollen grains collected by one bee species is highly variable for different plant species because grains vary widely in size and shape (Free and Williams 1972, Stanley and Linskens 1974, O'Neill and O'Neill 2011). Flowers trade-off pollen size and number of pollen grains (Harder 1998), which means that a bee can collect a large number of small grains from one plant species or a small number of large grains from another species with similar nutrient gain. This variance caused by plant species is apparently higher than the variance caused by bee body size. It is relatively difficult to separate the effect of body size and plant species since many bee species are oligolectic and forage only on one or several similar plant species. In order to compare plants of different families, one must select polylectic bee species of different size that forage e.g. on several abundant mass crops (see e.g. O'Neill and O'Neill 2011).

Some authors believe that large bees collect only large pollen because of hair structures that are adapted to collect large pollen (Thorp 1979, Schlindwein et al. 2009). This does not mean that small bees only collect small pollen. Small species cope with large pollen by moistening or agglutinating them with nectar (Thorp 1979, Neff 2008). Indeed, small and intermediate sized bees collect small and large pollen (large and small numbers, fig. 2.6.A). For large bees we did not find the very large number of pollen grains that one would expect for small pollen grains on large bodies (fig. 2.6.A). This could suggest that they indeed primarily collect large pollen, but with so few measurements is a conclusion premature.

Combined effects of other factors may be stronger than the effect of body size. Pollen provisions and loads are affected by temperature (Stone 1994a), sex ratio of brood cells (e.g. Maddocks and Paulus 1987, Bosch 1994) and age of the bee (wear of body hairs, Neff 2008). Pollen load per foraging trip is also affected by distance to a foraging site and time at the nest (Willmer and Stone 2004) which may trade-off the time for accurate pollen disposal and time needed for flying to more distant sites.

Brood cell provision volume

The high variance in brood cell provisions by pollen numbers can be reduced by correcting for plant species. Plant specific grain volume allows us to convert grain numbers to a volume (Müller et al. 2006). The variation in brood cell provisions for bees of the same size indeed clearly decreases when following this approach and the estimated brood cell volume clearly increases with body mass (Müller et al. 2006) and body length (fig. 2.6.B). Estimate grain volumes for different plant species (Müller et al. 2006) allowed us to convert the number of grains to a volume for three further bee species (fig. 2.6.B). These points confirm the clear positive relation between body length and brood cell pollen volume. However these bee species have somewhat higher pollen volumes, which may reflect the difference between polylectic bee species (as selected by Müller et al. with moderate volumes from mixed pollen loads) and oligolectic and monolectic species (additional points, one pollen grain size). This difference may be even stronger for true pollen ball volumes (rather than estimates based on grain counts), since pollen of different size can be packed closer together than pollen grains of one size. We also used the (plant) species specific pollen volumes to estimate pollen grain numbers backwards (only approximately by bee-specific pollen preferences). We could compute these grain numbers to compare them with the other collected grain numbers from the literature (fig. 2.6.A). Again, these provisions scatter in the wide (but similar) range of grain numbers, not exceeding the range of the other data points. Pollen volume is clearly the superior unit for provisions.

The shape of the body size - pollen load relationship remains unclear. Body length and provision volume provide a satisfying and significant ($p < 0.01$) linear fit (fig. 2.6.B and appendix A table A.1.5). The alternative fit is based on double log-transformed body mass and provision volume, resulting in a power relation for both untransformed body mass and body length which we favour for two reasons. The power fit of body mass and pollen volume was significant at a higher significance level ($p < 0.001$) than the linear fit for pollen volume and body length ($p < 0.01$). Further, the pollen volume that can be carried per foraging trip probably increases non-linearly with body length due to the faster increase of surface (with more hairs that can carry pollen). Although one of both fits is favoured, it is not possible to give an accurate estimation of pollen provisions beyond the body size range from 6 to 15 mm, due to the lack of data.

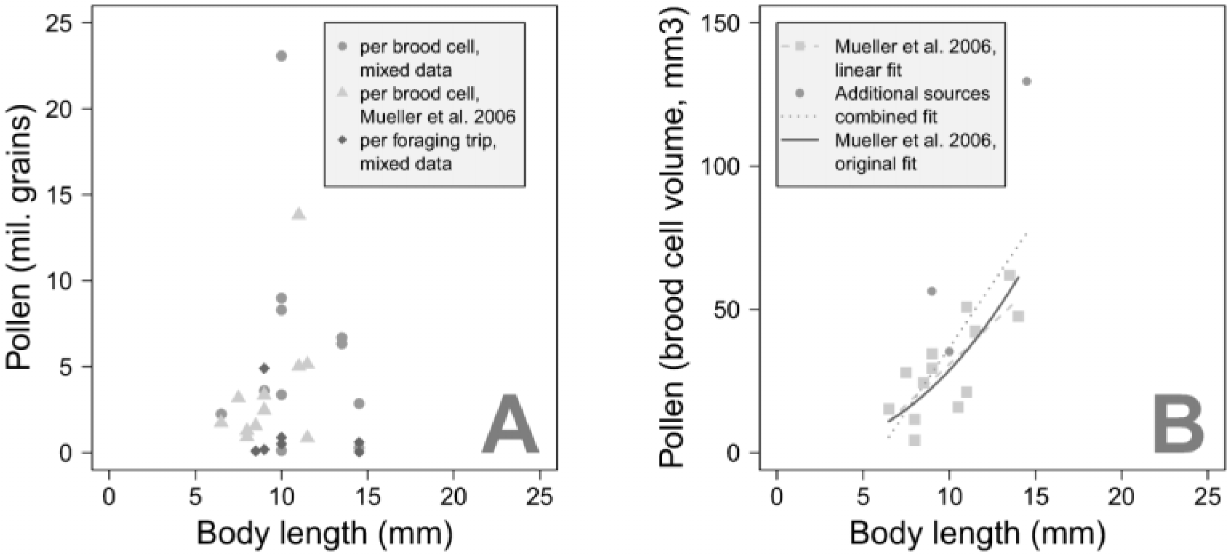

Figure 2.6: Pollen provisions of differently sized bees. A: Number of pollen grains; for brood cell provision and per foraging trip. B: Pollen brood cell volume with different fits in response to body size.

2.3.2. Flower handling time

Handling time for pollen and nectar collection

Solitary bees either visit a flower to collect pollen or nectar as brood cell provision or to collect nectar as energetic resource for flying. Solitary bees often collect the pollen and the nectar from different plant species (e.g. Tasei 1973, Bernardino and Gaglianone 2008) at different foraging trips (Thorp 2000, Willmer and Stone 2004). Some solitary bees also drink nectar at the flowers from which they collect pollen (Benedek et al. 1973, Gerling et al. 1983, Willmer and Stone 2004) and bumblebees may rarely visit flowers exclusively for pollen collection (Heinrich 1976). We focus here on studies with flower visits for pollen or mixed pollen and nectar collection. Detailed focus on nectar collection is out of the scope of this review. For many species is pollen the primary brood cell provision resource (Linsley 1958). In order to increase the amount of studies for comparison, we also used measurements of flower visits per minute. Since flying between flowers takes relatively little time compared to handling time (2-4 s, e.g. Pyke 1978) we directly (over-) estimated the amount of time they were visiting the flowers.

Large bees collect more pollen (fig. 2.6.B) and need more nectar as energy resource for flying. It makes sense that they also need more time to collect this, and a straightforward hypothesis is that they therefore spend more time on flowers. Only few studies (Strickler 1979, Chagnon et al. 1993, Javorek et al. 2002, Schlindwein et al. 2005) report handling times for pure pollen collection visits (fig. 2.7). If all bees had the same handling time, this would mean that the amount of pollen they extract per flower is relatively constant and large bees compensate for this by visiting more flowers. Our data show, however, that large bees have shorter handling times than small bees (fig. 2.7.A). It is possible that large bees can extract the pollen more effectively. Large bees have more and longer hairs which may take up pollen easier. Enhanced electrostatic force may even further increase pollen uptake. Alternatively, it may mean that large bees take up less pollen per flower than small bees as a result of the shorter visits. To compensate, they have to visit more flowers. Large bees may also try to visit more flowers per time unit than small bees, which is easier with better flight capabilities. Pollen uptake efficiency (pollen removal per time unit) decreases with time spent on the flower (Harder and Thomson 1989). Large bees may leave the flower as soon as the efficiency decreases and fly to the next flower as fast as possible in order to maximize the pollen collected per time unit. Small bees on the other hand may collect as much pollen per flower as they can because flying between plants is much more costly (in energy and time units) than for large bees. The optimization of the amount of pollen collected per time unit and per energy unit invested may be very different for large and small bees.

The studies we compared differ considerably in the duration of pollen handling (fig. 2.7.A). For bees of the same size handling times vary with flower type, but handling times for bees decrease with body size, regardless of the plant species. The shape of the curve may be an exponential decay (as fitted here), but it is also possible that it are two or more separated relationships with body size. Some bees transport dry pollen (more common in large bees heavier than 20 mg) while others agglutinate the pollen (Neff 2008). As figure 2.7.A shows, if we separate the data in slow and fast (small and large) bees for within these groups, data points connect even better (a fast decreasing handling time for small bees and a slowly decreasing handling time for large bees). A separation of bees based on social class (solitary bees, bumblebees and honeybees) does not show differences in handling time, except those related to body size (fig. 2.7.A). Note, however, that the largest solitary bee for which we have a handling time for pollen is only 12 mm (intermediate size).

Schlindwein et al. (Schlindwein et al. 2005) measured handling times for pollen and nectar separately, allowing us to compare handling times directly (fig. 2.7.A). The two *Chelostoma* species spent significantly more time on pollen than on nectar collection, which is more often the case for solitary bees (Nachtigall 1994).

Other studies did not specify whether bees collect pollen or nectar (Benedek et al. 1973, Nachtigall 1994, Richards 1996), but provide more data on handling time (fig. 2.7.B). The duration of the flower visits is generally low (compare with fig. 2.7.A) and it probably considers nectar handling in most of the cases. Two cases show a slight increase of handling time with body size, which are not significant and span a small range of body sizes. Those that span a wider range show an exponential decrease with body size similar to that for pollen handling time. A negative relation between nectar handling time and body size is probably driven by other mechanisms than for pollen collection. Large bees have larger tongues (Benedek 1973) which may make them faster in nectar collection (Benedek et al. 1973) as an optimization for the higher energy requirements (O'Toole and Raw 1991). However not only tongue length but also nectar collection behaviour may differ between large and small bees (Benedek et al. 1973), which means that there may be (as for pollen collection) several curves instead of one.

Further similarities with pure pollen collection are present. Handling times are different for different plant species. The estimation of handling time by flowers per minute does also not clearly differ from directly measured handling times (but note that the difference in value with flying between flowers is much lower than for pollen collection). Honeybees now (in contrast to pure pollen collection) seem to have longer handling times than other bees. This is may be the reason that one curve (bees on Astragalus cicer, Richards 1996) is more steep than the others. Honeybees are known to collect nectar even slower than pollen on some plants (Weaver 1957, Richards 1996) in contrast to solitary bees. It is sometimes suggested that collecting pollen differs not qualitatively from collecting nectar or any other energetic resource (Rasheed and Harder 1997) but we think that the mechanisms may be quite different despite similar patterns.

Handling time for pollen and nectar collection is also related to other factors than body size. We found here that difference in plant species highly affects handling time, which is known from other studies as well (Nachtigall 1994, Chittka et al. 1997). Also previous pollen removal is known to affect pollen handling time negatively (Harder and Thomson 1989) so that handling times differ throughout the day (Richards 1996) also influencing whether to collect pollen or nectar at a certain time of the day (e.g. Gerling et al. 1983, Giovanetti and Lasso 2005). Further it may relate to flower size, since it is easier to collect the required amount of pollen on larger flowers and a longer handling time may be more profitable than on a small flower. Moreover, larger pollen can be collected faster than small pollen (Schlindwein and Martins 2000). Pollen collection is a specialized behaviour. Bees from different taxonomical groups collect pollen on different body parts (O'Toole and Raw 1991). In essence the traits of the bee have to fit to the pollen-dispensing mechanism of the flower. Pollen specialists have stereotyped motor skills that allow faster pollen collection (Raine and Chittka 2007), so there may also be differences between bees from different families or genera.

This multidimensional parameter space has not been systematically investigated so far. To give a demonstration of the complexity we plotted data from Richards (1996) in detail for three bee species (*Bombus huntii*, *Bombus nevadensis* and *Apis mellifera*) that had five data points in common (fig. 2.8). All three bee species have a similar handling time on *Lotus corniculatus*, but the handling time on *Astragalus cicer* differs between the bee species. *Bombus huntii* has a similar handling time on both plant species, while *Bombus nevadensis* has a clearly different handling time on both plant species. *Apis mellifera* has a larger handling time than both bumblebee species in all cases, even though it is of the same body size as *Bombus huntii*. This is probably due to a relive short tongue of *Apis mellifera* for its body length (O'Toole and Raw 1991). The differences in handling times of *Apis mellifera* on both plant species is less pronounced, while site and year seem to have an effect. Although none of the species is solitary, it probably reflects quite well the difference between bee species in general. Body size has a weak effect (largest bee species lowest handling time), but plant species has a very strong effect which stresses the important of species related adaptation. The effect of site and year is probably related to resource-availability effects.

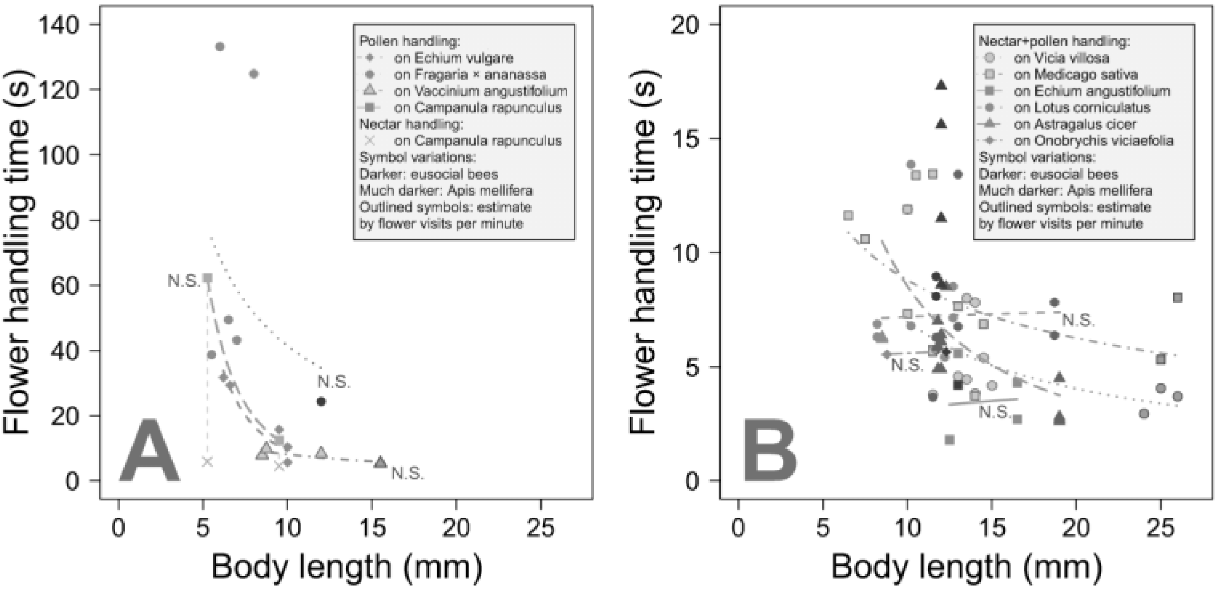

Figure 2.7: Flower handling time for differently sized bees on different plant species. A: Handling time measurements separated for pollen and nectar collecting behaviour. B: Handling time measurements without distinction between pollen and nectar collection. Handling times represented by open symbols (60 divided by flower visits per minute) are a slight overestimation since they include flight time between flowers. Statistical information can be found in appendix A.1. N.S. stands for "not significant" and is supplied in the figure. Complete references are given in the main text and appendix A.2.

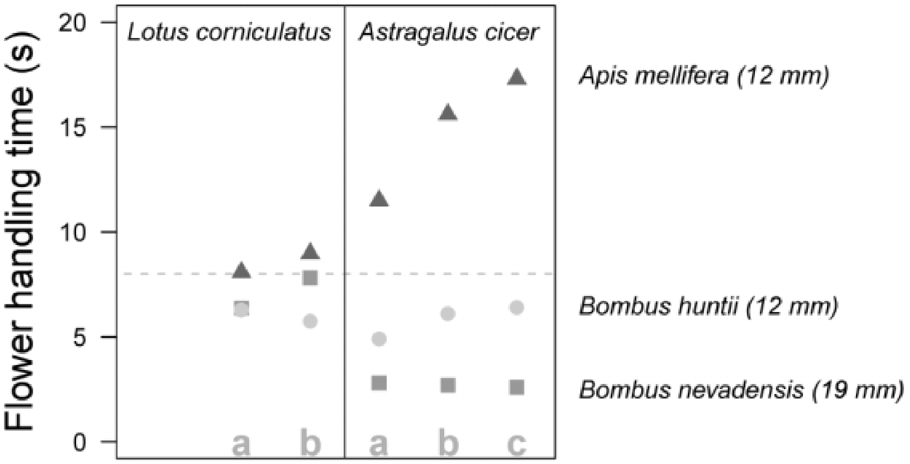

Figure 2.8: Handling time of three bee species on two different plant species, for different sites and years (*L. corniculatus*: a: 1989, b: 1990; *A. cicer*: a: 1980 at site one, b: 1981 at site one, c: 1981 at site two) per plant species. Handling time is not separated for nectar and pollen handling. Data from Richards (1996).

Choice of flower size

From the perspective of niche theory, one would expect that small bees forage on small flowers and large bees forage on large flowers so that all bees have their exclusive niche. Resource competition on the other hand leads to the fact that bees use as much resources as they can regardless of flower size. Data suggest that there is no strong relation between pollinator size and flower size, if any. Flowers of a certain size have a rich composition of foraging bees of all sizes (e.g. Hoehn et al. 2008, Vivarelli et al. 2011). Small bees can forage on large flowers (e.g. Minckley et al. 1994, Benevides et al. 2009) and large bees can forage on small flowers (e.g. Javorek et al. 2002, Denisow 2004, Goodell and Thomson 2007).

However, visitor composition may be somewhat shifted for flowers of different sizes. Absence of body size related preference of flower size does not mean bees have no limits in the size range of flowers they can visit (Blarer et al. 2002). This is particularly clear for nectar foragers: larger bees have longer proboscises (Benedek 1973) and therefore can drink nectar from larger (especially elongated) flowers. There is a strong size matching between nectar depth and proboscis length in pollinators (Stang et al. 2009). Large flowers for longer-tongued bees also produce more nectar (Pyke 1978), so that flower size, nectar production and bee size are all positively correlated. This is different for pollen gathering. Pollen collecting bees visit flowers independent of nectar related floral traits. Pollen collection often requires the whole body and the larger the bee, the more difficult it will fit "into" a small flower.

2.4. Time budgets

2.4.1. Foraging time and daily activity time

How long a bee forages per day varies widely between species. Foraging time or species activity time vary for most species between 8-12 hours (Linsley 1978, Danforth 1990, Bosch and Blas 1994, Teppner 1996), but may be half of this (4-6 hours) when the peak activity of a bee population is considered (Danforth 1990, Teppner 1996). Foraging time may relate to body size since large species can generate more body heat needed to start earlier (Stone 1994b). Larger species that start earlier in the day often also forage late, but have reduced foraging activity around noon (Willmer and Stone 2004) which may cancel out effects of body size. Daylight, flower opening times, and temperature course during the day may also affect foraging time. Animals often restrict their food search to the most optimal time as response to the periodic nature of temporal resource distribution (Bell 1990) and the effective foraging time may be similar for different species of bees. Indeed, many species forage mainly for pollen during the first hours of the day (Gerling et al. 1983, Neff and Danforth 1991, Giovanetti and Lasso 2005). Other bees stop foraging when they have provided one brood cell, regardless of the number of hours it takes (Danforth 1990, Schlindwein and Martins 2000).

2.4.2. Time at the nest

Solitary bees remain some time at the nest between pollen foraging trips. The time spend at the nest can be clearly separated into two types, time after a foraging bout and time after collecting the required amount of pollen for one brood cell (Danforth 1990). After a foraging trip a bee discards the pollen from the body hairs. Larger bees have to discard more pollen than small ones and can therefore be expected to need more time to do so. The nectar to pollen ratio may affect how sticky the collected material is and may also affect disposal time. When a bee has collected a complete brood cell provision it spends time at the nest to lay an egg and close the brood cell (i.e. making a protective shield with mud or other material) before starting a new cell and a new pollen foraging trip. This type of behaviour requires more time than the former and may be more constant for all bees. Alternatively, larger bees often use larger tube diameters (Budriene et al. 2004) and making a closing disk may require more time.

The time spent at the nest for pollen disposal varies from half a minute to 30 minutes (Franzén and Larsson 2007), but a time below 5 minutes is more often reported (Tasei 1973, Danforth 1990, Neff and Danforth 1991, Teppner 1996). In contrast, it takes over an hour to lay eggs and close cells (Danforth 1990). Mixing activities can result different mean values for non-foraging activities at the nest, illustrated by two studies on same solitary bee species (Bosch 1994, Teppner 1996). It is questionable whether all studies separated between activities at the nest, but we assume that most did. We did not find an indication of a relation with body size based on these studies.

2.5. Discussion and conclusion

In this review we have compiled body-size related data for wild bees, aiming at a synthesis of current knowledge. This information is an important building block for enforcing our understanding of bee ecology and of the many activities and behaviours of solitary bees.

We have shown clear relationships with body size. Large bees have a higher velocity, have a larger foraging and homing range, have a better perception of the environment (larger eyes and more facets, more light per facet and more contrast between facets), a larger brood cell provision and a shorter flower visiting (handling) time. This provides both advantages and limits to the foraging behaviour of large bees (table 2) and affects their performance in multiple ways. Some of these performance conflicts are probably more prominent for daily foraging tasks than others. We developed a diagram (fig. 2.9) that links all body-size relationships and the remaining factors that affect pollen collection behaviour. The diagram shows that the body-size relationships highly affect time budgets of bees. Our synthesis of body-size related traits can therefore also be a building block for modelling approaches that study bee foraging and pollination at the landscape scale.

The allometric relationships (given in appendix A.1) are in most cases only meant as preliminary indicators of the possible relationships between body-size and trait and therefore not given in the figures themselves. The available data for most of the discussed topics leaves space for speculation. We have shown that there is not a single best fit for some of the relationships such as for foraging ranges and pollen requirements. The compared data from different studies was often gathered with various methods and did not enable us correct sufficiently for violation of statistical assumptions (such as normality of data and residuals of fits). Estimations for small or large species from our fits can therefore be misleading or even false. This having said, we think that broadening the perspective for a trait to the whole range of body sizes for solitary bees was a big step forward. However, additional data is urgently needed and this review is a good start for more extensive field experiments.

A first recommendation is to include small species in studies. Measurements on small bees can provide a great deal of information on other bees. For example the insight that small bees can cross roads (Zurbuchen et al. 2010a) makes it likely that large bees can also do this. When this experiment would have been performed with bumblebees, there would be no conclusion possible for small bees. A second recommendation is to abandon solitary bees as a single pollinator group. Patterns of species richness can lack significance because the species taken together respond differently (e.g. Cane et al. 2006). Body size and nesting preference are important traits to consider how they respond to landscape parameters (Cane et al. 2006). We think that providing information about the composition of the group of solitary bees that was studied (size composition and proportion of ground-nesting bees) helps understanding why a correlation was (not) significant. Recent studies still do not provide this kind of information (e.g. Arthur et al. 2010, Taki et al. 2010), leaving a gap for interpretation of results.

We still know only little about the foraging behaviour of solitary bees and cost of time budgets (Neff 2008). This review contributed by identifying relevant body-size relationships. The data we presented is "the best we have" until now and we hope that new research follows to refine our findings (or reject them). We hope that this review motivates both experimental and theoretical research to understand how wild bees interact with landscapes and how to protect these bees, which should have a research priority in the context of pollinator declines (Biesmeijer et al. 2006)

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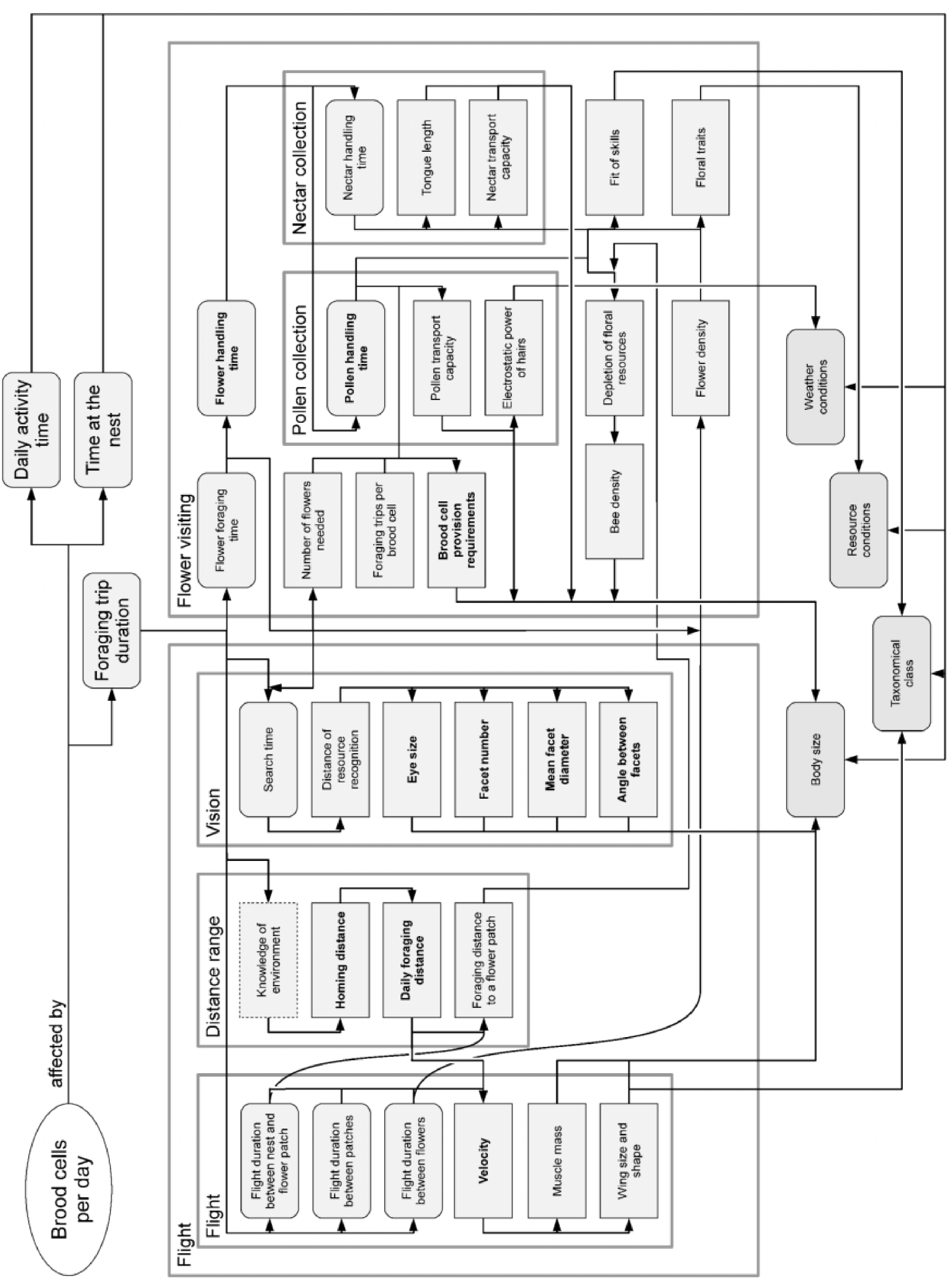
Table 2.2. Direct and indirect advantages and limitations for a large bee compared to a small bee.

	Advantages (large bee)	Disadvantages (large bee)
direct	• flies faster • has shorter handling times per flower • can collect more pollen before returning • can fly farther away from the nest • recognizes foraging resources from farther away	• needs more pollen for one brood cell • needs more or larger flowers • has to fly farther between nest and foraging resources
indirect	• has better gap-crossing abilities in patchy landscapes	• has to fly farther and longer in order to collect enough pollen • has to visit more flowers and loses time • may have to reduce velocity to profit from better visual abilities

Figure 2.9 (following page): Diagram with time budgets of bees and their components, separated for flight related behaviour and flower visiting behaviour ("on the way to" versus "at" the resource site). This diagram follows back the time budgets that relate to the number of brood cells. All components ultimately point back to (affected by, arrow direction) either body size, taxonomical class, resource conditions, weather conditions (rounded boxes in darker grey) or a combination of them. Other rounded boxes represent time budgets. Arrows represent "affected by" and should be read in downward direction unless otherwise indicated. Factors in bold are presented in a figure in this review.


Brood cells per day
affected by
Daily activity time
Time at the nest
Foraging trip duration
Flight
Flight
Flight duration between nest and flower patch
Flight duration between patches
Flight duration between flowers
Velocity
Muscle mass
Wing size and shape
Distance range
Knowledge of environment
Homing distance
Daily foraging distance
Foraging distance to a flower patch
Vision
Search time
Distance of resource recognition
Eye size
Facet number
Mean facet diameter
Angle between facets
Flower visiting
Flower foraging time
Flower handling time
Number of flowers needed
Foraging trips per brood cell
Brood cell provision requirements
Pollen collection
Pollen handling time
Pollen transport capacity
Electrostatic power of hairs
Nectar collection
Nectar handling time
Tongue length
Nectar transport capacity
Depletion of floral resources
Bee density
Fit of skills
Flower density
Floral traits
Weather conditions
Resource conditions
Taxonomical class
Body size

CHAPTER 3

A simulation model for pollen foraging solitary bees in a spatially explicit landscape

Bees nest either below ground or above ground, roughly said in the soil (upper left) or in dead wood (upper right). They collect pollen and nectar for their offspring and vary in body size (lower left and right). How can pollen foraging behaviour of different bee types be integrated in a spatially explicit foraging model?

3.1. A Simulation model for bees in fragmented landscapes

We describe in this chapter the model SOLBEE, a spatially-explicit individual-based simulation model that mimics solitary bees in agriculturally-dominated landscapes. Our goal was to develop a mechanistic description of the pollinator-plant interaction at the landscape scale with relevant parameters. We implemented several body-size related features that determine flight and pollen-collection behaviour of the bees (chapter 2). The behavioural rules are implemented in an if-else format that is intuitive to follow. The reason for such a simulation model is that solitary bees forage for pollen individually without communication about food locations (in contrast to honeybees and bumblebees, which try to optimize foraging tasks by communicating, see chapter 1). This favours a more stochastic, non-optimized foraging model. The landscape, with patches of flowering plants providing pollen to the bees, has several features from coarse grained structures to fine scaled pollen release per flower. We follow the standardized ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006, Grimm et al. 2010) to describe our individual-based model. It provides overview, general concepts and case-specific model details in such a way that a model becomes more reproducible.

3.2. Purpose of the model

This rule- and individual-based model aims at understanding how wild bees with different life-history traits interact with landscape structure and to give insight into the bee's perspective of a landscape. We have shown in chapter 2 that many of the bee's traits, and therefore behaviour as well, related to body size. Some traits improve performance with body size (such as velocity, handling time and resource recognition distance), while others moderate their performance (such as required pollen for a single brood cell). We expect that bees of different size perform differently when they collect pollen in a spatially explicit environment. This may also be influenced by the spatial allocation of the resources. We compare fitness differences by simulating the behaviour and time allocation of solitary bees that determine the amount of pollen brought to the nest.

3.3. Entities, state variables and scales

The model has two dynamic levels: a spatially-explicit grid-based landscape with a given resource distribution and a community of pollen-collecting bees. Table 1 shows an overview of the most important system properties and their values.

3.3.1. Entities and state variables of the landscape (environment and spatial units)

The landscape is described at two levels; at the coarse landscape level and the more detailed vegetation level (habitat units). We use for the first level a landscape generator, which enables the separation of habitat loss and fragmentation as different processes and allows for a wider range of foraging habitat availability and fragmentation than do images obtained from real land-use maps. Habitat availability (or loss) and fragmentation are focal variables for our simulations. The landscape is divided into habitat-units that are either suitable or unsuitable for foraging. Agriculturally dominated landscapes are a mosaic of sharply contrasting habitat types (Tscharntke and Brandl 2004). Suitable habitat units (second level) are described by flower density, amount of pollen per flower, and the proportion of pollen that is available per pollinator visit (regulation of flower depletion). These different vegetation-level parameters serve the fine detail that is needed at the individual bee level (pollen uptake, flying intra-flower distances) and represent homogeneous vegetation (fixed values). Auxiliary parameters describe the average distance between flowers and the initial amount of pollen for each habitat unit. We track during simulation the remaining pollen volume and the number of bee visits per grid cell.

3.3.2. Entities and state variable of the bees (the individuals)

We consider six different types of solitary bees according to three body sizes (body length of 6, 12, and 24 mm) and two nesting preferences. Each simulation deals with a bee population of one type. Several bee traits are directly calculated from body size with allometric scaling rules. These include pollen capacity, flight velocity, flower handling time, perception distance, length of flight units ("step-lengths") and return distance (table 3.1 and table 3.3). Several of the bee traits are unrelated to body size such as memory size, tortuosity of the flight path, patch leaving thresholds and the amount of time spent at the nest for non-foraging activities. In appendix B, we give an overview of the main parameters with biological ranges and simulated values, accompanied by explanation and references.

We implemented above ground (wood and cavity) nesting and subterranean (soil) nesting as two distinct nesting preferences (or nesting guilds). Wood-nesting bees nest in our model at the border of foraging habitat and unsuitable habitat. Such habitat edges are often suitable for nesting in natural landscapes (Banaszak 2000, Ewers and Didham 2006), since they provide shrubs and trees at nesting substrate. Soil-nesting bees nest in the soil at bare spots in the vegetation, and nest in our model in aggregations everywhere in the foraging habitat. The nesting preference in our model has consequences for the spatial distribution of bees. Each bee has a fixed start location (nest) to which it must return (central place foraging).

The six different bee types represent a wide range of bee genera in nature: Soil-nesting small bees (6 mm): *Dufourea*, some bees from *Halictus* and *Lasioglossum*; soil-nesting medium sized bees (12 mm): most bees from *Andrena*, *Anthophora*; soil-nesting large bees (24 mm): *Centris*, *Euleama*, *Oxaea*, *Habropoda*, *Xenoglossa*; wood nesting small bees (6 mm): *Ceratina*, *Chelostoma*, *Heriades*, *Hyleaus*; wood nesting medium sized bees (12 mm): several *Osmia*, *Megachile*; wood nesting large bees (24 mm): *Xylocopa*. For further considerations on selecting these body sizes see appendix B.3.

Different state variables are recorded for each foraging trip (used synonymously with foraging bout) for each bee: pollen collected during the trip, distance from the nest, number of unsuccessful and successful flower visits per trip, most recently visited locations, quality of last visited location, flight direction, start time of the foraging trip, "future time" for the next behavioural element and current spatial location. Data of different foraging trips is collected at the nest; here we record (per bee) the number of returns to the nest, pollen delivered to the nest, number of flowers probed, maximum distance from the nest, and time spent per behavioural module. Other auxiliary variables keep track of the total distance flown and trip duration. At the end of the simulation the mean amount of pollen collected per is converted into the (size related) number of brood cells. We do not use population level variables.

We link the landscape and the bee population with a parameter that describes the overall landscape quality for bees, which is used for calculating the total number of bees in the landscape (initializations, section 3.6).

3.3.3. Scales

The simulated landscapes have a spatial extent of 1 km, because solitary wild bees respond to landscape structures on scales up to 1000 m (Steffan-Dewenter et al. 2001). We used a grain size of 50 m that mimics raster-based land-use maps and is used in landscape-scale studies with solitary bees (Monsevičius 1995, Williams and Tepedino 2003). Lower grain sizes result in very fragmented, grainy landscapes that do not realistically represent agriculturally-dominated landscapes. However, bees perceive landscape structures in more detail (Lonsdorf et al. 2009) especially nesting substrate in strips with shrubs and trees (Franzén et al. 2009) and on small tree islands (Artz and Waddington 2006). Bees show differences in behaviour at a fine scale (e.g. Joshi et al. 2006, Diekötter et al. 2007). We therefore subdivided the landscape maps into 5x5 m cells. Our model landscapes thus consist of 200 by 200 grid cells. From the perspective of the bee, the landscape contains foraging habitat and matrix. The foraging habitat is split up in edge (5 m wide strips, which wood nesting and soil-nesting bees use for nesting and foraging) and interior (used for foraging by both bee types and for nesting by soil-nesting bees only).

Our model landscape has reflecting rather than absorbing boundaries, because we deal with central-place foragers that have to return to their nests. Consequences of this implementation are discussed in appendix B in the section "Concept details of several submodels".

We use 14,400 time steps of one second, which equals a foraging period of four hours. A behavioural unit of a bees last from one to several seconds. The decision of the exact time horizon is based on a tuning with the time spent at the nest, which is discussed in simulation experiment 1 (chapter 4).

Table 3.1. List of input variables and parameters used in the model with abbreviations, definitions and values used. In appendix B, this table is continued with the biological parameter ranges and the selection process of parameter values is explained there in detail**.** Asterisk indicates parameters that are explored in the global perturbation analysis (simulation experiment 2, chapter 4).

Variables and parameters	short	unit	used value	definition
Landscape variables:				
foraging habitat availability*	am		0.05 to 0.95	proportion of the landscape that is suitable foraging habitat
landscape fragmentation*	fr		0.05 to 0.95	amount of fragmentation, reverse of "terrain smoothness" (Hurst exponent), synonym with habitat fragmentation
landscape stochastic factor*	seed			initial number for pseudo-random number generator
Bee variables:				
body length*	size	mm	6, 12, 24	body length of a bee
nesting preference*	nest		wood, soil	category of nesting preference
Landscape parameters:				
landscape element size	esize	m	50	length of the most detailed landscape element (grain size of coarse grid)
flower density*	fd	m^{-2}	50	number of flowers
pollen per flower*	ppf	mm^3	0.5	pollen volume that one flower has available during one day
pollen availability	plimit		0.3	proportion of pollen of a flower that is extractable per pollinator visit
landscape quality*	bdc		30	maximum number of brood cells that can build from the available pollen in the landscape per individual
Bee parameters:				
pollen capacity per bee	pcap	mm^3	by size	maximum amount of pollen that can be carried per foraging bout per bee
pollen per brood cell	ppb	mm^3	by size	pollen volume that is needed to build one brood cell
velocity medium/low	vmed	$m \cdot s^{-1}$	by size	flight velocity for flying in suitable habitat
velocity high	vhi	$m \cdot s^{-1}$	by size	flight velocity for flying in unsuitable habitat
handling time per flower	ht	s	by size	time needed to remove pollen from flower
perception distance*	sightm	m	by size	distance radius at which bees can recognize habitat cells with flowers
length of flight units*	flightm	m	by size	mean length of a flight unit of which a flight path is built
general return distance	r50	km	by size	the distance for which the probability of returning is 50%
flower memory*	fmem		3	minimal number of most recently visited flowers that can be memorized
habitat cell memory*	cmem		10	number of most recently visited habitat units that can be memorized
ignorance	ig		0.1	probability of (non)ignoring flower location within sight or at the present location, the inverse of habitat cell memory
flight path tortuosity*	CRW		0.9	density parameter of the wrapped cauchy distribution that determines the relative amount of small turning angles during flight
lower patch leaving threshold	l_plt		0.5	value of relative habitat cell quality below which a bee must leave the habitat cell
upper patch leaving threshold	u_plt		1.0	value of relative habitat cell quality above which a bee must stay in the habitat cell
time at the nest*	ntime	s	30	time spent at the nest for non-foraging activities
flytime	tt	s	14400	total time of activity during a foraging day

3.4. Process overview and scheduling

After the initialization phase, in which a landscape is generated, a bee community is defined (bee traits regulated by allometric scaling, see "submodels", section 3.8). A nest site is assigned to each individual, upon which a foraging day starts. The virtual bees exhibit five types of behaviour. The behaviour of one individual is strictly sequential in time, and lasts at least for one second (discrete time steps). When an individual performs a behavioural type, state variables are changed. When a behavioural type lasts longer than one second a waiting time is set for that individual. Individuals are processed in random order at each time step (fig. 3.1.A). Waiting times imply asynchronous updating of individuals. When a foraging day is completed values are averaged per bee and written to an output file.

The five behaviours are (fig. 3.1.B):
1. FORAGE FLOWERS (Forage flowers within a landscape grid cell)
A bee flies from flower to flower directly (spatially implicit), encounters stochastically a full or empty flower (based on present resources), collects pollen, and decides about leaving the grid cell. Behavioural states can change into FLY AROUND (3) (current resources very low) and NEIGHBOURING CELL (2) (current resources low) or FLY BACK (4) (enough pollen collected).
2. NEIGHBOURING CELL (Fly to a suitable neighbouring landscape grid cell)
The bee considers the eight neighbouring landscape grid cells for foraging. It accepts one of them randomly when it contains flowers and if it has not been visited recently. The behavioural state changes back to FORAGE FLOWERS (1) after moving there. On rejection of all eight cells, the behavioural state changes into FLY BACK (4) (far from the nest) or in FLY AROUND (3).
3. FLY AROUND (Fly around and look for unknown foraging areas)
The bee performs a correlated random walk (changes direction and moves one step). The behavioural state changes to FORAGE FLOWERS (1) if either the new landscape grid cell is suitable (contains flowers and has not been visited recently) or if a suitable landscape grid cell has come within sight (move second step) or it can change into FLY BACK (4) (too far from the nest). With a certain probability suitable cells are ignored, leading to a more realistic foraging behaviour (better matrix crossing and better foraging of interior habitat, see "pattern oriented modelling", section 3.9).
4. FLY BACK (Fly back to nest)
The bee performs a directed random walk (correlated random walk in the direction of the nest). Eventually the state changes into NEST REACHED (5).
5. NEST REACHED
The bee delivers the pollen to the nest and spends time on non-foraging activities (while other bees still deplete the landscape). Afterwards the behavioural state is set to FORAGE FLOWERS (1).

During the behaviours 1, 3 and 4 bees leave visitation marks, which are used as a measure of pollination potential in the later analysis. Time penalties for each bee are given in table 3.2. A full description of the model with pseudo-code is presented in appendix B.

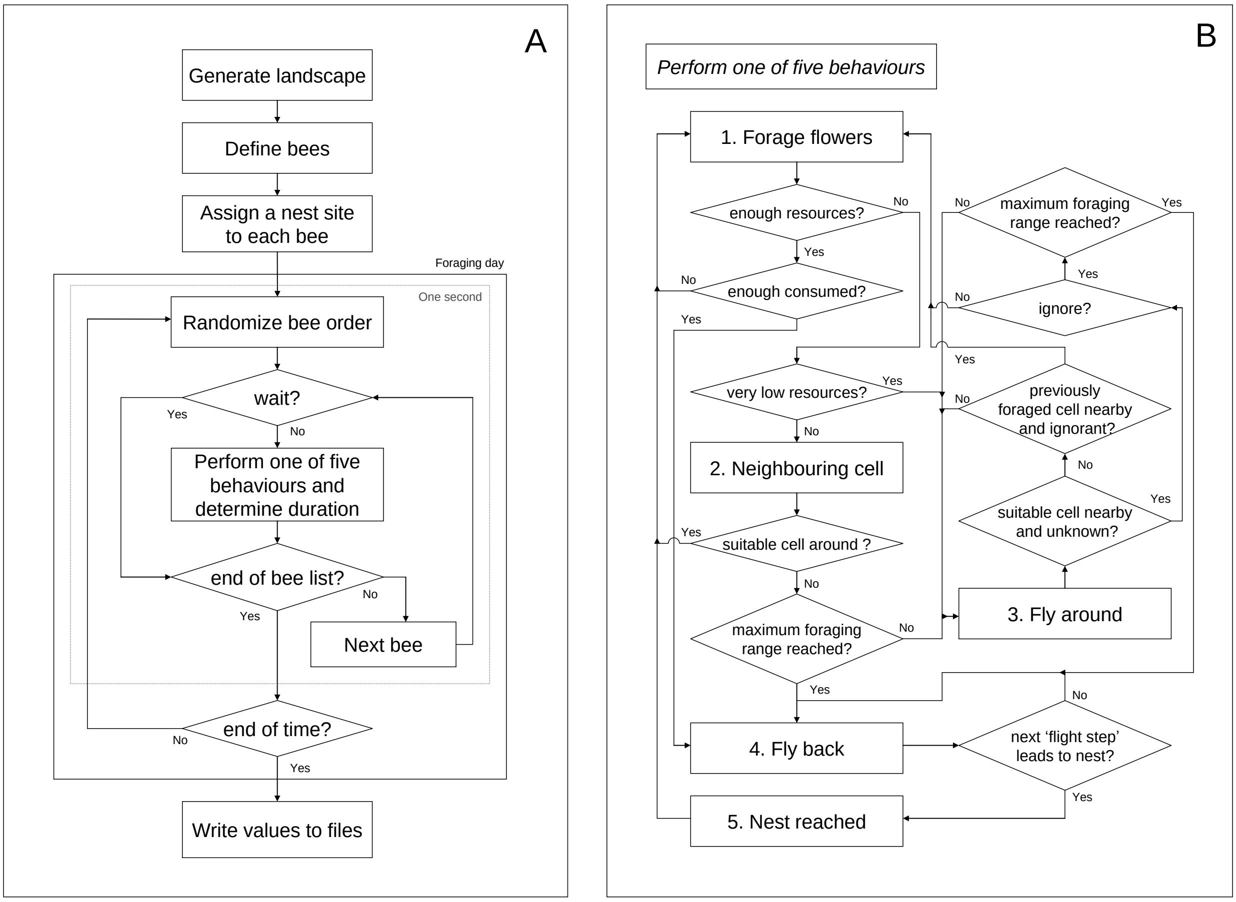


Figure 3.1. Flowchart diagrams of the model flow. A: Basic model frame. B: Relationships between the five behavioural modules. The relative resource quality is based on comparison of currently encountered and remembered resource quality (ration of full and empty flowers). The complete set of rules and details can be found in appendix B.

Table 3.2. Overview of time penalties. More details on the selection of values can be found in appendix B.

Behaviour	time penalties for:	value (minimal 1 s)
1. Forage flowers	poor habitat grid cell:	
	- assessing patch quality	1 s
	good habitat grid cell:	
	- flying to a flower	based on medium/low velocity (size)
	- full flower: removing pollen from a flower	based on handling time (size)
	- empty flower: assessing flower	1 s
2. Neighbouring cell	- accepting or denying a surrounding cell	1 s
	- flying to a surrounding cell	based on medium/low velocity (size)
3. Fly around	- distance flown per flight unit	based on high velocity (size)
4. Fly back	- distance flown per flight unit	based on high velocity (size)
5. Nest reached	- pollen deposition and other non-foraging activities	30 s (parameter *time at the nest*)

3.5. Design concepts

Basic principles: We use several known foraging principles such as area restricted search for resource items (e.g. Pyke 1983) and a patch "giving up time" (e.g. Charnov 1976). Area restricted search means that the animal has a limited knowledge and memory of the environment and "scans" the local environment with a fixed-sized search window and inevitably chooses close resource points (Pyke 1983). The decision of an individual to leave patch is based on actually probed flowers and the estimated resource level, rather than by time spend in a patch. Resource-based "departure rules" may be more realistic than time-based ones (Pyke 1983) and we used resource ratios and thresholds to determine departure (Basset et al. 2002). In a spatially-explicit individual-based model, this means that bees react on the rapidly changing resource levels caused by other foraging individuals. We use the concept of near-far foraging as an optimization which is relevant in large patchy environments (Motro and Shmida 1995). This means that bees generally forage on nearby flowers, but switch to foraging resources further away when nearby resource levels get low. Such behaviour has been shown for solitary bees (Williams and Tepedino 2003, Beil et al. 2008). Not considered concepts that are known for nectar foraging honeybees or bumblebees include "majoring and minoring" (Heinrich 1979), the "Matching Law" and the "Ideal free distribution" (e.g. Thuijsman et al. 1995), because they are not likely to apply to oligolectic (foraging on one plant species) pollen foraging solitary bees. We do not explore or compare the used principles; they only serve realistic foraging behaviour.

Emergence: Complex behaviour of bees emerges from five behavioural rules, posing differences on individuals during simulation (i.e. different behaviours coexist). Differences in nest positions (and bee densities) cause differences in local competition for foraging resources. The amount of pollen collected (or number of brood cells), the mean distance flown from the nest (or foraging distance) and the number of flowers visited are not coded into the model. Also a spatial "visitation map" emerges from behavioural rules and landscape structure and is used to calculate the percentage of the foraging habitat that has been visited by a bee community.

Adaptation: The individuals adapt to changing local resource conditions. After visiting and memorizing the status of a pre-defined minimal number of flowers (*flower memory*), the habitat cell quality (ratio of full to empty flowers encountered) is compared with the quality of the last visited habitat grid cell. According to the relative quality and an upper and lower patch leaving threshold, a bee stays (relative quality better than upper patch leaving threshold) or leaves.

Objectives: We measure the performance of an individual by how much pollen it can collect within a fixed time span. The costs consist of time penalties for each behavioural rule (table 3.2). The amount of pollen collected at the nest is at the end converted to a number of brood cells according to body size. For solitary bees, efficiency (and hence fitness) can be formulated as "potential number of offspring produced from the pollen per unit time on the flower" (Eickwort and Ginsberg 1980), represented in the model by the number of brood cells.

Learning: The behavioural rules are static without learning component (the same conditions in later foraging trips lead to the same decisions) because solitary bees are considered primitive foragers and display less efficient behaviour than honeybees (Campan and Lehrer 2002). The memory of the bees is used for memorizing locations and quality, and changes constantly (limited memory), but the application of this memory is not optimized by learning. The sequence of behavioural modes and the outcome of decisions change with time as a result of local depletion of flowers and patches.

Prediction: The individuals cannot predict any future condition, except for the fact that they memorize recently visited habitat cells and avoid them because they predict that food condition are low there.

Sensing: Bees assess (when foraging in suitable habitat) neighbouring landscape grid cells for suitable foraging habitat (resource availability) by vision and remember if they have visited them recently. When flying around in unsuitable matrix, they assess the environment with a square-shaped search window based on vision. Furthermore they sense the distance to the nest and can fly back anytime when they are too distant. The bees do not sense each other and therefore experience local competition only indirectly.

Interaction: Interaction between individuals exists indirectly through competition for resources, but highly affects bees near the nest. Since the nest location is determined by landscape structure and nesting preference, the magnitude of interaction differs between landscapes, bee types and within a simulation in space and time.

Stochasticity: We used stochasticity for different goals:
1. To generate landscapes: The fractal algorithm is partly based on stochastically generated noise.
2. To randomize the sequence and decisions of bees: We randomize the sequence of individuals at each time step, assign a random direction at start of foraging trip, choose randomly from suitable habitat cells around, and choose randomly when there are more "nearest locations" within sight.
3. To produce natural variability in behaviour and nesting: Natural variability is a major element of the correlated random walk (wrapped Cauchy distribution for turning angles and a normal distribution for flight unit lengths) and different leaving thresholds. Nest sites are selected randomly. A landscape grid cell is drawn randomly until one is suitable for nesting according to different nesting preferences. Furthermore, we use specified frequencies (or a specified fraction) for ignoring suitable habitat grid cells, for determining the binary full or empty status of a flower, for clumping of nests (soil-nesting bees), and for the probability distribution of maximum return distances. In specific cases we use stochasticity for rounding to integers (when the frequency distribution between two is not uniform).

Collectives: We do not use collectives in our model. Each bee forages solitarily without direct interaction to other bees.

Observation: We record bee performance for each individual as total pollen collected, mean, realized and mean foraging range (distance flown from the nest), number of returns to the nest and mean trip duration. For each behavioural module we recorded the amount of time spent in it. As output variables we use the arithmetic mean over all individuals and the standard deviation. At the landscape level we record total number of flower-visits and visitation marks (grid cells visited, including those without flowers). From these visitation marks we calculated the percentage of the semi-natural habitat that was visited. We record the number of flower visits per bee, as indicator for how the pollen vector behaves (but not as a performance of the bee, because here we do not distinguish between full and empty flowers).

3.6. Initializations

Landscapes and habitat

We use "noise" from a random number generator (*landscape stochastic factor*) and a Hurst exponent for fractional Brownian motion (*landscape fragmentation*) and a threshold (*foraging habitat availability*) to generate a landscape (Saupe 1988). We generate landscapes symmetrically and wrapped (With et al. 1997). Symmetry prevents the entire foraging habitat to be in one corner, and wrapped boundaries give the landscape the appearance to be part of a larger landscape.

Suitable habitat cells are assigned an initial pollen volume based on *flower density* and *pollen per flower*. We do not assess a range of landscape metrics for the landscapes, because most landscape metrics are highly correlated in artificial landscapes (Hargis et al. 1998). Instead we calculate the proportion of available nest habitat (landscape grid cells suitable for nesting) according to the nesting preference of the bee.

Individuals

We assume our bee community to be in balance with the amount of foraging resources. In natural communities bee density is often related to flower cover (Banaszak 2000, Calabuig 2000) or flower diversity (Pawlikowski 1989, Gathmann et al. 1994). We used pollen volume as resource parameter (Müller et al. 2006) and scale the number of individuals to the total amount of pollen present in the landscape. More specifically, the total number of individuals is calculated by dividing the pollen volume present in the landscape by the pollen volume available per individual (table 3.4). The latter is calculated with the help of the parameter *bdc* (*bee density control* or *landscape quality for bees*) as the "potential offspring (brood cells) per individual". We set this value at 30 which means that each bee can build potentially 30 brood cells from the amount of pollen in the landscape independent of its size (equal performance potential for all bees). A large value means fewer bees, but also a higher landscape quality for bees since there are more excess resources. The chosen value (see appendix B for a short review) results in realistic bee densities in the landscape with high bee numbers for small bees and lower numbers for large bees and an increase with increasing foraging habitat. A disadvantage of this approach is that model runtime varies several orders of magnitude for different parameter settings (*body length* and *foraging habitat availability* as well as *flower density* and *pollen per flower*).

Each simulation uses one bee type (according to size and nesting preference) and the initially calculated number of individuals remains constant during simulation (one foraging day without population dynamics). Each individual has several initializations. The most important is the nest assignment, which is in the model always near foraging resources (Westrich 1996). Wood-nesting bees accept a (randomly chosen) location to nest when it is at the edge of the foraging habitat and soil-nesting bees accept a location all over the foraging habitat but preferably in the vicinity of another bee nest in the soil (see appendix B for details). Nest distribution depends thus directly on landscape configuration. Each bee was additionally initialized with a random direction (used in the behaviour "fly around") and a maximum distance allowed to fly (knowledge of the environment).

3.7. Input data

The model does not use input data to represent time-varying processes.

3.8. Submodels for the regulation of allometric scaling

Allometric scaling

All size-related traits were calculated based on *body length* (table 3.3). In order to use the allometric relationships from the literature, we first converted *body length* to intertegular-span (shortest linear distance between the wing tegulae, see Cane 1987) and to dry body mass (data taken from Müller et al. 2006). Several traits are directly based on a certain publication (*pollen per brood cell*, *general return distance*, *far return distance*) while others were calculated with own collected data from multiple studies (*velocity medium/low*, *velocity high*, *handling time per flower*). We use these parameters subsequently to calculate *pollen capacity per bee*, *perception distance* (and perception area) and *length of flight units* (table 3.3). Additional discussion and data can be found in appendix B.

A more complex allometric trait is the maximum distance allowed to fly per foraging trip, based on homing distance. Homing distance can be considered as the maximum distance with knowledge of the environment, which differs between individuals and in different directions. Allometric scaling of homing distance of bees is known from the literature for typical homing distance (*r50*) and far or maximum homing distance (*r90*) (Greenleaf et al. 2007). We connect these two parameters by a (saturation) curve (table 3.4) after calculating a shift parameter which represents a certain minimal knowledge for which a bee of a given size will never return by the distance argument (but only by full pollen load). The concept of using homing distance as a boundary for maximum foraging was also discussed in chapter 2.

Table 3.3. Allometric rules that were used in the model. All bee traits (y) are directly or indirectly related to body size (x) and in the model all determined by the variable *body length*. Parameters are explained in table 7.1 and appendix B. The scaling relationships are based on the same concepts as in chapter 2, but in the model we used single studies and preliminary data sets.

x	y	formula	data source
body length (mm)	dry body mass (mg)	$y = 0.0398 \cdot x^{2.589}$	(data taken from Müller et al. 2006)
dry body mass (mg)	intertegular-span (mm)	$y = 0.77 \cdot x^{0.405}$	(Cane 1987)
dry body mass (mg)	pollen per brood cell (mm^3)	$y = 10^{(0.433+ 0.868.\log_{10} x)}$	(Müller et al. 2006)
pollen per brood cell (mm^3)	pollen capacity per bee (mm^3)	$y = x/10$	10 foraging trips, appendix B
body length (mm)	velocity medium/low ($m \cdot s^{-1}$)	$y = -0.214+0.135 \cdot x$	appendix B
body length (mm)	velocity high ($m \cdot s^{-1}$)	$y = 1.48+0.218 \cdot x$	appendix B
body length (mm)	handling time per flower (s)	$y = 919.62 \cdot x^{-1.914}$	appendix B
velocity high ($m \cdot s^{-1}$)	perception distance (m)	$y = 10 \cdot x$	distance of ten seconds flight forward
perception distance (m)	perception area (m^2)	$y = (2 \cdot x)^2$	search window around the bee
perception distance (m)	length of flight units (m)	$y = x/2$	perception distance flown in two flight units
intertegular-span (mm)	general return distance (km)	$y = 10^{(-1.643+ 3.242.\log_{10} x)}$	(Greenleaf et al. 2007)
intertegular-span (mm)	far return distance (km)	$y = 10^{(-1.363+ 3.366.\log_{10} x)}$	(Greenleaf et al. 2007)

Table 3.4. Body size-based calculation of individuals and maximum flight range of a foraging trip.

multiple x	calculation of	formula	notes
foraging habitat availability (am), landscape area, *flower density (fd)*, *pollen per flower (ppf)*, *landscape quality (bdc)*, *pollen per brood cell (ppb)*	individuals	$(am \cdot \text{total area} \cdot fd \cdot ppf) / (bdc \cdot ppb)$	The pollen volume available to the entire bee community (numerator) and the pollen volume available to one bee (denominator) are calculated in cm^3. The total area is 1 km^2.
general return distance (r50), *far return distance (r90)*	probability (of reaching a distance from the nest without knowledge of the environment)	$(\text{distance} - shift) / (Km + \text{distance} - shift)$	$shift = 1.125 \cdot r50 - 0.125 \cdot r90$ $Km = r50 + shift$
	maximum distance from nest (allowed to fly per foraging trip)	$(U \cdot Km/1 - U) + shift$	Inverse of distance probability; U is drawn from a uniform distribution.

3.9. Pattern oriented modelling

We used the pattern oriented modelling (POM) approach (Grimm et al. 2005) to parameterize the behavioural rules of the model. The visitation pattern (grid cells where bees left one or more visitation marks) showed that bees with area restricted search and a limited memory easily fly back to old patches and grid cells and never cross the matrix (fig. 3.2.B). We considered the behaviour "too locally optimized". Foraging resources appear "in sight" when flying parallel to the vegetation and such a grid cell is visited when it is not memorized (ten last visited grid cells are in memory). We added a parameter (*ignorance*) that lets the bee ignore decisions with a certain probability (details in appendix B). This probability assumes an innate preference of solitary bees to occasionally take the risk of crossing the matrix for finding far resource patches with higher resource abundance instead of optimizing the short-term profit. We decided that a value of 0.1 (ignoring 10% of the optimal decisions) results in a more plausible foraging pattern (fig. 3.2.C). Bees now sufficiently cross the matrix and search for better patches outside the local patch. They also visit more often the interior of flower field.

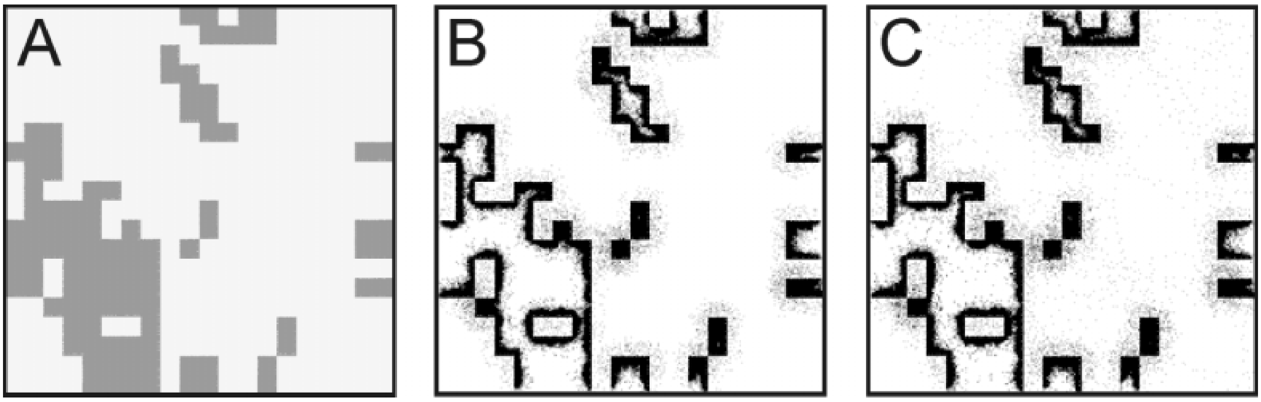


Figure 3.2. An example landscape and two visitation responses for bee communities with slightly different foraging behaviour. A. An example landscape with fragmented (meadow like) fields. The darker shade of grey represents the foraging habitat in an unsuitable matrix. The smallest patch measures 50 by 50 metres (0.25 ha). In this example around 1400 individuals (large bees) nest in woody structures at the border of the vegetation (nests represented by small white dots). B. Visitation by a community of large bees, in the first 8000 seconds of simulation. The darkest shades of grey represent the highest total visitation and white no visitation (excluding nest sites). There is only flight activity around the border where the bees nest, where they find sufficient foraging resources. The greyscale is optimized to visualize single "visitation marks" as well. C. Visitation of a bee community similar as in B but with introduced ignorance. Single flight paths can be recognized and the bees cross occasionally the matrix (more grey dots in the matrix) and the interior of fields with foraging habitat.

CHAPTER 4

Simulation experiments for basic model understanding

Foraging behaviour of wild bees can include extreme situations. Very small bees can forage on very large flowers (such as sunflower, *Helianthus annuus*, left) and large bees sometimes forage on very small flowers (*Dasypoda hirtipes* on *Euphrasia*, right). How does the model respond to extreme parameter settings?

4.1. Description of simulation experiments

Before scientific questions can be tested and answered with a simulation model, it needs to be explored. We therefore performed four simulation experiments in order to gain basic understanding of the model and to understand the influence of the different parameters. These experiments include the basic calibration and validation of the model as well as exploration of global perturbations within the parameter space and quantifying local sensitivity of the parameter values. All parameters are listed in table 4.1 and for each simulation experiment the used values are given. Statistical analyses on simulated outputs were performed with R (R Development Core Team 2009). Statistical analysis of simulated results is relatively unusual since most parts of the model are deterministic (all parameters have a significant influence). However, the model has many rules that interact so that we could not predict "a priori" which of the parameters would have most effect on the response variables and statistical tools help in ranking the impact of different parameters. We look at different response variables; number of brood cells, number of flower visits, mean distance from the nest and foraging habitat visitation. In simulation experiment we additionally look at the mean trip duration and the maximum foraging distance.

4.1.1. Exploration of time series and validation of response variables (simulation experiment 1)

First we performed a systematic exploration of the model. We assessed how the model behaves over time, and how well output parameters overlap with literature data. There are two parameters in the model that determine the global time budget for bees: foraging time (*flytime*) and the time spent at the nest for pollen deposition (*time at the nest*). Since biological values have a wide range (appendix B), we investigated whether different combinations have only quantitative or also qualitative effects.

We simulated three time-budget scenarios: a foraging day of four hours with 6 seconds at the nest after each foraging bout, a foraging day of 8 hours with 60 seconds at the nest, and a foraging day of 16 hours with 600 seconds at the nest. We used unequal intervals for *time spent at the nest* for two reasons. First, it suits biological values best (appendix B) and second we expect that with longer foraging days the relative effect of time at the nest decreases (have longer foraging trips, need to forage further). We varied *body length* (6, 12, 24 mm) and explore the results for the three bee sizes separately. We simulated four combinations of *nesting preference* (two types) and *foraging habitat availability* (0.05 and 0.95). This gives twelve time series per bee size. Within each time-budget scenario we ranked the four time series (their values at the end of the simulated time) to trace qualitative difference of the three time budget scenarios.

4.1.2. Global perturbation analysis (simulation experiment 2, sensitivity I)

The goal of this simulation experiment is to quantify parameter effects within their estimated biological range and identifying the most important ones. We analysed the relative effect on brood cells for fifteen parameters (*flower density (fd), landscape quality for bees (bdc), pollen per flower (ppf), scaling parameter for perception distance (sightm), scaling parameter for length of flight units (flightm), flight path tortuosity (CRW), flower memory (fmem), habitat cell memory (cmem), time at the nest (ntime), and landscape stochastic factor (seed)* and included the focal parameters *body length (size), nesting class (nest), foraging habitat availability (am), and fragmentation (fr)*). We used two values for each parameter representing the biological range (appendix B). The values for *flower density*, *pollen per flower* and *landscape quality for bees* were restricted by simulation resources (parameter combinations that resulted in millions of bees) and cover an acceptable extent of biological range rather that the complete range (see appendix B). We generated a set of parameters for each possible combination (2^{14} combinations) and selected 2000 of these sets randomly for simulation.

4.1.3. Robustness of bee-related parameters (simulation experiment 3, sensitivity IIa)

The effect of wide biologically plausible parameter ranges does not give information about parameter effects close to the chosen values. In this simulation experiment we therefore investigate the effect of small standardized changes in model parameters related to flight and decision behaviour of the bee and those related to the body size of the bee (*vhi, vmed, ht, r50, sightm, flightm, CRW, pcap, cmem, ig, fmem, l_plt, u_plt*). We varied each parameter by ± 10%. For parameters that normally range between 1 and 0, we used 0.1 increments instead of 10%. We shifted for *CRW* and *u_plt* the default value by -0.1 (technical restriction). For *general return distance* (*r50*) we shifted the probability curve to the left or to the right (moving both *Km* and *shift* by 10% of *r50*) after *Km* and *shift* were calculated. Since most of the bee parameters are calculated from *body length* in different steps, we first calculated the default value, and then applied the deviation (none, -10%, or +10%) randomly. Note that in case of *ig*, *sightm* and *flightm* there were more than three levels due to dependencies with other parameters, leading to multiple applied deviations. We generated 1000 parameter sets and checked for replicate sets, as alternative for generating all possible combinations. We considered wood-nesting bees of intermediate size. We repeated the analysis for soil-nesting bees (altered *nesting preference*, 1000 new parameter settings) and a longer foraging period (*flytime* 8 hours, same 1000 parameter sets).

The analysis proceeded in two steps. A: We determined which parameters were most important for variation in brood cells using a multiple regression model and checked for interactions between parameters. We simplified the linear model by minimising the BIC. B: We calculated the arc-elasticity of the input parameters, i.e. the percentage change in the response variable divided over the percentage change in input variable, measured against the average of two subsequent levels. A parameter was deemed elastic when the arc-elasticity is >1 (Bradley and Patton 2002, page 72-80). We corrected for non-simulated parameter combinations (far more than the 1000 simulated combinations) by predicting the response variable with the regression model. The model parameters were considered robust, when all elasticity values remained under 1.0.

4.1.4. Robustness of landscape-related parameters (simulation experiment 4, sensitivity IIb)

In this simulation experiment we investigated the effect of small standardized changes in model parameters that altered the landscape and the vegetation (*am, fr, esize, seed, bdc, fd, ppf, plimit*). We followed the same protocol as for the sensitivity of bee parameters in simulation experiment 3.

Table 4.1. Simulated parameter values for the different simulation experiments. Grey parameter values are not varied in that simulation experiment, but are given for comparison. Italic numbers show parameters that got special attention in the analysis. See table 3.1 for parameter explanation. For parameters with asterisk (*sightm* and *flightm*) we varied in simulation experiment 1 and 2 their regulator parameter (x seconds and x units respectively) and in simulation experiment 3 their calculated value.

		Simulation experiment													
		1			2		3			4			5		
		Exploration of time series			Sensitivity I: Global perturbations		Sensitivity IIa: bee parameter robustness			Sensitivity IIb: landscape analysis			Main experiment		
Parameter	short	value 1	value 2	value 3	value 1	value 2	value 1	value 2	value 3	value 1	value 2	value 3			
landscape stochastic factor	seed	821			821	188	821			-10%	100	+10%	x5		
flytime	tt	*14400*	*28800*	*57600*	*14400*	*28800*	*14400*	*28800*		*14400*	*28800*		14400		
Landscape:															
landscape element size	esize	50			50		50			-10%	50	+10%			
foraging habitat availability	am	0.05	0.95		0.05	0.95	0.5			-0.1	0.5	+0.1	0.05	to	0.95
landscape fragmentation	fr	0.5			0.05	0.95	0.5			-0.1	0.5	+0.1	0.05	to	0.95
flower density	fd	50			10	100	50			-10%	50	+10%			
pollen per flower	ppf	0.5			0.1	2	0.5			-10%	0.5	+10%			
pollen availability	plimit	0.3			0.3		0.3			-10%	0.3	+10%			
Bee:															
landscape quality for bees	bdc	30			10	50	30			-10%	30	+10%			
body length	size	*6*	*12*	*24*	6	24	12			12			*6*	*12*	*24*
nesting preference	nest	*"wood"*	*"soil"*		"wood"	"soil"	*"wood"*	*"soil"*		*"wood"*	*"soil"*		*"wood"*		*"soil"*
flight path tortuosity	CRW	0.9			0.1	0.9	-0.1	0.8	+0.1	0.8					
lower patch leaving threshold	l_plt	0.5			0.5		-0.1	0.5	+0.1	0.5					
upper patch leaving threshold	u_plt	1			1		-0.1	0.9	+0.1	0.9					
habitat cell memory	cmem	10			2	30	-10%	10	+10%	10					
flower memory	fmem	3			3	10	-10%	3	+10%	3					
general return distance	r50						-10%	size related	+10%						
velocity high	vhi						-10%	size related	+10%						
velocity medium	vmed						-10%	size related	+10%						
pollen capacity per bee	pcap						-10%	size related	+10%						
handling time per flower	ht						-10%	size related	+10%						
perception distance*	sightm	10			10	20	-10%	size related	+10%						
length of flight units*	flightm	2			2	1	-10%	size related	+10%						
ignorance	ig						-10%	memory related	+10%						
time at the nest	ntime	*6*	*60*	*600*	1	600	30			30					

4.2. Simulation results

4.2.1. Exploration of time series and validation of response variables (simulation experiment 1)

A. Time series

We visualized the 36 simulated combinations for each response variable and separated by bee size resulting in 12 time series per plot (three time-budget scenarios times two nesting preferences in two different landscapes). We explored a system that is unsaturated with bees (where there is more pollen than bees collect in one day, defined by *bdc*). Bees performed differently due to time constraints before the landscape is depleted. Visualizing the three different time-budget scenarios of *flytime* and *ntime* in time series for different response variables gave first insights in important processes in the model.

Number of brood cells (fig. 4.1, A and B)

The pattern for different time-budget scenarios was similar between small bees (fig. 4.1.A) and large bees (fig. 4.1.B). The *flytime* determined the absolute number of brood cells that could be built in one day and the *time at the nest* determined how fast (change in slope) a certain number of brood cells is built. The relative distance between different values for the *time at the nest* (6-60-600) was the same as the relative distance between the curves. Both time-related parameters did as expected affect the remaining available time for pollen collection. The number of brood cells increased linearly for soil-nesting bees in all cases which means that they were not resource limited by competition. Wood-nesting bees performed badly when they faced a high *foraging habitat availability*. The increase was not linear in time, but levelled off. This was also the case for wood-nesting bees in landscapes with low foraging habitat, but the effect was weak. This may be related to the different distribution of nests, which induced other time constraints (fig. 4.3). Small bees were able to build more brood cells than large bees and no bee was able to collect the pollen for 30 brood cells (as defined in *bdc*). The ranking of the performance of the bee types (ranking of the four response curves) was the same for all three time-budget scenarios.

Number of flower visits (fig. 4.1, C and D)

Large bees (fig. 4.1.D) visited many more flowers that small bees (fig. 4.1.C). The number of flowers visited per bee (full and empty flowers) increased exponentially, not linearly. Hence, bees encountered more empty flowers later on the day (probed more flowers per time unit). This effect was much stronger for small bees (fig. 4.1.C, clear exponential increase) than for large bees (fig. 4.1.D, increased almost linearly). Large bees visited more flowers almost linearly in time and had thus good access to full flowers. The same applied for soil nesting small bees. Wood-nesting small bees showed a different pattern, and visited much more flowers per time unit later on the day (steeper increase). They built less additional brood cells per time unit (fig. 4.1.A) and thus faced more empty flowers, leading to a higher flower visitation rate. Their nest position at the border of the habitat and their higher numbers and lower flight capability may have limited their access to less depleted areas. The ranking of the response for the different bee types was the same again under the three time-budget scenarios, except for large bees with *ntime* 600. At this point we cannot give a sufficient explanation for that. Time budgets for flower visits were apparently not the same time constraints that determined the pattern for the number of brood cells (fig. 4.1, A and B).

We discuss the following response variables for large bees only, since the pattern was the same for small bees.

Normal foraging activity and far foraging activity (fig. 4.2, A and B)

Far foraging distances (fig. 4.2.B) were in most cases about twice as large as mean foraging distances (fig. 4.2.A). Foraging experience (distance) increased almost linearly for soil-nesting bees and did not reach high values indicating that they found foraging resources close to the nest. Wood-nesting bees flew farther than soil-nesting bees, especially when they were in a landscape with much foraging habitat (fig. 4.2, A and B). Wood-nesting bees were forced to nest in edge structures, while soil-nesting bees were more or less evenly distributed over the foraging habitat. Depletion around the nest was therefore more likely for wood-nesting bees and resulted in farther foraging from the nest. In landscapes with high *foraging habitat availability* there were more bees and less edge (fig. 4.3), increasing the depletion effect around the nest. For these bees we observed two more things, their far foraging distance was not twice as large as their mean foraging distance and their expansion rate decreased with time (fig. 4.2, A and B). The *r90* values (far homing distance, used to rule out exceeding this foraging distance for 90% of the flight trips) were 120 m for small bees, 1386 m for midsize bees and 16017 m for large bees (for *r50*, the typical homing distance, 60, 640 and 6760 m). Large bees never reached these distances (fig. 4.2.B) and this hard coded foraging rule cannot have been the cause for the decrease in expansion rate. All the patterns in figures 4.2.A and B were in agreement with figures 4.1.A and B and may indicate that longer flights directly resulted in less brood cells. There were no qualitative differences (same ranking) between the three time-budget scenarios. Far foraging distances (fig. 4.2.B) were based on rarer expansion events and the increase was therefore less smooth and more stochastically.

Expansion over the foraging habitat (foraging habitat visitation, fig. 4.2.C)

The model tracked at the landscape level how much of the foraging habitat was visited by the bee community (fig. 5.1.C, large bees). Soil-nesting bees covered within 3000 seconds the complete vegetation (100%) in landscapes with low *foraging habitat availability* and 90% of the vegetation in landscapes with high *foraging habitat availability*. This means that they had good access to all foraging resources without depleting it within a foraging day (brood cells increase with the same rate throughout the day, fig. 4.1.A). Wood-nesting bees that nested at the border of the foraging habitat did not cover the whole foraging habitat. In a landscape with low *foraging habitat availability* the bee community reached 85% within a foraging day, but in a landscape with high *foraging habitat availability* the bees never covered more than 40% of the foraging habitat in these simulations. The ranking remained the same for all three time-budget scenarios.

Trip duration (fig. 4.2.D)

The average trip duration increased during the day for all situations (fig. 4.2.D), but were generally low (below 10 minutes). Soil-nesting bees had the shortest trips and wood-nesting bees had the longest trips, especially those in landscapes with a high *foraging habitat availability*, in agreement with longer foraging distances (fig. 4.2.A). The ranking of the four responses did not change for the three time-budget scenarios.

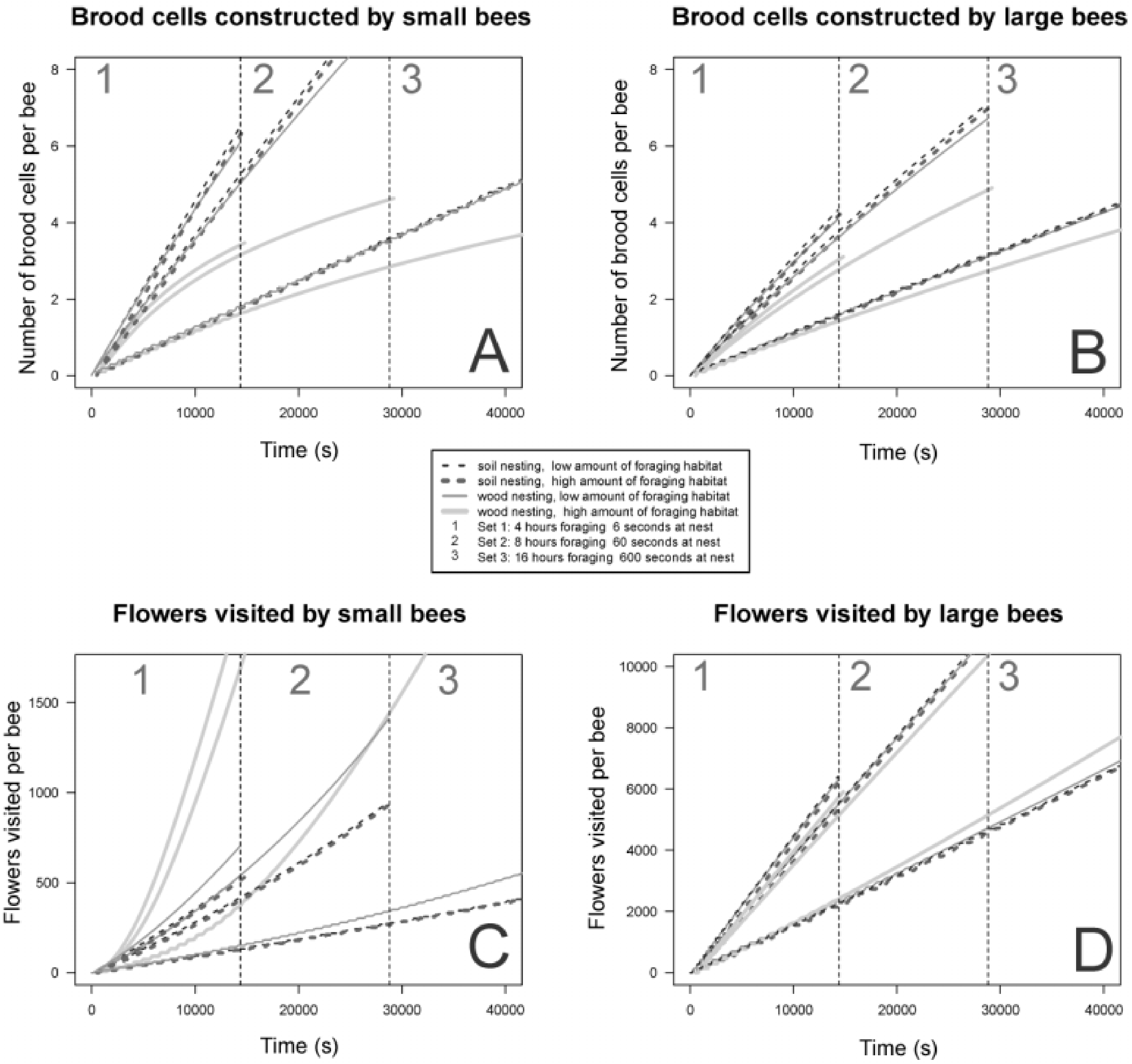


Figure 4.1. Development of different response variables during simulation time. Each graph contains 12 time series, of which 4 end at 14400 seconds, another 4 at 28800 and the last 4 outside the graph (at 57600). Each subset of 4 represents a different scenario according to *nesting preference* and *foraging habitat availability*. The lines of each of the 4 scenarios are directly comparable with the lines in the two other time-budget scenarios (set 1 to 3). We shifted the lines for "high *foraging habitat availability*" with 500 seconds to make them distinguishable from other lines. A. Brood cells built by small bees; B. Brood cells built by large bees, C. Flowers visited by small bees, D. Flowers visited by large bees.

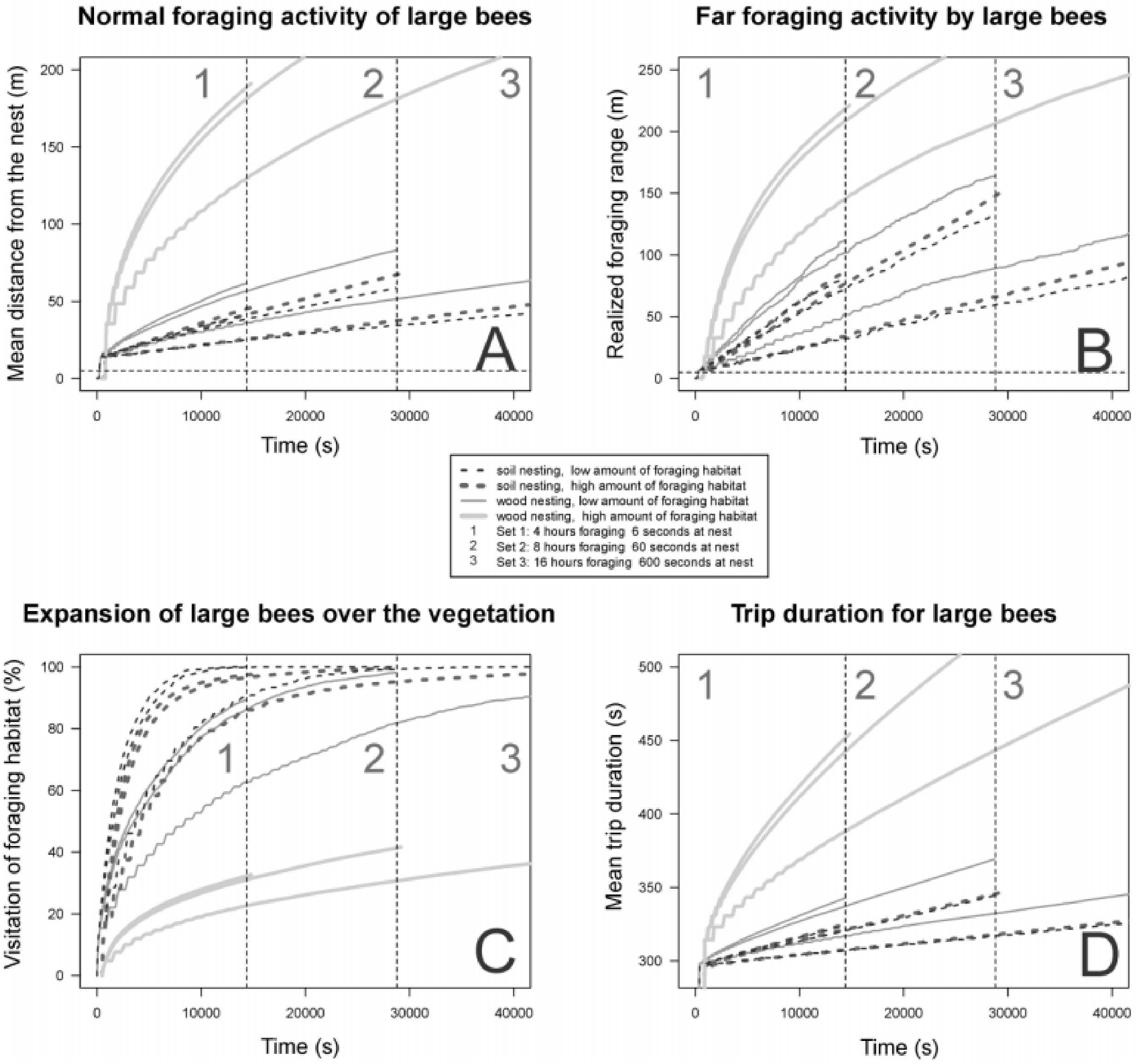


Figure 4.2. Progress during simulation time of expansion-related parameters for large bees. Again, each graph contains 12 time series, as in figure 4.1. A. Mean distance from the nest; B. Maximum realized foraging range (averaged over the bee community), C. Visitation of foraging habitat. D. Mean trip duration for large bees. Plot A and B start actually at a minimum of 5 m indicated with a dashed line, because the minimal distance is larger than one grid cell. Because, The mean foraging distance seems in the beginning to be higher than the maximum foraging distance due to slightly different assessment methods in the model, but this is cancelled out after a short time. Plot D starts at the "emerged" minimal trip duration.

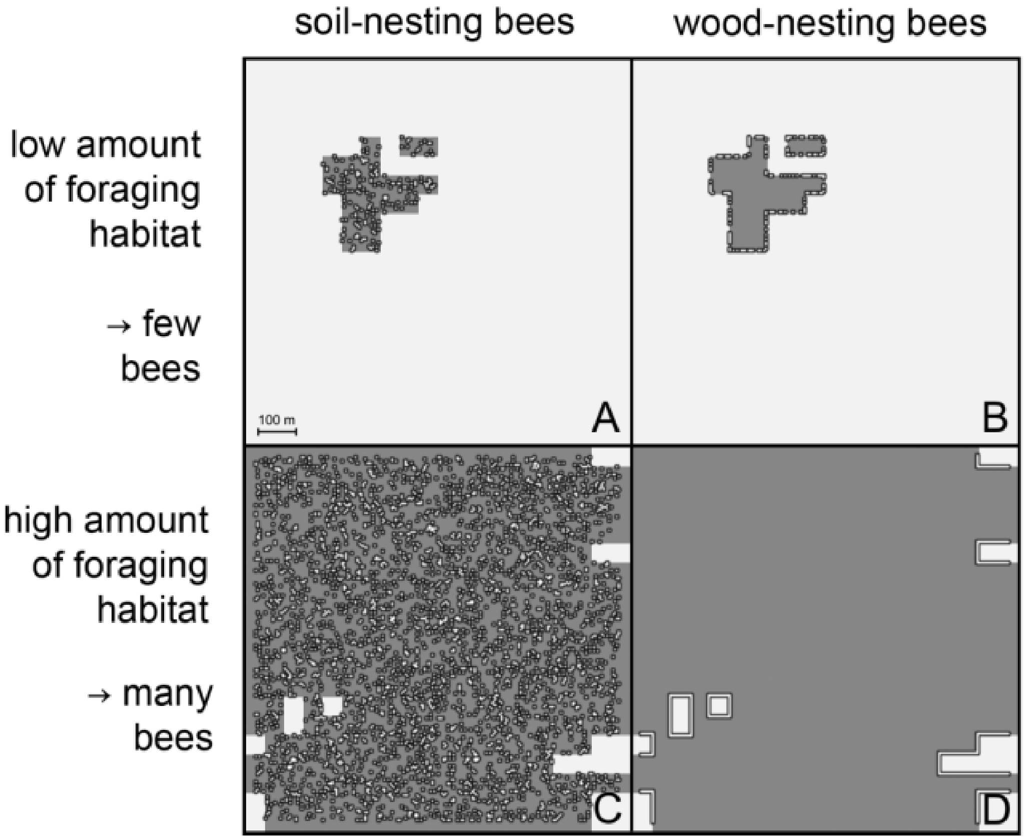


Figure 4.3. Four simulation examples after the initialization phase. The panels represent the four combinations of *nesting preference* and *foraging habitat availability* from simulation experiment 1. These landscape realizations have a certain amount of foraging habitat (darker grey areas in an matrix without foraging resources), an intermediate fragmentation level and a population of large bees. A bee's nest is represented as a white dot with a dark border. High nest densities appear as merged circles (white stripes with a dark border). A. Population of soil-nesting bees with a low *foraging habitat availability*. B. Population of wood-nesting bees in a landscape with a low *foraging habitat availability*. C. Population of soil-nesting bees in a landscape with a high *foraging habitat availability*. D. Population of wood-nesting bees in a landscape with a high *foraging habitat availability*.

B. Basic validation with literature values

We collected data from the literature with a focus on pollen collecting solitary bees for several response variables: brood cells per day, foraging trip duration, flowers visited (per day and per trip), mean distance from the nest and far foraging distances in a day (appendix B). We present here a summary of the found ranges and compare them with the ranges from the simulation model (table 4.2). In order to use and discuss the sparse data effectively we grouped the values for three bee size classes. The model reproduced values quite similar to those of natural systems with overlapping ranges in the majority of the cases. For all responses, the direction of change between small and large was correct and also the intervals between the three bee sizes were similar between modelled values and real values. There were however also differences. The modelled bees built more brood cells per day than in natural systems, had shorter foraging trips and flew shorter distances. These responses were related to each other in the time series (section 4.2.1). The number of flower visits in the model overlapped well with literature values for intermediate sized bees, but not so well for small and large bees. The literature data for flower visits was sparse and based on very loose estimations without specification of the type of flower visits (only successful vs. all visits). The model values were based on all flower visits during pollen foraging.

Table 4.2. Value ranges from response variables of the model compared with ranges from the literature. Modelled ranges are rounded to the widest range. Between brackets are uncertain numbers. See *appendix B* for references.

	Literature value ranges			Modeled value ranges		
bee size:	small	medium	large	small	medium	large
Brood cells per day	2 - 6	0.5 - 3 (7.1)	0.2 - 3	3.0 - 10.5	3.5 - 9.5	3.0 - 7.5
Foraging trip duration (min)	(3) 4 - 46	1 - 35	14-190	3.5 - 8.0	4 - 8	5 - 9
Flowers visited per day	fewer	4500 - 10000	180 - 9000	500 - 5000	1500 - 6000	6000 - 11500
Flowers visited per trip	few	50 - 90	4 - 150	8 - 95	30 - 105	150 - 220
Mean distance from nest (m)	(15) 20 - 27	40 - 100	18 - 447	15 - 120	20 - 180	40 - 250
Realized foraging range (m)	40	80 - 200	(100) 460 - 710	25 - 170	45 - 225	80 - 285

4.2.2. Global perturbation analysis (simulation experiment 2, sensitivity I)

We present here the most important parameter effects and parameter interactions based on linear models for the different response variables (appendix C, table C.1.1) under more extreme parameter settings.

Brood cells

The number of brood cells was most affected by the *pollen per flower*, *time at the nest* and *landscape quality for bees*. More total pollen (*pollen per flower*) and more pollen available per bee (*landscape quality for bees*) resulted in more brood cells. A longer *time at the nest* reduced the time available for collecting pollen and building brood cells. Several interactions between parameters were important (appendix C, fig. C.1.1): a longer *time at the nest* reduced the effect of pollen per flower, a high amount of *pollen per flower* reduced the effect of *body length* to almost none and a long *time at the nest* as well as a low amount of *pollen per flower* reduced the effect of bee density (*landscape quality for bees*) to almost none. For a longer foraging period, the order of importance of the discussed parameters and interactions did not change (appendix C, table C.1.1).

Flowers visited

The number of visited flowers per bee was affected by *body length*, *time at the nest* and *pollen per flower*. Larger bees visited more flowers, and flower visitation was also higher for a high amount of *pollen per flower*. A longer *time at the nest* decreased the number of flower visits. There was a positive effect of *pollen per flower* on flower visits when bees spend a short *time at the nest* and a negative effect when bees spend a long *time at the nest* (important interaction, appendix C, fig. C.1.2.A). The number of flower visits was counted on an aggregated level where we did not separate between visits of full flowers and empty flowers. This may explain some of the patterns, because visits of empty flowers must have increased for situations with increased competition pressure (such as an increased number of bees by a high amount of *pollen per flower* or more foraging activity by a short *time at the nest*). A longer foraging period did not change the importance order of the parameters.

Foraging habitat visitation

Foraging habitat visitation of the bee community was affected by *pollen per flower*, *nesting preference*, *landscape quality for bees* and *flower density*. The percentage of the foraging habitat visited is higher for a higher amount of *pollen per flower* (also more bees flying around) and soil-nesting bees (better distribution over the vegetation). A low bee density (high *landscape quality for bees*) decreases foraging habitat visitation. *Flower density* has also a positive effect on foraging habitat visitation, probably also by an increased number of bees. For soil-nesting bees the effect of *foraging habitat availability* is almost absent in contrast to wood-nesting bees (interaction, appendix C, fig. C.1.2.B). For a longer foraging period, the effect of *foraging habitat availability* got more important (appendix C, table C.1.1). More foraging habitat meant that bees were less able to visit the complete foraging habitat area.

Mean distance flown

The mean distance flown from the nest per bee was most affected by *nesting preference*, *body length*, *foraging habitat availability*, *time at the nest* and *landscape quality for bees*. Large wood-nesting bees in landscapes with a high *foraging habitat availability* flew the farthest. A low bee density (high *landscape quality for bees*) and a long *time at the nest* decrease the mean distance flown from the nest. The effect of *foraging habitat availability* was low for soil-nesting bees (appendix C, fig. C.1.2.C). The importance of parameters for a longer foraging period did switch for pairs with very similar importance (*nest-size* and *bdc-ntime*, appendix C, table C.1.1).

In this simulation experiment with more extreme parameter values we found also that in some cases (in 5 of the 2000 simulations) the landscape got depleted and bees built the amount of brood cells as given by *bdc* (but not exceeded this value).

4.2.3. Robustness of bee-related parameters (simulation experiment 3, sensitivity IIa)

The full results of the analysis can be found in appendix C (ANOVA tables for regression models in table C.1.2 and tables for parameter elasticity in table C.1.3). We present here the relevant effects of the small standardized changes of the bee-related parameters.

A. Linear regression model
We found different patterns for three scenarios (wood-nesting bee, soil-nesting bee and an elongated foraging time). *Handling time per flower* caused most variation in number of brood cells and the number of flowers visited under all three scenarios. *Handling time per flower* had probably a similar negative effect as *time at the nest* (simulation experiment 1); it prevented time being available for other activities. For habitat visitation and distance flown there were differences between bee types. Foraging habitat visitation was most affected by *length of flight units* and distance flown by *perception distance* for wood-nesting bees. For soil-nesting bees, both were most affected by the two patch leaving thresholds (*lower patch leaving threshold, upper patch leaving threshold*). There was no effect of a longer foraging period on any of the important predictors. Parameter interactions had a negligible effect, which means that the parameters in this experiment acted additively.

B. Elasticity
Elasticity values were in general low (<0.5) across the response variables, which means that they were quite robust against small changes in bee-related parameters. The parameters causing most variance for each of the response variables (see regression results at 3.A) were also causing the highest sensitivity in response (elasticity value > 0.5), but never exceeded one. The highest values were for *handling time per flower* (both for wood- and soil-nesting bees) and the model can be considered moderate robust against this parameter. A longer foraging period did slightly decrease elasticity values. Habitat visitation was most robust against changes in bee-related parameters (all values below 0.5).

4.2.4. Robustness of landscape-related parameters (simulation experiment 4, sensitivity IIb)

The full results of the analysis can be found in appendix C (ANOVA tables for regression models in table C.1.4 and tables for parameter elasticity in table C.1.5). We present here the relevant effects of the small standardized changes of the landscape-related parameters.

A. Linear regression model

The *pollen per flower* and *pollen availability* negatively affected the number of brood cells across all three scenarios (wood-nesting bee, soil-nesting bee and an elongated foraging time). Both parameters described the local vegetation properties (as well as *flower density* and *foraging habitat availability* which only had a low impact). Three response variables (number of flowers visited, foraging habitat visitation and the mean distance flown) were most affected by the same parameter(s), which however differed for both bee types. For wood-nesting bees *foraging habitat availability* and *landscape stochastic factor* were most important (also for a longer foraging period). These landscape level parameters determined the spatial distribution of foraging and nesting resources. An increases in *foraging habitat availability* resulted in more flowers visited, a lower percentage of foraging habitat visited and longer distances flown. Note that we could change the *landscape stochastic factor* only in random increments and the direction of the effect on the response did not have much meaning. For soil-nesting bees the *landscape quality for bees*, which determined the landscape-level bee density, was important. None of the parameter interactions had an important effect compared to the main effects.

B. Elasticity

Elasticity was also for landscape parameters in general low (<0.5) across the response variables, which means that they were quite robust against small changes in landscape-related parameters. The parameters causing most variance for each of the response variables (see regression results at 4.A) were also causing the highest sensitivity in response, but values never exceeded one. An exception was the elasticity of *landscape stochastic factor*, exceeding one. We used the set 90-100-110 for this analysis, but the set 99-100-101 would lead to the same response (due to the random effect of this parameter) and reduce the elasticity values by a factor ten (due to 1% change instead of 10% in the independent variable). The meaning of its elasticity value can therefore be neglected. Other high values were for *pollen per flower* and *pollen availability* (both for wood and soil-nesting bees) and the model can be considered moderate robust against these parameters. A longer foraging period did slightly decrease elasticity values. The total number of flowers visited per bee was most robust against changes in landscape-related parameters.

4.3. Discussion and conclusions

4.3.1. Exploration of time series and validation of response variables (simulation experiment 1)

A. Time series

The model shows realistic patterns in time such as increasing foraging trip duration during the day, a well-known time effect for pollen foraging bees that face local pollen depletion (Willmer and Stone 1989, Minckley et al. 1994, Franzén and Larsson 2007). The three different time-budget scenarios for *flytime* and *time at the nest* had only quantitative effects and did not change the relative difference between the different bee types in different landscapes. The only exception was the number of flowers visited by large bees during the day. We therefore consider it acceptable to shorten *flytime* to 4 hours and to use a relative short *time at the nest* (30 seconds) in future simulations. We found clear differences for bees of different size and for soil nesting and wood-nesting bees, which are worth exploring further.

B. Basic validation with literature values

The modelled response variables yielded realistic values for small, intermediate sized and large bees and the modelled ranges generally overlapped well with real systems. The model bees were however more efficient than in most natural systems. A (too) high number of brood cells may have arisen from less realistic model assumptions such as the exclusion of nectar foraging trips. Also collecting mud and other nest material can take considerable time (Willmer and Stone 1989) that is not available for collecting pollen. Some solitary bees only build one cell per day regardless of pollen availability and remaining time (Neff and Danforth 1991) and are rather egg-limited (O'Toole and Raw 1991). Another assumption was that bees collect pollen for one brood cell within ten foraging trips (used to define the loading capacity per trip) and bees always had a full load when they return (except when flying too far), which is often not the case (Pitts-Singer and Bosch 2010). Probably the largest difference with real systems is that the model bees always nest near foraging resources (because they would when they could). Wood-nesting bees nest at the border of the field and soil-nesting bees distribute evenly over suitable nest and foraging habitat. This is often not the case in agricultural landscapes where much of the data originates from and distances between nest and foraging habitat are large. In this sense it is realistic that the model bees are "in the more effective range" of natural systems. We think that the model yield realistic output and that the overlap with literature data is satisfactory, also considering the fact that we used detailed, literature-based input values without fitting any parameter.

4.3.2. Global perturbation analysis (simulation experiment 2, sensitivity I)

The analysis showed that *pollen per flower* (*ppf*) has a disproportionate effect on the number of brood cells and interacts with the effect *body length*. This could mean that on small flowers small bees are better and on very large flowers large bees are better. However the other performance responses did not show a strong interaction between *ppf* and *size*. The *time at the nest* (*ntime*), and *landscape quality for bees* (*bdc*) had predictable effects on the number of brood cells and showed no important interactions with other parameters. The other response variables were also affected by *ppf*, as well as by *size*, *nest*, *ntime*, *bdc*, *fd* and *am*.

The most uncertain and unknown parameters (*sightm*, *flightm*, *CRW*, *fmem*, *cmem*) did not have strong effects on the response variables and do not require further study. The strong effect of *pollen per flower* (*ppf*) implies that the model would be usable for comparing different vegetation types such as fields of clover (little pollen) with fields of sunflowers (very much pollen). The model does however require very long running times for large flowers (due to the high number of bee individuals) and large flowers are not common in most landscapes. We consider simulations with meadow-like vegetation populated by moderately sized flowers (moderate pollen production) to be a legitimate and realistic scenario without large flowers. We also consider a moderate value for *time at the nest* (instead of incorporating extreme values in simulation experiments), since it is biologically more plausible (appendix B). A longer foraging time did not affect the relative impact of parameters and a value of four hours is suitable to measure performance within a foraging day. Also the selected value for *bdc* (30, see appendix B) is considered biologically more plausible than its extremes. The other important parameters *size*, *nest* and *am* are incorporated in the main simulation experiment(s). The parameters show within the biological parameter space for this model system with a community of foraging bees shows interesting effects on the response variables, even for a single bee species and single plant species system. The model seems to have a high potential for exploring multiple biological questions.

4.3.3. Robustness of bee-related parameters (simulation experiment 3, sensitivity IIa)

A. Linear regression model

For soil and wood-nesting bees of intermediate size did small changes in *handling time per flower* affect the number of brood cells and flowers visited most. This parameter has a high time penalty and probably reduces time being available for other activities. Habitat visitation and distance flown were less affected by such time budget related parameters and more by the flight and sight parameters (wood nesting) and patch leaving thresholds (soil nesting). Expansion over the landscape was apparently not governed by the same processes as for the number of brood cells.

B. Elasticity

The four response variables were robust against small changes in bee-related parameters and had generally low elasticity values. As an exception, they were moderately robust against *handling time per flower*.

4.3.4. Robustness of landscape-related parameters (simulation experiment 4, sensitivity IIb)

A. Linear regression model

We found that *pollen availability* (*plimit*) and amount of *pollen per flower* (*ppf*) were most important for the number of brood cells. Of moderate importance were *foraging habitat availability* and *landscape stochastic factor*. Some of the effects seem contradictory. An increase in local resource availability (*plimit*, *ppf*) decreased the number of brood cells. An increase in *foraging habitat availability* increased the distance flown, but decreased the percentage of the foraging habitat visited. We suspect that local bee density is around the nest (fig. 4.3) is important for these patterns and may be affected by different parameters for both bee types (wood-nesting bees responded most to *bdc*) and should be considered in future analyses. The *landscape stochastic factor*, used for adding spatial structure in the landscape generation process, had a stronger effect than *landscape fragmentation* and *landscape element size*. The latter two were varied only 10% while *landscape stochastic factor* could only be varied randomly, likely causing this.

B. Elasticity

The four response variables were robust against small changes in landscape-related parameters and had generally low elasticity values. The most influencing two parameters, *ppf* and *plimit* had a moderate robustness (value between 0.5 and 1).

4.3.5. Conclusions

The responses of a bee community were dominated by the effects of vegetation-related and other landscape-related parameters. Within the natural parameter space (simulation experiment 2) the *pollen per flower* and *landscape quality for bees* had most effect, likely by affecting the number of bees in the landscape. The landscape related parameters also had slightly higher elasticity values than bee-related parameters showing more moderate robustness against small changes (simulation experiment 4) compared to bee-related parameters (simulation experiment 3). The number of flowers visited was however more sensitive to bee-related parameters (high elasticity values, simulation experiment 3). From the bee-related parameters had the time penalty by *handling time per flower* most effect on brood cells and caused relatively high elasticity values for small changes (simulation experiment 3). Bees were mainly limited in time, since they rarely built the possible amount of brood cells (simulation experiment 1). Other responses showed saturation processes with time as well (simulation experiment 1). The model seems to be driven by local bee densities (affected by vegetation parameters) and performance limitations of the bee (affected by size).

The simulation experiments yielded basic model understanding and more detailed simulation experiments can now be performed to answer specific questions. The balance between modelling robust results and computational power required to do so (costs) remains an issue. On one hand did a modern computation cluster enable us to analyse this individual-based simulation model extensively, but on the other hand were we still limited in the number of parameter combinations and replicates. The *landscape stochastic factor*, which we used to set our stochastic replicates, had a noticeable effect on the output variables. This means that the required number of replicates for robust results still needs to be tested.

CHAPTER 5

The effect of landscape fragmentation on solitary bees of different sizes

A large meadow offers abundant foraging resources for many bees (background). Single individuals fly from flower to flower to collect pollen and nectar for their offspring (foreground, photo compilation). Does their performance depend on their body size and where they nest? How does the area of the meadow (proportion in the landscape) and landscape structure affect their performance?

5.1. Description of the simulation experiment

The goal of this experiment is to investigate how different types of bee respond to habitat fragmentation in landscapes with different foraging habitat availability. For assessing our questions we used the simulation model SOLBEE (chapter 3) that uses detailed and realistic foraging rules (that apply specifically to solitary bees) and has been thoroughly tested (chapter 4). This model is capable of reproducing realistic values and patterns (chapter 4). We simulate populations of six different bee types (scenario-like) to compare their performance over a gradient of habitat fragmentation and habitat availability. We focussed on two general landscape features: foraging habitat availability and landscape fragmentation. We used 10 unique values for each with equal intervals (0.05 to 0.95 for both habitat availability and fragmentation), simulated all combinations and used 5 replicates of each. For each of these 500 landscapes we let six different bee types (body length of 6, 12, and 24 mm combined with two nesting preferences) nest and forage for pollen, which makes a total of 3000 simulations. The default values of other parameters are listed in table 3.1.

We analysed the main response variable "number of brood cells" with R (R Development Core Team 2009). We used a GLM approach to determine the importance, effect and interaction between the parameters. We use other response variables such as nest habitat availability, number of bees and mean distance flown per foraging trip to explore the causes of different performance. Due to long simulation times of various parameter combinations we were limited in the number of pure replicates. We repeated the analysis for additional replicate sets (increments of 5 replicates, or 3000 simulations, see also table 4.1), and found that 15 to 20 replicates are needed for more reliable results (appendix C2) and hence the better trade-off between costs and robustness of results. We therefore present the results based on 20 replicates.

We ask the following questions with regard to the number of brood cells bees build: Do different bee types perform differently? Does a bee of a certain type perform differently in different landscapes? Does the response to different landscapes differ between bee types? What is the effect of body size and what is the effect of nesting preference? Can we explain differences by other response variables?

5.2. Results

5.2.1. Solitary bee fitness in different landscapes

We measured the fitness of bees by mean number of brood cells that a bees constructed within in a certain landscape based on 20 replicate simulations. Bees built up to 6 brood cells (fig. 5.1), although the amount of pollen per individual would suffice for about 30 brood cells (*bdc*, table 3.1). This means that time budgets were the main constraints for pollen collection and that performance differences between bee types are related to the bee's body size and *nesting preference*.

From the variables that we investigated were *body length* and *nesting preference* far more important than *foraging habitat availability* and *landscape fragmentation* (table 5.1). *Body length* and *nesting preference* interacted with all other factors (table 5.1) and we therefore explore the interaction between *foraging habitat availability* and *landscape fragmentation* for each bee type separately.

Small bees (fig. 5.1, A and D) were able to build more brood cells than large bees (fig. 5.1, C and F). The relative difference between the three bee sizes was similar for wood-nesting (fig. 5.1, A-C) and soil-nesting bees (fig. 5.1, D-F). Soil-nesting bees did build slightly more brood cells in the same amount of time than wood-nesting bees of the same size.

Foraging habitat availability was more important than *landscape fragmentation* (table 5.1). Soil-nesting bees showed a negligible response to this gradient (fig. 5.1, D-F). Wood-nesting bees respond very strongly to *foraging habitat availability* and only weak to *landscape fragmentation* (fig. 5.1, A-C). They built most brood cells in landscapes with a low amount of foraging resources and their performance decreases with increasing *foraging habitat availability*. The decrease was steepest in landscapes with very high amounts of foraging habitat. Wood-nesting bees built more brood cells in more fragmented landscapes (fig. 5.1, A-C).

The standard errors were generally low (maximum 0.088) compared to the value for brood cells and were close to zero for soil-nesting bees (fig. 5.1, D-F). Despite their low value they revealed for wood-nesting bees a clear gradient for different landscapes similar to that of the amount of brood cells. The landscapes with the lowest number of brood cells (with the highest *foraging habitat availability*) in each panel had the highest standard error (fig. 5.1, A-C). This means that the difference between replicates in performance of bees was highest in such landscapes.

Table 5.1. Analysis of variance for the number of brood cells. Analysis is based on 20 replicates, i.e. 12000 simulations. The predictors are sorted by importance. Df stands for degrees of freedom. The sum of squares (sum sq) indicates the importance of the predictor and "effect" indicates the direction of the effect of the predictor. See table B1 for predictor abbreviations.

Model response: number of brood cells

Predictor	Df	Sum Sq	effect
size	1	5469.5	−
nest	1	1386.5	+
am×*nest*	1	507.9	+
am	1	497.2	−
size×*nest*	1	94.2	−
am×*size*	1	58.9	+
fr×*nest*	1	40.5	−
fr	1	40.4	+
am×*fr*	1	4.6	+
fr×*size*	1	4.6	−
Residuals	11989	441.4	

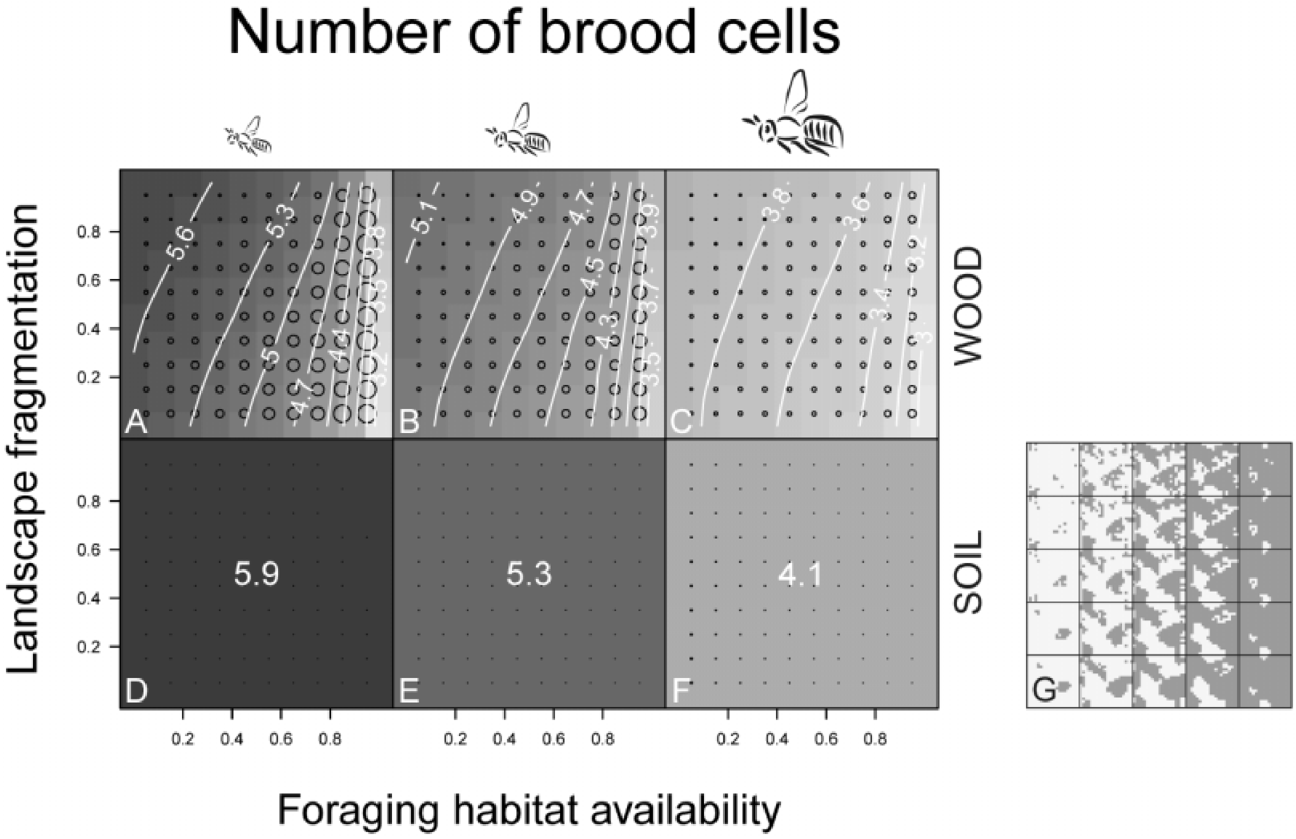


Figure 5.1. The number of brood cells that different bee types (panel A-F) build in different landscapes within a foraging day. Within each panel are different landscapes displayed and characterized by a gradient of *foraging habitat availability* (left to right) and *landscape fragmentation* (bottom to top); in total hundred combinations per bee type. Darker shades of grey (third dimension) represent a higher number of brood cells scaled over all bee types. To guide the different shades of grey absolute numbers and contour lines are depicted. Each of the hundred values represents the mean of 20 replicate simulations. The standard error (absolute value) is indicated by scaled circles (smallest circle represents zero, and the largest circle a value of 0.088). The panels depict from the left to the right small (A,D) to large bees (C,E) and from top to bottom wood- (A-C) and soil- (D-F) nesting bees. The most right panel (G) shows 25 example landscapes (5 by 5 instead of the 10 by 10 in the other panels) to visualize the gradient of *foraging habitat availability* (dark grey) and *landscape fragmentation*.

5.2.2. Alternative measures to explain the number of brood cells

Soil-nesting bees had their nests evenly over the foraging habitat distributed in the model, while wood-nesting bees only nested at the border, which inevitably affected foraging distances. Soil-nesting bees indeed had very short foraging distances while wood-nesting bees had a large gradient of short to long foraging distances (fig. 5.2.A, x-axis) caused by different landscape configuration. The number of brood cells for large bees decreased slowly with foraging distance, while the number of brood cells for small bees decreased steeply with foraging distance (fig. 5.2.A). With *body length* as co-factor, mean foraging distance and mean number of brood cells were highly correlated (r = 0.999, *p* <0.001, see appendix C.2 for model fit).

Another aspect that allowed a large variation for wood-nesting bees and a narrow variation for soil-nesting bees was nest-habitat availability. Nest-habitat availability for wood-nesting bees was positively affected by *landscape fragmentation* (r = 0.478, *p* <0.001) due to more edge habitat to nest in. Nest habitat availability was also correlated with *foraging habitat availability*, due to a reduction of habitat edge to nest in for high amounts of foraging habitat (r = −0.286, *p* <0.001, third power of *am* for focus on higher availability). Nest habitat availability did indeed partly explain the number of brood cells (fig. 5.2.B). The correlation with brood cells was not as high as for mean foraging distance (r = 0.916, *p* <0.001, see appendix C.2 for model fit), but the number of brood cells clearly increased with nest-habitat availability. Soil-nesting bees had higher nest habitat availability than wood-nesting bees (fig. 5.2.B) but this only partly explained their different number of brood cells. The effect of *body length* for the relation between the number of brood cells and nest habitat availability was not so clear, especially for wood-nesting bees (fig. 5.2.B).

Bees were never nest-site limited, because they always got a place to nest. They nested however in different densities due to differences in nest-habitat availability and total number of bees. The number of individuals was not only related to *body length*, but also positively to *foraging habitat availability* (r = 0.447, *p* <0.001). When we account for the mean number of individuals per available grid cell nest habitat, a clear pattern appeared for explaining number of brood cells (fig. 5.2.C). A higher number of individual per square metre nest habitat strongly decreased the number of brood cells. The remaining variance was explained by *body length* and the model fit is quite strong (r = 0.998, *p* <0.001, see appendix C.2 for model fit).

The effects of *foraging habitat availability* and *landscape fragmentation* on brood cells were apparently linked to local resource availability of both nest and foraging habitat. The ratio of nest-site availability to foraging availability incorporates both required habitats. This ratio varied for the model landscapes from 0 to 1 since the amount of grid cells suitable for nesting never exceeded those for foraging. An increasing in this ratio (which means more nest habitat grid cells per foraging habitat grid cells) increased the number of brood cells (fig. 5.2.D). The ratio was in combination with *body length* also highly correlated with the number of brood cells (r = 0.998, *p* <0.001, see appendix C.2 for model fit).

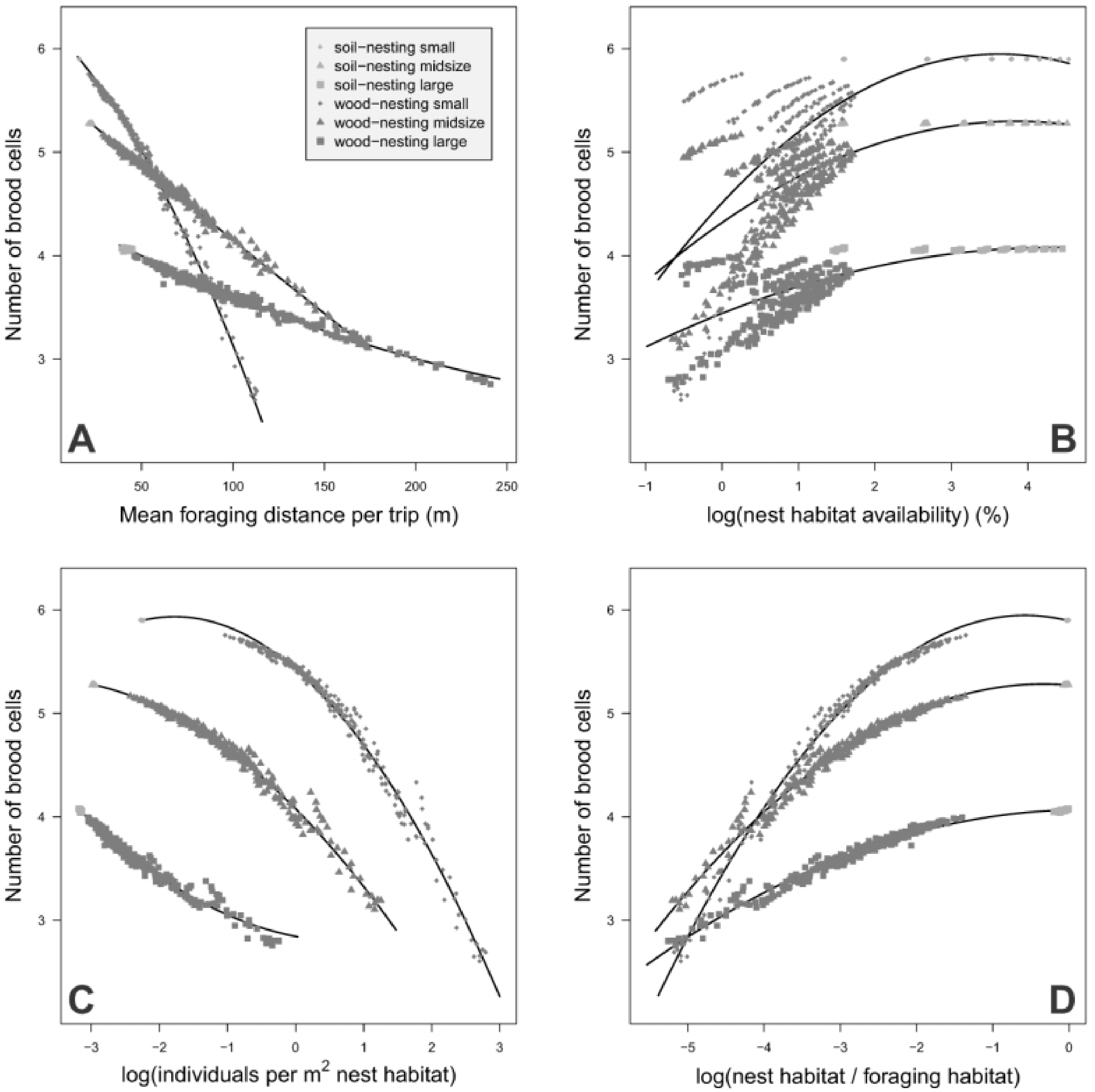


Figure 5.2. Four alternatives for explaining the number of brood cells with fewer parameters. A: mean distance flown, B: nest site availability, C: local bee density, D: habitat complementarity of nesting and foraging habitat. Dark grey points are wood-nesting bees and lighter grey points are soil-nesting bees, plotted for three replicate simulations. Lines are based on linear models (appendix C.2, 20 replicate simulations) and are separated for different body sizes.

5.3. Discussion and conclusions

5.3.1. Foraging habitat availability and landscape fragmentation

Bees were expected to build the same number of brood cells when the landscape effect is negligible, as we observed for soil-nesting bees that neither responded to *foraging habitat availability* nor to *landscape fragmentation*. In contrast, wood-nesting bees responded negatively to *foraging habitat availability*. Our model confirms that time can be more limiting than foraging resources for wild bees (e.g. Westphal et al. 2006b). An exception are oligolectic and monolectic bees that forage on uncommon native plant species and are probably always limited by availability of plants (Larsson and Franzén 2007), especially when the number of individuals is not scaled with the available pollen as in the model.

Wood-nesting bees responded positively to *landscape fragmentation*. The results support the hypothesis that small fragments in fragmented landscapes may have an advantage for bees due to their increased nest site availability and disproportional diversity (Donaldson et al. 2002, Tscharntke and Brandl 2004). Bees were indeed positively affected by nest habitat availability (fig. 5.2.B).

Some studies did not find a significant effect of fragmentation on bees (Gathmann et al. 1994, Donaldson et al. 2002, Exeler et al. 2008). We showed that it is important to separate between different bee types (nesting preferences and body sizes) when studying the effect of landscape fragmentation on solitary bees in agreement with other studies (Steffan-Dewenter and Tscharntke 2001, Cane et al. 2006). However, we also recognize that the effect of *landscape fragmentation* can be low compared to other landscape level parameters (chapter 4, simulation experiment 2 and 4).

Due to the moderate effect of *foraging habitat availability* and weak effect of *landscape fragmentation* compared to the effect of bee type (table 5.1) we considered four other measures for explaining the number of brood cells: mean foraging distance, nest habitat availability, local bee density, and ratio of nest habitat availability to foraging habitat availability. Nest habitat availability was the least good predictor. Mean foraging distance and local bee density can be measured in the field and were both good predictors. The difference between both is that the mean foraging distance is actually a response to local bee density (more bees per square meters forces bees to forage farther). They require both high measurement efforts in the field. The ratio of nest habitat to foraging habitat availability (an implementation of habitat complementarity for wild bees, Westrich 1996), explains the number of brood cells also very well. The ratio of nest habitat to foraging habitat availability successfully replaces *nesting preference*, *foraging habitat availability* and *landscape fragmentation* into a single measure with a more informative gradient of values, giving a clear picture of landscape quality from those components. It satisfies the need of a landscape measure hat is more suitable in describing the resource needs of solitary bees (Cane and Tepedino 2001). It means that surveys need to include identification of nest habitat instead of foraging habitat alone.

5.3.2. Body size

Body length was the most important predictor for the number of brood cells. Smaller bees performed on average better than large bees, both wood-nesting bees and soil-nesting bees. This is also supported by the literature (chapter 4, table 4.2. and appendix A). All bee types had the opportunity to build the same number of brood cells by resource availability. Large bees must have therefore stronger time limitations, despite the shorter handling times per flower. The time allocation diagrams for the different bees (appendix C.2) shows that the bees spend most of their time visiting flowers and flying between them at intermediate velocity. Small changes in flower handling time affected the number of brood cells by far the most (chapter 4, simulation experiment 3). It may be that the smaller handling time does not compensate enough for the number of flowers (pollen) that large bees require. The difference in number of brood cell is lower when bees of different size forage on larger flowers with more *pollen per flower* (chapter 4, simulation experiment 2), due to less time spend on flying when flowers are large. This would favour the velocity as main cause for the differences between bees of different size. Additional simulation experiments are required to study the effect of body size in detail.

Large bees were expected to perform better than small bees in fragmented landscapes because of their better dispersal abilities (Tscharntke and Brandl 2004), but we found that small bees performed better independent of fragmentation level. Soil-nesting bees did not respond to *landscape fragmentation* and wood-nesting bees (independent of size) performed better in more fragmented landscapes (fig. 5.1). The interaction between *landscape fragmentation* and *body length* was lowest of all tested (table 5.1). Bee traits related to dispersal ability (*return distance, velocity high*) were in the model not so important (chapter 4, simulation experiment 3) as those affecting local efficiency (*velocity medium, pollen capacity per bee, handling time per flower*). However large wood-nesting bees were less affected by *landscape fragmentation* (fig. 5.1.C) than small wood-nesting bees (fig. 5.1.A). The ratio of nest habitat availability to foraging habitat availability (fig. 5.2.D) shows this even clearer. A decrease in ratio results in a much steeper decline of brood cells than for large bees (fig. 5.2.D). Large bees are thus less sensitive to a decrease in the nest habitat to foraging habitat. We also think that when landscape fragmentation leads to separation of nest habitat and foraging habitat (which was in the model never the case) the response of large and small bees may be different that in our simulations.

In some cases small bees performed worse than large bees (wood nesting). When small bees were forced to forage larger foraging distances (fig. 5.2.A) and in in cases where the ratio of nest habitat to foraging habitat availability was very low (fig. 5.2.D) small bees performed worse instead of better than large bees. This is in cases where small bees have exceptional high nest densities (fig. 5.2.C).

The result that "large solitary bees are worse performers" may imply evolutionary consequences. The lower efficiency of large bees may be a driver to develop a social structure with higher efficiency and explain why large bees are more often social than small bees. In central Europe there are e.g. more species of eusocial bumblebees than large bees from the genus *Xylocopa* and *Anthophora* in contrast to very small bees from which most are solitary. The performance constraint may thus be an additional driver for sociality in combination with other drivers such as climate change (Bradley et al. 2009) and time (lineage age, Cardinal and Danforth 2011).

5.3.3. Nesting

Nesting preference caused the second most important contrast between the bee types. Soil-nesting bees hardly responded to *foraging habitat availability* and *landscape fragmentation*. They were more evenly distributed over the semi-natural habitat (foraging habitat) and always found enough foraging resources near the nest (fig. 5.2.D). A low impact of the surrounding landscape was expected for cases where soil-nesting bees primarily benefit from sunny open spots anywhere (Tscharntke and Brandl 2004). Wood-nesting bees responded in contrast very strong to different landscapes. They performed worst in landscapes with a high *foraging habitat availability* and a low degree of *landscape fragmentation*, an effect likely related to nest density (fig. 5.2.C) and ratio of nest habitat to foraging habitat (fig. 5.2.D). In general did both nesting preferences appear not to be a bimodal contrast between bees, but merely causing a gradient of habitat use where both nesting preferences are part of the same relationship for a bee of a certain size (fig. 5.2, A-D).

Field data from semi-natural meadows suggested that the effect of landscape parameters may be explained better when bees were separated by nesting preference than by body size (Steffan-Dewenter and Tscharntke 2001), because of the different nest-site availability for soil-nesting bees in the different successional stages of the meadows. We found a higher contrast between bees of different size than of different nesting preference, but modelled homogeneous vegetation. However, when we would model different nest-site availabilities for soil-nesting bees, we would observe an even lower contrast between both nesting preferences. Alternatively, our range of body sizes may be relatively high. Another study showed a similar pattern as in the model (Cane et al. 2006) where body size had more impact on the response than nesting preference. Both studies looked at species diversity and individual numbers and not at a fitness measure such as the number of brood cells and are thus of limited value for comparison. Anyhow, the model clearly confirms that both nesting preference and body size are important and cause differences between bees in how they respond to landscape configuration.

CHAPTER 6

Pollination by different solitary bee types in fragmented landscapes

When plants are not or rarely visited by pollinators they produce deformed fruits, here exemplified with blackberry (*Rubus* cf. *fruticosus*) and raspberry (*Rubus idaeus*). How does landscape structure affect the movement of pollinators in the landscape?

6.1. Description of the simulation experiment

The aim of this simulation experiment is to investigate how communities of different solitary bee types (differing in nesting preference and body length) provide pollination services. We also ask whether pollination services change with landscape composition (foraging habitat availability) and configuration (landscape fragmentation). For answering our questions we used the simulation model SOLBEE (chapter 3) with the same methods, parameter settings and simulation configuration as in chapter 5. Instead of number of brood cells (chapter 5) we analyse the responses number of flowers visited, percentage of the foraging habitat visited and mean distance flown. We consider these pollinator-centred measures potentially useful for assessing pollination services at the landscape scale. The mean number of flowers visited per bee gives an indication of how bees (pollen vectors) behave under different conditions. The percentage of the foraging habitat (in grid cells) that has been visited by at least one bee is a measure of pollination coverage. The mean distance flown from the nest provides information on how far pollen is transported.

We present the results based on the same 20 replicates as in chapter 5. Additionally we explore the effect of the ratio of nest habitat availability to foraging habitat availability for these three responses. This landscape measure performed better in explaining bee performance (the number of brood cells) than foraging habitat availability or landscape fragmentation alone (chapter 5).

We focus on the following central questions: Do different bee types provide pollination services differently? How do foraging habitat availability and landscape fragmentation affect pollination services? Do the chosen responses show a similar pattern for different bee types and landscapes, or is one representative for pollination services better that the others?

6.2. Results

6.2.1. Foraging habitat availability and landscape fragmentation

The mean number of flowers visited per bee was most affected by *body length* (table 6.1) with large bees visiting more flowers than small bees (fig. 6.1, left and right). Soil-nesting bees did not respond to landscape composition and configuration (fig. 6.1, D-F). *Landscape fragmentation* slightly reduces the number of flower visits for wood-nesting bees (fig. 6.1, A-C). Small and intermediate sized wood-nesting bees visited exponentially more flowers in landscapes with a high *foraging habitat availability* (fig. 6.1, A and B) and more than soil-nesting bees of the same size (fig. 6.1, D and E). In contrast, large wood-nesting bees visited fewer flowers in landscapes with a high *foraging habitat availability* (fig. 6.1.C) and about the same number of flowers as soil-nesting bees of the same size (fig. 6.1.F).

The percentage of foraging habitat that a bee community visited was most affected by the *nesting preference* (table 6.1). Soil-nesting bees almost or completely covered the foraging habitat (96-100%, fig. 6.2, D-F), without any visible landscape effect. For wood-nesting bees foraging habitat visitation decreased in a rather gradual linear than exponential fashion, but strongly, with *foraging habitat availability* (fig. 6.2, A-C). Wood-nesting bees covered slightly more of the foraging habitat for higher *landscape fragmentation* (fig. 6.2, A-C). The effect of *body length* was very low (table 6.1, rank 8). The effect of *body length* was clearest for wood-nesting bees in landscapes with a high *foraging habitat availability*, where large bees covered a higher percentage of the foraging habitat (fig. 6.2, A-C).

The mean distance flown from the nest was most affected by *nesting preference* and *body length* (table 6.1). Soil-nesting bees flew very short distances compared to wood-nesting bees (fig. 6.3, top and bottom) and large bees had longer foraging distances (fig. 6.3, left and right). The mean distance from the nest increased exponentially with *foraging habitat availability* for wood-nesting bees (fig. 6.3, A-C) and is also slightly lower for higher *landscape fragmentation* (fig. 6.3, A-C). For soil-nesting bees were foraging ranges not affected by landscape composition and configuration (fig. 6.3, D-F).

6.2.2. An alternative measure for landscape structure

The ratio of nest habitat to foraging habitat as a single variable replacing *foraging habitat availability*, *landscape fragmentation* and *nesting preference* did in combination with *body length* explain the number of flowers visited satisfactory (fig. 6.4.A). This also applied for foraging habitat visitation (fig. 6.4.B) and mean distance from the nest (fig. 6.4.C), with high correlation values for all three responses (appendix C.3). The effect of *body length* was most obvious for the number of flowers visited (fig. 6.4.A). Intermediate sized bees visited up to three times more flowers than small bees and large bees visited up to three times more flowers than intermediate sized bees. In unfavourable landscapes with a low ratio of nest habitat to foraging habitat, small and intermediate sized bees visited more flowers than landscapes with a higher ratio. For large bees was this opposite, visiting slightly more flowers in landscapes with a high ratio (fig. 6.4.A). The mean distance from the nest also depended on *body length* (fig. 6.4.C). Large bees flew about twice as far as small bees. In unfavourable landscapes with a low ratio of nest habitat to foraging habitat, bees flew farther from the nest. Foraging distance decreased exponentially with increasing ratio (fig. 6.4.C). *Body length* had the lowest effect on foraging habitat visitation (fig. 6.4.B), varying maximally 10% between bees of different size. The ratio of nest habitat to foraging habitat had a much stronger effect than *body length*, covering almost the complete span from 10% foraging habitat visitation for a low ratio to 100% for a high ratio (fig. 6.4.B).

Table 6.1. Analysis of variance for three model response related to pollination. Analysis is based on 20 replicates, i.e. 12000 simulations. Df stands for degrees of freedom. The sum of squares (sum sq) indicates the importance of the predictor and "*" indicates the direction of the effect of the predictor. See table B1 for predictor abbreviations.

Response:	Flowers visited (thousands)				Foraging habitat visitation (%)				Mean distance from the nest			
Predictor	df	sumsq	rank	*	df	sumsq	rank	*	df	sumsq	rank	*
am	1	96	5	+	1	1003215	3	−	1	2427243	3	+
fr	1	6	9	−	1	77732	5	+	1	160825	7	−
size	1	59976	1	+	1	4141	8	+	1	3563939	2	+
nest	1	201	3	−	1	4389882	1	+	1	6370929	1	+
am×fr	1	1	10	−	1	125	10	−	1	9298	9	−
am×size	1	108	4	−	1	11362	7	+	1	206547	6	+
am×nest	1	95	6	−	1	1011815	2	+	1	2304946	4	−
fr×size	1	8	7	+	1	1081	9	−	1	8431	10	−
fr×nest	1	6	8	+	1	78032	4	−	1	150708	8	+
size×nest	1	256	2	+	1	55545	6	−	1	366922	5	−
Residuals	11989	1247			11989	286187			11989	1386256		

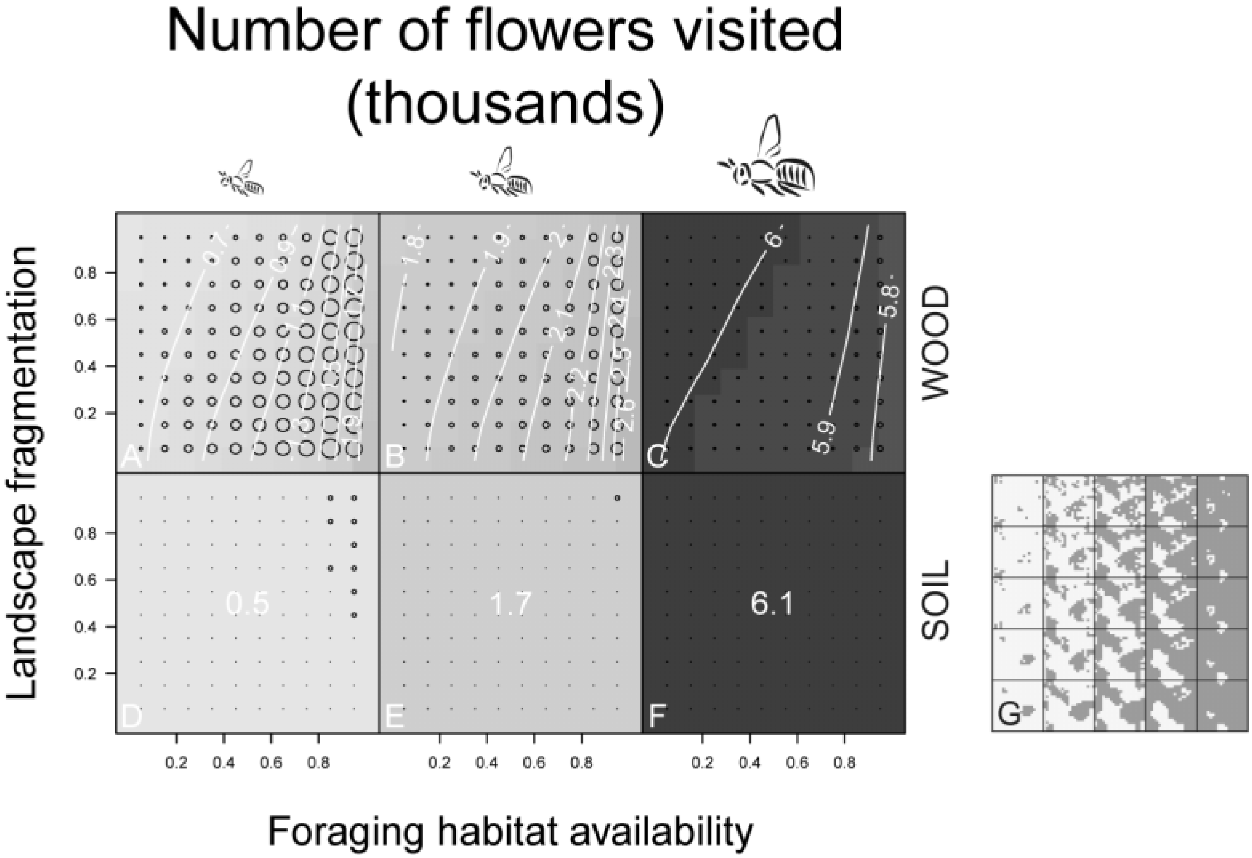


Figure 6.1. The mean number of flowers visited per bee (in thousands) during a foraging day for different bee types (panel A-F). Within each panel are different landscapes displayed and characterized by a gradient of *foraging habitat availability* (left to right) and *landscape fragmentation* (bottom to top); in total hundred combinations per bee type. Darker shades of grey (third dimension) represent a higher number of flowers scaled over all bee types. To guide the different shades of grey absolute numbers and contour lines are depicted. Each of the hundred values represents the mean of 20 replicate simulations. The standard error (absolute value) is indicated by scaled circles (smallest circle represents zero, and the largest circle a value of 0.047, i.e. 47 flower visits). The panels depict from the left to the right small (A,D) to large bees (C,E) and from top to bottom wood- (A-C) and soil- (D-F) nesting bees. The most right panel (G) shows 25 example landscapes (5 by 5 instead of the 10 by 10 in the other panels) to visualize the gradient of *foraging habitat availability* (dark grey) and *landscape fragmentation*.

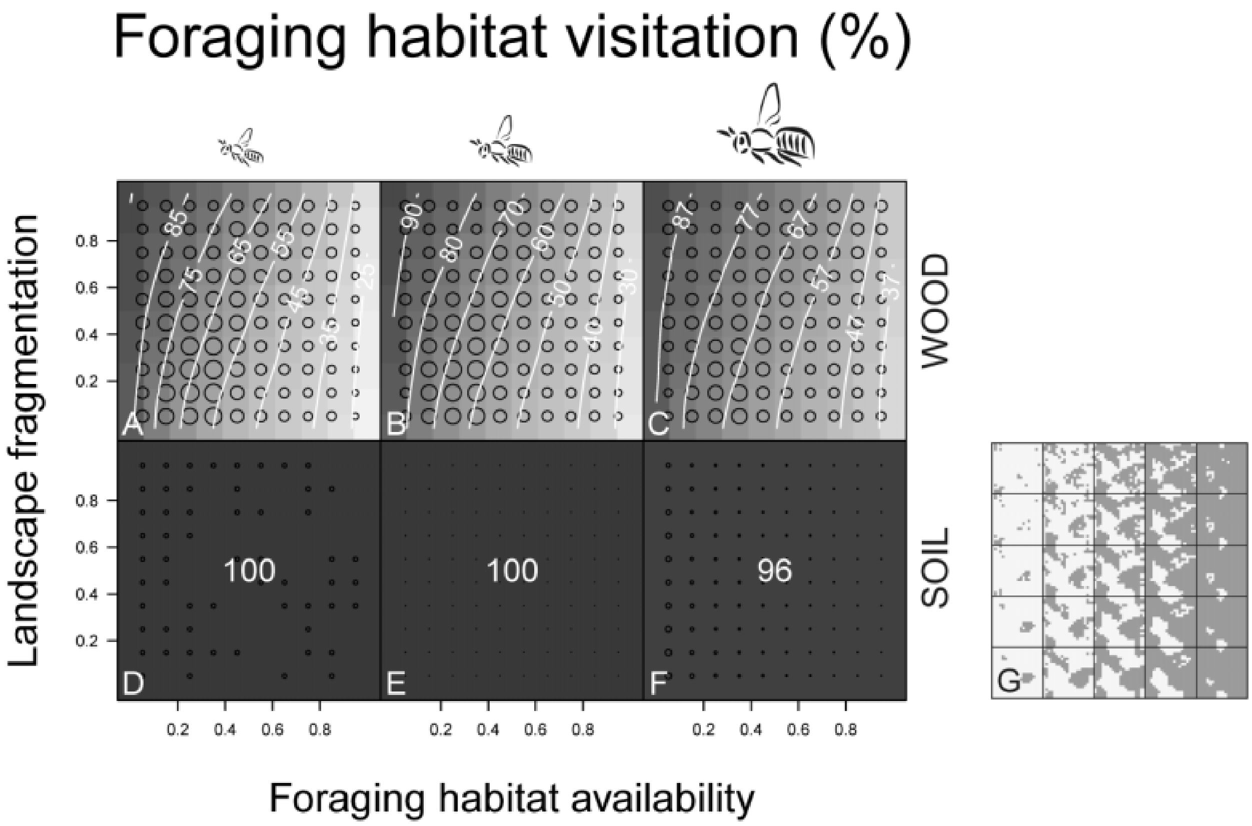


Figure 6.2. Percentage of foraging habitat visited by the bee community (during a foraging day) for different bee types (panel A-F). Within each panel are different landscapes displayed and characterized by a gradient of *foraging habitat availability* (left to right) and *landscape fragmentation* (bottom to top); in total hundred combinations per bee type. Darker shades of grey (third dimension) represent a higher visitation scaled over all bee types. To guide the different shades of grey absolute numbers and contour lines are depicted. Each of the hundred values represents the mean of 20 replicate simulations. The standard error (absolute value) is indicated by scaled circles (smallest circle represents zero, and the largest circle a value of 2.3). The panels depict from the left to the right small (A,D) to large bees (C,E) and from top to bottom wood- (A-C) and soil- (D-F) nesting bees. The most right panel (G) shows 25 example landscapes (5 by 5 instead of the 10 by 10 in the other panels) to visualize the gradient of *foraging habitat availability* (dark grey) and *landscape fragmentation*.

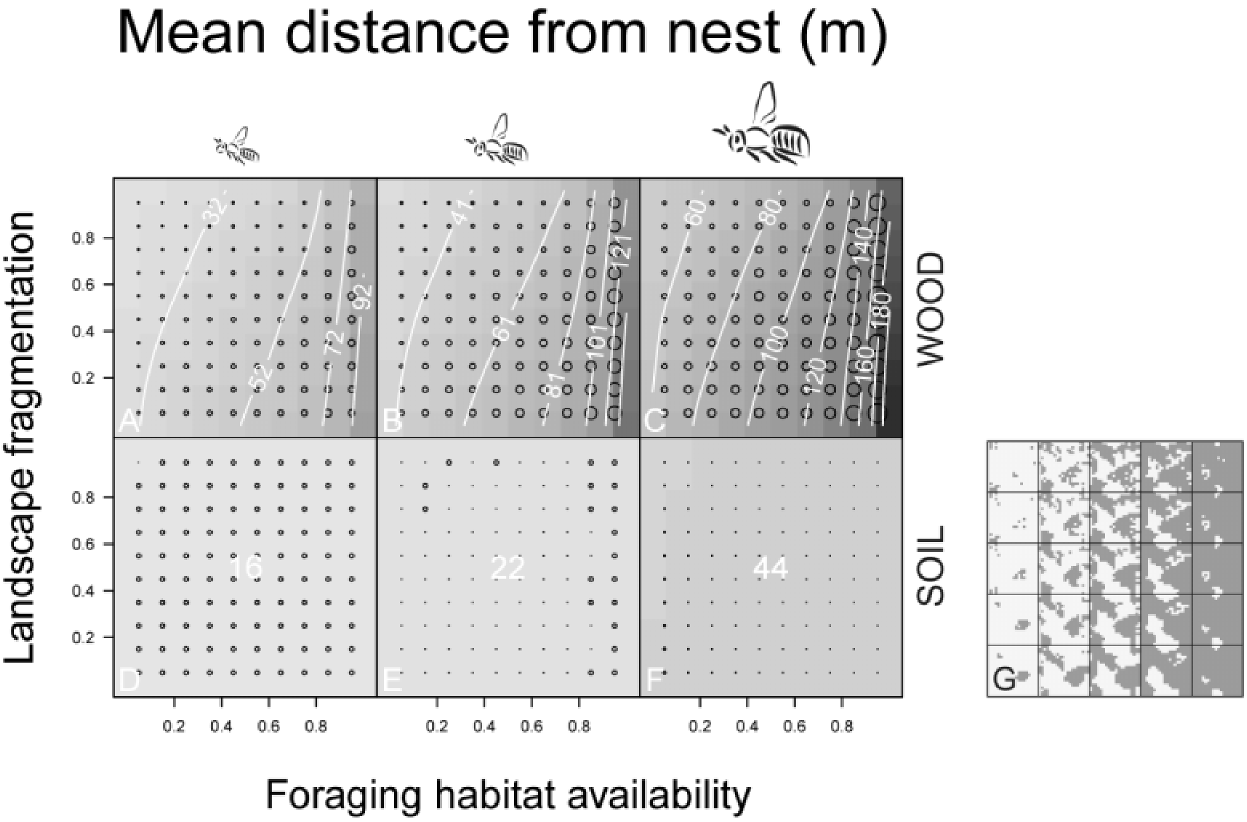


Figure 6.3. Mean distance flown from the nest per bee (during a foraging day) for different bee types (panel A-F). Within each panel are different landscapes displayed and characterized by a gradient of *foraging habitat availability* (left to right) and *landscape fragmentation* (bottom to top); in total hundred combinations per bee type. Darker shades of grey (third dimension) represent foraging distances further from the nest scaled over all bee types. To guide the different shades of grey absolute numbers and contour lines are depicted. Each of the hundred values represents the mean of 20 replicate simulations. The standard error (absolute value) is indicated by scaled circles (smallest circle represents zero, and the largest circle a value of 4.9). The panels depict from the left to the right small (A,D) to large bees (C,E) and from top to bottom wood- (A-C) and soil- (D-F) nesting bees. The most right panel (G) shows 25 example landscapes (5 by 5 instead of the 10 by 10 in the other panels) to visualize the gradient of *foraging habitat availability* (dark grey) and *landscape fragmentation*.

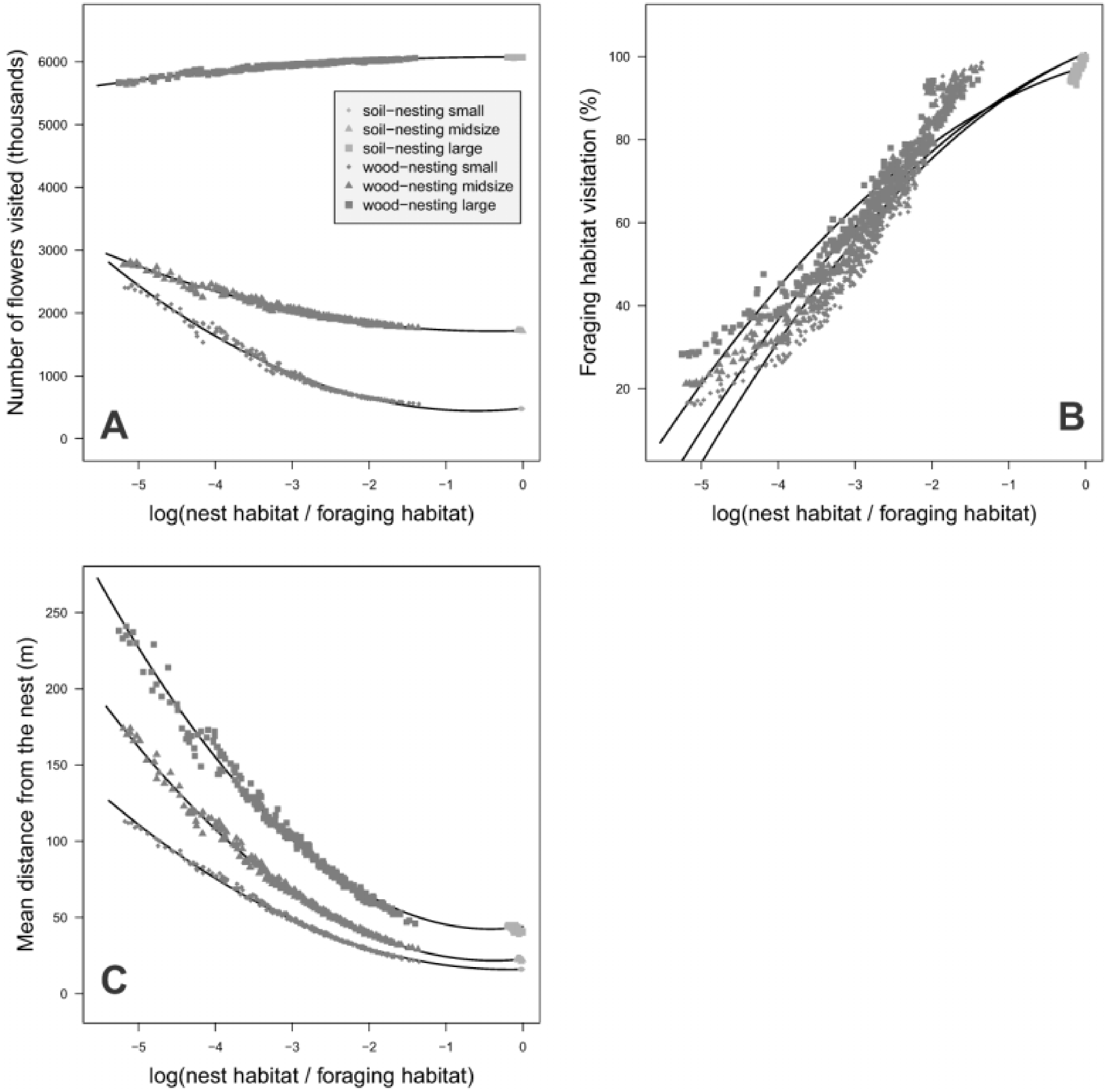


Figure 6.4. The effect of the ratio of nest habitat availability to foraging habitat availability on three pollination-related responses. A: number of flowers visited, B: ratio of nest habitat availability to foraging habitat availability, C: mean distance from the nest. Dark grey points are wood-nesting bees and lighter grey dots are soil-nesting bees, plotted for three replicate simulations. Lines are based on linear models (appendix C.3, 20 replicate simulations) and are separated for different body sizes.

6.3. Discussion and Conclusions

6.3.1. Individual centred pollination measures

The three pollinator-centred measures for pollination have all their own value, with different responses and different ranking of factor importance (table 6.1). The results for the number of flower visits, mean distance from the nest and foraging habitat visitation hold therefore different messages. We also found that the ratio of nest habitat availability to foraging habitat availability was a good replacement for the effect of *foraging habitat availability*, *landscape fragmentation* and *nesting preference* (fig. 6.4) with high correlation values for the three pollination measures. We have also shown that very small solitary bees can contribute to pollination. They cover the foraging habitat almost as much as large bees (fig. 6.2) although they fly on average less far from the nest (fig. 6.3). The pollination potential of small insects is often underestimated and they transfer enough pollen for sufficient seed set (Taki et al. 2009).

More flower visits per individual bee indicates that more flowers received pollen. As expected do large bees visit more flowers than small bees (fig. 6.1) in accordance with the literature (e.g. Sih and Baltus 1987, Hoehn et al. 2008). Flower visits increased with *foraging habitat availability* and *landscape fragmentation*, better explained as more flower visits for a low nest habitat to foraging habitat ratio and less flower visits for a high ratio (soil-nesting bees) (fig. 6.4.A). For an equal amount of brood cells, bees of a certain size require the same amount of flowers. The number of flowers visited showed however an opposite pattern to the number of brood cells, which increased with the ratio of nest habitat to foraging habitat (chapter 5, fig 5.2.D). The number of brood cells is thus lower when more flowers have been visited. This only makes sense when the bees visited many empty flowers, which we did not separate from visit of flowers still offering pollen (but got different time penalties, table 3.2). The number of flower visits per bee was found to decrease for solitary bees with an increasing number of flowers (Sih and Baltus 1987) comparable to an increase in foraging habitat in the model. We found the opposite pattern, attributable to the fact that we also increased the number of bees in the model. The opposite response of large bees compared to intermediate sized and small bees (figs. 6.1 and 6.4.A) is remarkable and may be caused by a different ratio of full and empty flowers probed. Small and intermediate sized wood-nesting bees occurred in high local nest densities (chapter 5, fig. 5.2.C) and were likely to find many empty flowers near the nest-site. Large bees occurred in lower densities (chapter 5, fig. 5.2.C) and additionally had better flight capabilities to escape locally depleted patches near the nest, which could have led to more visits of full flower. Flower-visiting behaviour of large wood-nesting bees was very similar to that of large soil-nesting bees without a high impact of landscape composition and configuration (fig. 6.1, C and F).

The mean distance from the nest is a measure for how far pollen is transported, but it is focussed on the bee. Bees do generally not fly farther than needed, which can result in very short foraging distances (< 50 m, fig. 6.3) for soil-nesting bees. They were with their nest evenly distributed over the foraging habitat and found enough pollen within a short range from the nest in all landscapes. Large bees flew farther (50-200 m, fig. 6.3.C) than small bees (30-100 m, 6.3.A), but these distances are still relatively low. This is in agreement with the finding that that both large and small bees can have foraging distances below 200 m (Albrecht et al. 2007). Mean foraging distances are higher when conditions are unfavourable for bees (up to 800 m for large bees and 300 m for small bees, data from simulation experiment 2, chapter 4). The mean distance flown was in most cases several times lower than the mean homing distance that we used (*r50*). Foraging distances are thus very different for different conditions and landscapes. A maximum performance value such as homing distance is indeed not suitable as substitute for foraging activity (Guédot et al. 2009).

The patterns of foraging habitat visitation make sense. Soil-nesting bees that nest well distributed over the foraging habitat could also cover the foraging habitat very well (96-100%, fig. 6.1). Wood-nesting bees that nest at the border of the habitat and covered less foraging habitat when there was more foraging habitat to cover in the landscape (down to 25% for high *foraging habitat availability*, fig. 6.1). Bees nesting at field edges did not reach the interior of the fields in those cases. Remarkable is the low effect of *body length*, which makes foraging habitat visitation a very practical pollination service measure that can be approached by the landscape level measure of nest habitat to foraging habitat ratio (fig. 6.4.B). We re-fitted the relationship between foraging habitat visitation and the ratio nest habitat to foraging habitat with a sigmoid function (fig. 6.5.A, inlay). We then untransformed the ratio which gives a clear picture that foraging habitat visitation is rapidly reduced when the ratio becomes below 0.2 (fig. 6.5.A, main plot), independent of the body size of the bee.

The abrupt rate of change for pollination services that we modelled (fig. 6.5) and the value for which below pollination services are clearly reduced may be common in natural systems. However, we should be cautious with interpretation since we simulated only one type of vegetation. The flower density and amount of pollen per flower were important system parameters for foraging habitat visitation (chapter 4, simulation experiment 2). We therefore repeated the simulation experiment (5 replicates) with different vegetation parameters. This altered vegetation is characterized by a lower flower density (*fd* = 25) and larger flowers with a threefold of pollen per flower (*ppf* = 1.5), which is released in at least 5 pollen packages (*plimit* = 0.2). The results are virtually the same (fig. 6.5.B) with the main difference in the minimal coverage of the foraging habitat. Hence, there may be a general pattern for different vegetation types, but more extreme values still need to be explored.

The responses mean distance from the nest and foraging habitat visitation showed an opposite pattern, and highlights a conflict between the bee's perspective of the landscape and the pollination at the landscape level. In the best landscapes for bees with a high ratio of nest habitat to foraging habitat, the number of brood cells was high (chapter 5, fig. 5.2.D) and due to a better spatial distribution the coverage of foraging habitat was also high (fig. 6.4.B). The foraging distances were lowest in those cases (fig. 6.4.C), and pollen was thus inevitably transported over shorter distances. The two pollination measures (mean distance from the nest and foraging habitat visitation) were thus negatively correlated (compare figs. 6.4.B and 6.4.C). This seems contradicting but has a logical explanation. Larger fields (low nest habitat to foraging habitat ratio) are not visited in the interior (lower foraging habitat visitation). Due to more bees (high *foraging habitat availability*) nesting in the same border of the same field bees have a high local density (chapter 5) forces the bees to fly a bit further from the nest than for small fields. These increased foraging distances are not enough to cover the whole foraging habitat. Due to this contradiction. the mean foraging distance may not be the best measure for pollination. Additionally bees do most of the time move between near habitat grid cells and do mainly exchange pollen with plants over this short distance.

6.3.2. Practical applications

A strong result is that the ratio nest habitat to foraging habitat seems very suitable for measuring pollination services, especially the foraging habitat visitation. Some studies with wild bees already experimented with similar measures. The surface to circumference ratio of agricultural fields in agriculturally dominated landscapes was suggested to increase the value for wild bees (Banaszak 2000) and a wild bee community was indeed positively affected by the (squared) edge to area ratio and performed as measure better than area or habitat isolation (Brosi 2008). The use of such ratios is promising, since they include both nesting and foraging requirements, but more field studies are needed to quantify their practical value.

The main issue in the field is the right classification of the different habitats, because it differs for bee species and in biogeographical regions. Mistakes in classification of habitat requirements for both nesting and foraging are easily made, due to a lack of experience with wild bees. Forest is sometimes interpreted as foraging habitat and nest habitat for bees, which is true for tropical forests. Temperate forests hardly provide foraging resources and alone forest edges serve as nest habitat, not the entire forest (Calabuig 2000, Steffan-Dewenter 2002), at least concerning human dominated landscapes. A good example of classifying land-use maps into habitat classes for wild bees is given by Lonsdorf et al. (2009). They also recognize in line with our findings that for studying pollination services by bees at the landscape scale, biological detail about body size, foraging resources, and nesting resources are essential.

Our results probably apply to mass crops as well. We modelled meadows with a moderate flower density and without disturbance, so that we could fairly compare different bee types. The main differences with agricultural crop fields are that soil-nesting bees are not able to nest in disturbed soils (Osborne et al. 1991) and that the foraging resources (crop) are not available during the complete lifetime of most bee species (Banaszak 2000, Potts et al. 2010a). A (too) short availability of foraging resources does not affect pollination services during a foraging day, nor does it affect the number of brood cell built during a foraging day. Bees may even search for a new nest site after mass crop flowering since they have no brood care and can safely close a nest tube or tunnel with completed brood cells. Soil-nesting bees may not nest in agricultural fields, but nest at least in field edges as well, together with wood-nesting bees. This highlights the importance of undisturbed field strips along agricultural fields with both shrubs and open spots with bare soil.

The minimum requirement for good pollination services corresponds to a nest habitat to foraging habitat ratio of 0.2 (fig. 6.5). A 5 m wide natural strip at the (inner) border of a 1 ha crop field, yields a ratio of 0.19 , at the border of a 49 ha field a ratio of 0.028. Since most crop field are larger than one ha and have no field strips, most agriculturally dominated landscapes are really poor and a hostile environment for solitary bees, despite mass flowering crops. We assumed for example that bees nest near their foraging habitat and bee numbers were in balance with the amount of resources, which may not be true (e.g. Wojtoski et al. 1995). We also assumed that there is always some nest habitat in our 1 square km landscapes. When this is not the case, there would be no pollination at all (instead of the 26% in the worst landscapes, fig. 6.5). An increase in field margins with woody structures and a decrease in field size could mitigate this. This increase in landscape fragmentation would benefit solitary bees.

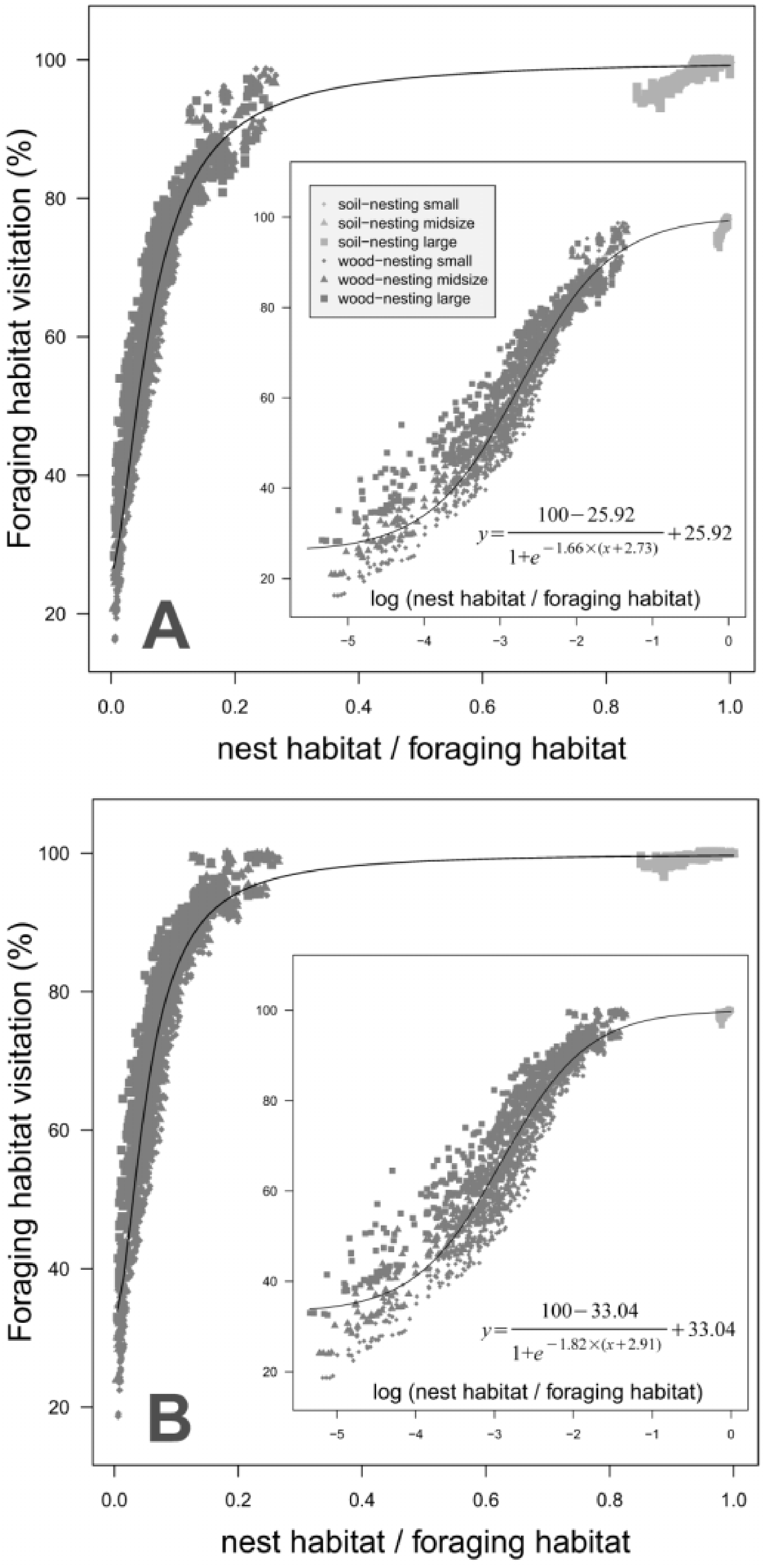


Figure 6.5. Percentage of foraging habitat visited in response to the ratio of nest site availability to foraging habitat availability. Darker shaded grey points represent wood-nesting bees that nest in field edges and lighter shaded grey points represent soil-nesting bees that can nest everywhere in the foraging habitat. Inlay: Foraging habitat visitation in response to the (natural) logarithm of the ratio. Data were fitted with a sigmoid curve and untransformed to the main plot. A: Data points from 5 replicate sets from the main simulation experiment, B: Data points from 5 replicate sets (the same *seed* as in A, i.e. same landscapes) with altered vegetation parameters. Pearson's correlation coefficients for A and B (between predicted curve and points) are 0.986 and 0.976 respectively.

CHAPTER 7

A case study:

Urban habitat selection of the red mason bee

published as: Everaars J., Strohbach M.W., Gruber B. and 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. Landscape and Urban Planning 103 (1): 15-23.

Bees are well able to survive in urban areas, especially in deserted areas with sufficient nesting substrates (left). Some species profit from stone walls that are warmed by the sun and build their nests at the bottom (right). How do solitary bees in urban areas cope with the high amount of fragmentation of foraging and nesting resources?

Urban bees "are those that lived in an area prior to urbanization and were able to adapt to anthropogenic (human) alterations to the environment."
(Frankie et al. 2009)

7.1. Case study methods

7.1.1. Study area

Leipzig is located in eastern Germany (51°20’ N, 12°22’ E). Climate characteristics are intermediate between temperate and continental with an average annual temperature of 8.8°C and 511 mm precipitation. Leipzig is a compact city with a population of approximately 500,000 people. The city core consists of a densely developed area with administrative and cultural facilities, little housebound green (gardens, balconies etc.) and several small parks. The core is surrounded by a residential ring, dominated by tenement blocks from the late 19th and early 20th century with green backyards and balconies with ornamental flowers. A second residential ring is formed around Leipzig consisting of terraced and detached houses with gardens, mainly built between 1900 and 1940, as well as socialist-era prefabricated multi-storey housing estates surrounded by lawns with very few flowers, but often with flower-rich balconies. Larger parts of the eastern and western sides of the city are covered by industrial and commercial land use with little green space.

Despite being compact, Leipzig has a significant amount of green space. The city has several large parks and a large floodplain forest is running past the core city. Many small allotment garden plots are situated along railway tracks and around the city. Former lignite open-cast mines that are being turned into an artificial lake district are located to the south of the city. Otherwise, the rural surrounding is dominated by intensively used agricultural land (fig. 7.1).

7.1.2. Bee sampling and microsite assessment

We sampled bees following a citizen-science approach. We handed out 350 trap nests to employees of the Helmholtz Centre for Environmental Research in Leipzig in March 2008. Participants were asked to hang their trap nest at or around their home and return it in June. Although this approach does not yield a perfectly balanced design, it covered the city well, reaching beyond public spaces. We gave the participants a questionnaire that enquired about microsite attributes describing nest site quality and abiotic conditions. The questionnaire included the address of the nest location, predefined categories about *trap orientation* (West, East, South, North, None), *sun exposure* (fully shaded, partly shaded, fully sunlit), *wind protection* (yes/no), *hang location* (house, garden, allotment, backyard, or specify other location), *object of attachment* (window, balcony, roof-terrace, tree/shrub, ground, wall, or specify other object), *floor* (if at a house), *flowers within 100 m* of the trap nest (yes/no) and flower types (*meadow flowers*, *ornamental flowers;* yes/no). In addition, we asked the volunteers to provide us with photographs of the trap location.

Each trap nest was constructed as a plastic tube, 20 cm long and 10.5 cm in diameter, filled with a bundle of approx. 33 bamboo tubes, each 20 cm long with a cavity diameter > 5 mm (which is the minimal diameter for O. bicornis: Budriene et al. 2004, Ivanov 2006).

The participants in the study returned 250 nests in June 2008 along with the questionnaires and counted the number of cells built by *O. bicornis* (excluding the vestibule). A trap nest is a unit where multiple females nest and each female uses one or more tubes, so that individual nests cannot be identified by this method. We used the number of brood cells to estimate the response to local resources since brood cells contain pollen and nectar from floral resources. The main flight period of *O. bicornis* is from the middle of April until the end of May (Maddocks and Paulus 1987, Teppner 1996). We only used trap nests that hung at least between 16 April 2008 and 25 May 2008. The locations of the 239 trap nests that met this criterion are shown in figure 7.1. These exposure days are characterized by a mean daily temperature of 12.8 ºC and 8.1 hours of sunshine and 0.6 mm of rainfall on average per day. We included the day of nest removal (Julian day – 145), the total number of bamboo tubes per trap and the proportion of tubes with an internode (which serves as additional nest protection) as correction factors in the analysis.

7.1.3. Habitat suitability and landscape factors

We quantified foraging and nesting resources at the landscape level since pollinators are mobile and operate at scales larger than the individual garden (Goddard et al. 2010). Solitary wild bees respond to landscape structure at scales up to 750 m in contrast to honeybees and bumblebees which operate at larger scales (Steffan-Dewenter et al. 2002). We classified the landscape based upon the most recent (2005) biotope map of Saxony (Sächsisches Landesamt für Umwelt, Landwirtschaft und Geologie 2008). The biotope map was derived from 1:10,000 colour-infrared ortho-photos by manual classification into biotopes with a minimal area of 0.25 ha. Biotope definitions are detailed land-use descriptions from a biological perspective and include (semi-) natural biotopes such as different forests types and water bodies as well as agricultural biotopes such as orchards and hedgerows but also urban habitats such as roads and different building types. This biotope classification was developed in Germany as a proxy for habitats that organisms use and is a useful and diverse classification when large areas are inaccessible for detailed plant surveys, as it is the case in urban areas where the majority of the land is private. We reclassified the land cover twice, focusing on estimated availability of foraging resources (areas with potential suitable bloom) and nesting resources respectively, based on rules given by Lonsdorf et al. (2009). *O. bicornis* forages on spring flowering vegetation (among others found at meadows with dandelion or areas having blossoming trees) and nests in cavities (found at places with dead stems). A summary of the re-classification rules is given in table 7.1. We re-classified into *abundant foraging resources* and *poor foraging resources*. Biotope classes that were not clearly rich or poor in foraging recourses were classified as *moderate* and not used for further analysis. We did likewise for nesting resources. Figures 7.1.B and 7.1.C show two enlarged areas of the re-classified map for foraging and nest habitat respectively.

We determined the minimum distance (flight effort) between the trap nest and each of the four suitability classes as well as their proportion (resource availability) within a 500 m buffer radius (typical foraging area of *O. bicornis*, see Gathmann and Tscharntke 2002) around the trap nest. We determined landscape structure (diversity and complexity) with basic tools from ArcGIS 9.3 and the Patch Analyst 0.9.4. We calculated the following landscape metrics within each buffer radius from the original biotope classes: *number of patches, mean patch fractal dimension, total edge length, edge density, mean patch size* and *mean shape index*, giving 14 different landscape factors in total.

7.1.4. Statistical analysis

Before analysing the data, we grouped hang locations by similarity. *Backyard* and *park* were joined into one class, as were *garden* and *allotment.* Likewise we grouped the attachment objects, including those that were not pre-defined: *balcony* and *roof terrace*, *carport* and *shed wall*, *window* and *stone wall*. All remaining objects except *tree or shrub* were grouped as *other object*. We used the statistical software R (R Development Core Team 2009) for analysis and proceeded in the following steps. First we addressed possible collinearity by reducing the number of variables so that all bivariate correlations were below a set threshold (Pearson's $r^2 < 0.49$; the ecologically more plausible predictor was retained). The parameters that meet this criterion are listed in table 7.2 and include both landscape-level variables and microsite attributes. Resource availability was incorporated into the presence-absence-analysis as minimal distance to a resource patch and in the abundance analysis as the proportion within 500 m radius. We then selected the most important variables, because our study had more predictors than could be fitted in a multiple regression. We used the machine learning approach of randomForest (Breiman 2001) to rank the variables by importance (separately for presence and abundance of *O. bicornis*).

With the six top-ranked variables we performed a (generalized) linear regression model selection based on the Bayes Information Criterion (BIC). We included quadratic responses and interactions between variables in the full model. The final regression model included only significant predictor variables. The number of observations for the final model is given in the results in brackets, since it depends on the missing values in the selected parameters. We used likelihood-ratio tests to compute significance values. Explained deviance was estimated as (null deviance – residual deviance)/null deviance. For the number of brood cells we fitted a negative binomial model. Trap nests were spatially independent (model residuals spatially uncorrelated). Two correction factors remained significant after model selection (table 7.2). The day of trap removal (Julian day – 145) increased the probability of trap-nest occupancy from 0.3 to 0.8 ($p = 0.011$) and the proportion of tubes with an internode had a slight, positive effect on the number of brood cells ($p = 0.004$). For significant factorial parameters we tested pair difference significance for all combinations with a Tukey's post-hoc test.

Table 7.1. Classification of nesting and foraging resources. The classification for *O. bicornis* into poor and abundant resources is based on the original biotope classes. Biotopes providing moderate resources were not considered.

New classification	Old classification
Abundant foraging resources	meadow (only those providing either a rich flora or abundant dandelions), hedgerow (often contain spring flowering trees), forest edge, orchard, riparian buffer zone, botanical garden, allotment area, garden, castle/monastery/estate area, mixed rural area
Poor foraging resources	water bodies without flowering vegetation, concrete buildings for non-living and non-public usage, industrial area, golf course, roads (all types), species-poor intensively-used grassland, coniferous forest
Abundant nesting resources	hedgerow, shrubbery, deciduous woodland (all types without conifers), forest edge, castle/monastery/estate area, reed bed, meadow orchard
Poor nesting resources	water bodies without reed beds, concrete buildings for non-living and non-public usage, industrial area, sewage field, golf course, road (all types), road ditch, intensively used grassland, sand plains, coniferous forest, afforestation area, agricultural fields

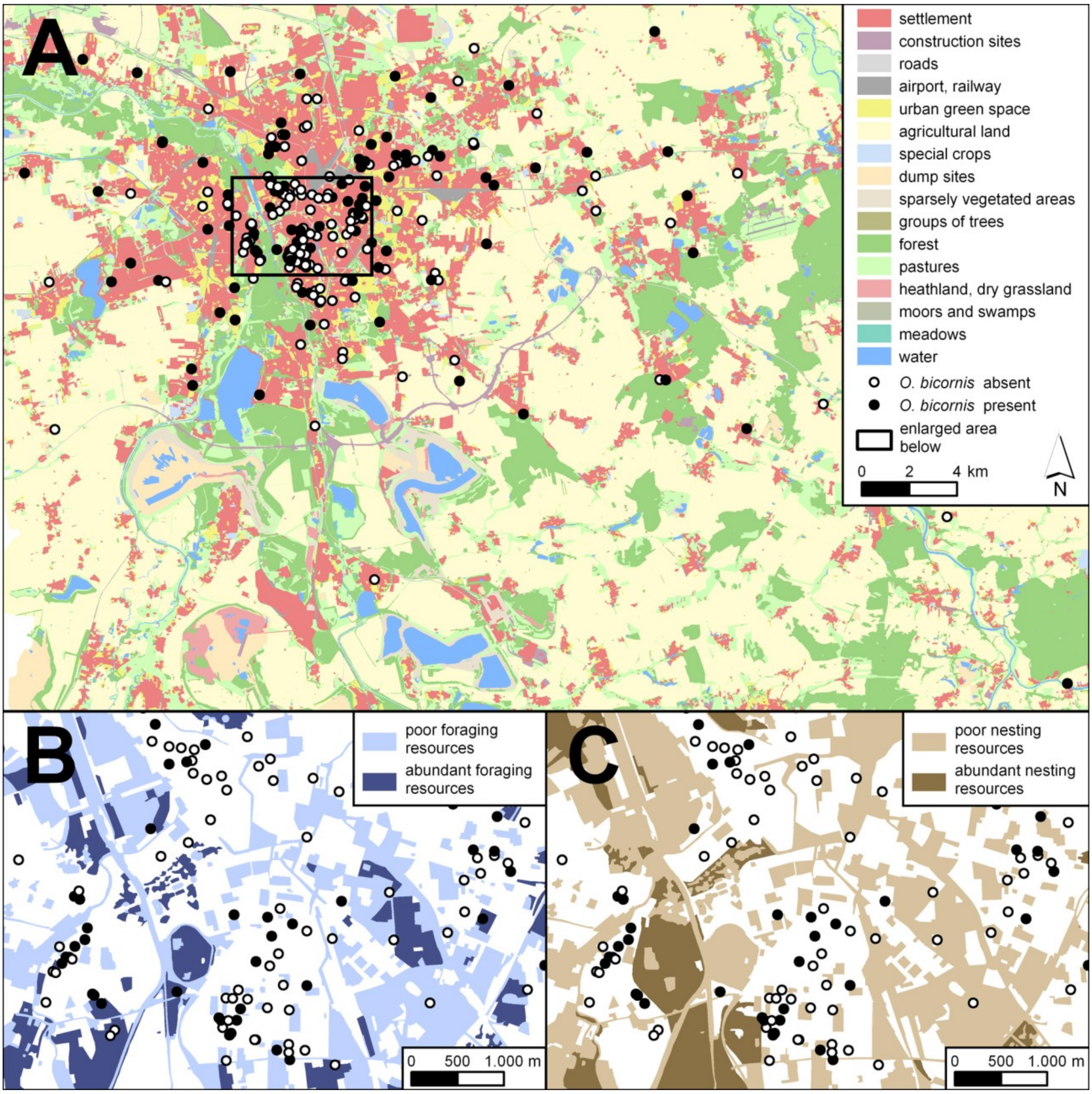


Figure 7.1. This map shows the major land cover classes in and around Leipzig and the distribution of the trap nests (A). B shows the classification of foraging resources and C of the nesting resources for *O. bicornis* (moderate foraging and nesting resources omitted, white space). Note that A, B and C are three different reclassifications of the detailed biotope classes.

7.2. Results

Out of the 239 trap nests amenable to analysis, 110 were occupied by *O. bicornis* (46%). There was no obvious spatial pattern of trap-nest occupancy (fig. 7.1; occupied trap nests are often close to non-occupied ones).

7.2.1. Presence-absence analysis

The regression model revealed the following significant parameters for the presence of *O. bicornis* (occupancy of a trap nest): the *object of attachment*, the amount of *sun exposure* and the minimal distance to *abundant foraging resources* (table 7.2, model A). Nests that were attached to *tree or shrub* showed a lower probability of trap-nest occupancy than those on balconies, at carports and other objects (fig. 7.2.a). Nests placed in the full sun were also more often occupied than nests located in the full shade (fig. 7.2.b). Trap nests located closer to abundant foraging resources were more likely to be occupied (fig. 7.2.c). The linear regression model (n = 222) explained about 30% of the deviance. A post-hoc analysis revealed that all three shade-groups were significantly different (fig. 7.2.b). The hang location *tree or shrub* differed significantly from *balcony or roof terrace* ($p < 0.001$), from *carport or shed wall* ($p < 0.01$) and *other object* ($p < 0.05$).

7.2.2. Abundance analysis

Abundance of *O. bicornis* refers to the number of brood cells within the 110 occupied nests. As for presence-absence data, the *object of attachment* had the largest impact. Nests that were attached to *tree or shrub* or *other object* showed a low abundance per nest and those to *carport or shed wall* a high abundance (fig. 7.3.a). In addition, there was a small but significant effect of nesting resources. An increase of the proportion of *abundant nesting resources* within 500 meters led to fewer cells and opposing to that, an increase in poor foraging resources led to more cells in the trap nest (fig. 7.3.b). Both had a significant effect by themselves, but not when taken together, since they provided similar information (despite a low correlation: Pearson's $r = -0.24$, $p < 0.05$, log-transformed data). We therefore used *abundant nesting resources* (and excluded *poor nesting resources*) in the regression model (table 7.2, model B, n = 90), which explained 25% of the deviance. A post-hoc analysis revealed that the hang location *tree or shrub* differed significantly from *carport or shed wall* ($p < 0.001$).

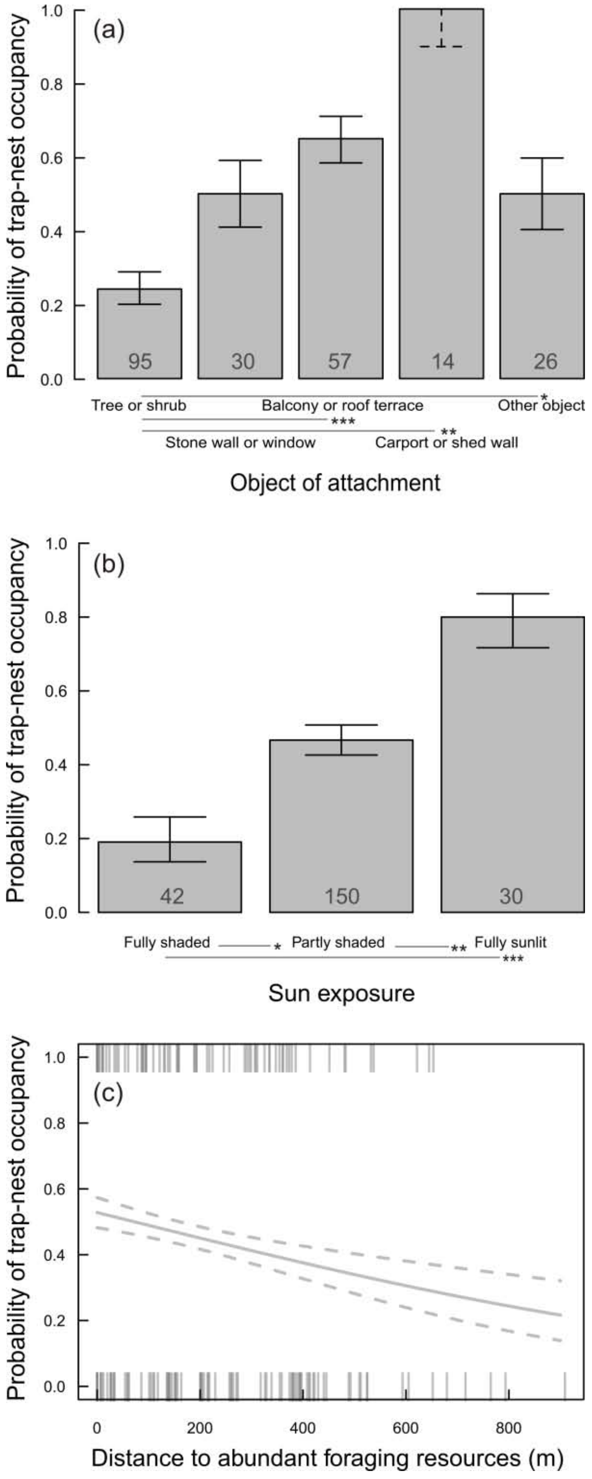


Figure 7.2: Variables explaining the presence of *O. bicornis* expressed as the probability of trap-nest occupancy. Probabilities ± SE are given based on the selected model. (a) Probability of trap-nest occupancy in response to the *object of attachment*. The number on each bar represents the number of observations. All trap nests for *carport or shed wall* were occupied and hence prevented an estimation of the error. We (over-) estimated this SE with an adjusted model with one observation changed from 'present' into 'absent'. Significant differences are indicated with a grey line (significance codes: *** < 0.001, ** < 0.01, * < 0.05, significances based on the adjusted model). (b) Probability of trap-nest occupancy in response to *sun exposure*. Error bars and contrast significance are based on the original model. (c) Probability of trap-nest occupancy in response to the minimal distance between trap nests and *abundant foraging resources*. Lines indicate the model prediction ± SE and the vertical marks (at zero and one) are the original presence and absence observations.

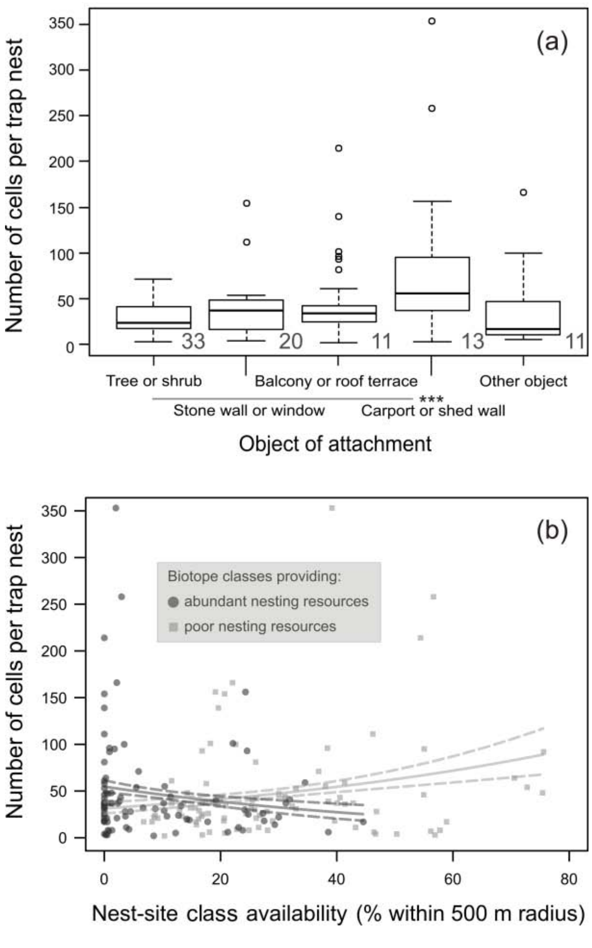


Figure 7.3: Variables explaining the number of *O. bicornis* brood cells per occupied trap nest. (a) Number of brood cells in response to the *object of attachment*. The number to the lower-right from each box represents the number of observations. Significant differences are indicated with a grey line (significance codes: *** < 0.001). (b) Number of brood cells in response to the amount of nesting resources. Lines indicate the model prediction ± SE. Each trap nest is represented twice (two of three nest site classes).

7.2.3. Interaction between the object of attachment and hang location

We initially assessed the hang location additionally to the object of attachment, but this was excluded from the final analysis due to collinearity, caused by the fact that balconies can only appear on houses while trees cannot. To reveal additional information, we separated each attachment class according to hang location (fig. 7.4). We plotted the proportion of occupied nests within each class for each of the ten new classes (fig. 7.4.a) and the mean number of cells for each class (unoccupied nests excluded) (fig. 7.4.b). Both show a similar pattern. *Garden or allotment* increased the probability of trap-nest occupancy and the number of cells in comparison to *backyard or park* as long as the trap nest was attached to a *tree or shrub*, a *stone wall or window* or *other object*. In both linear regression models we replaced *object of attachment* (five classes) by these ten classes (table 7.2, model C and D), increasing the explained deviance from 30% to 33% and from 25% to 33% for presence and abundance, respectively. To test whether the visual similarity between fig. 7.4.a and 7.4.b is statistically verifiable, we replaced the *object of attachment* in the regression model for abundance with the proportion of occupied nests within a class as new explaining variable for the number of cells (table 7.2, model E). This regression model explained 25% of the deviance.

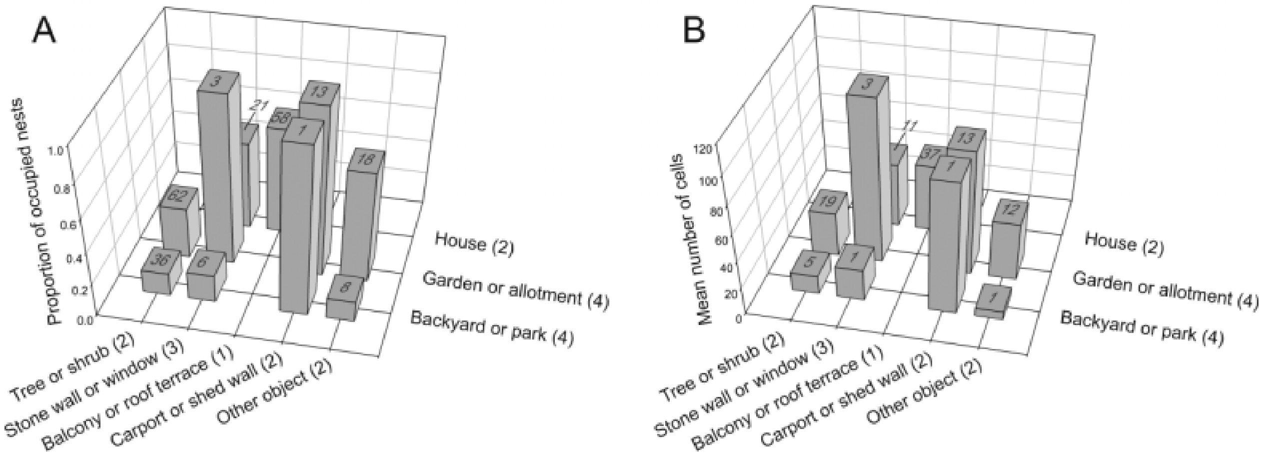


Figure 7.4. Effect of *object of attachment* and *hang location*. The number of bars in each row is given in brackets. The number on top of each bar represents the number of observations in each group. In total, 10 groups are displayed. A: Proportion of occupied trap nests within each group. B: Mean number of brood cells per trap nest in each group for occupied nests only.

Table 7.2: Selected regression models. The models for explaining presence and abundance of *O. bicornis* are based on model parameters that remained after correction for collinearity 1). Parameters describing microsite attributes are written in italics. Deviance, P-value and degrees of freedom (df) are given for each model.

Predictor	Df	Deviance	P-value
Model A: presence (1)			
null deviance: 306.30			
--------------------------------			
object of attachment	4	49.63	<0.001
sun exposure	2	26.15	<0.001
abundant foraging resources (distance)	1	8.13	0.004
day of removal 2)	1	6.51	0.011
model B: abundance (1)			
null deviance: 131.05			
--------------------------------			
object of attachment	4	20.44	<0.001
proportion of tubes with internode 2)	1	8.24	0.004
abundant nesting resources (500m radius)	1	4.46	0.035
model C: presence (2)			
null deviance: 306.30			
--------------------------------			
object of attachment with hang location	9	66.61	<0.001
sun exposure	2	23.45	<0.001
abundant foraging resources (distance)	1	3.75	n.s. (0.053)
day of removal 2)	1	6.78	0.001
model D: abundance (2)			
null deviance: 143.71			
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object of attachment with hang location	9	33.63	<0.001
proportion of tubes with internode 2)	1	9.06	0.003
abundant nesting resources (500m radius)	1	4.21	0.040
model E: abundance (3)			
null deviance 131.04			
--------------------------------			
proportion of occupied trap nests per class	1	20	<0.001
proportion of tubes with internode 2)	1	8.24	0.004
abundant nesting resources (500m radius)	1	4.96	0.026

1) Candidate predictors below bivariate correlation threshold ($r^2 < 0.49$): abundant foraging resources, abundant nesting resources, poor nesting resources, number of patches, mean shape index, *object of attachment, sun exposure, tube orientation, wind protection, presence of flowers within 100m, meadow flowers, ornamental flowers,* day of removal 2), proportion of tubes with an internode 2), total number of tubes 2)

2) Predictors used as a correction factor as explained in the methods section.

7.3. Conclusions and discussion

Our citizen-science approach revealed a dominance of microsite nest conditions over foraging resource distributions at larger scales. Sun-exposed and wall-mounted nests in private gardens were particularly attractive for bees.

7.3.1. Landscape effects and resource limitations

We expected that low levels of foraging resources at the landscape scale would have a negative effect on presence and abundance of *O. bicornis*. The probability of trap-nest occupancy decreased indeed slightly in response to the distance from abundant foraging resources (fig. 7.2.c), but foraging resources did not affect the number of cells. We believe that foraging resources (floral abundance) are not a major limitation in the urban area of Leipzig. There were always *abundant foraging resources* within the maximum foraging distance (900 m for *O. bicornis*: Gathmann and Tscharntke 2002, see fig. 7.2.c). Additionally, bees may have foraged on flowers in areas that we classified as *moderate foraging resources* (fig. 7.1.b). Note that most of the participants (97%) affirmed there were flowers within 100 m, strengthening the idea that abundance was affected more by local resources.

Nesting resources around the trap nests affected abundance. The most straight-forward hypothesis is that areas poor in nesting resources have lower population densities and affect abundance negatively. We found the opposite: the number of cells increased with decreasing *abundant nesting resources* (fig. 7.3.b), probably due to a concentration effect. Bees are observed in high concentrations on flower patches in flower-poor areas (Veddeler et al. 2006, Williams and Osborne 2009). A similar inversely proportional relationship between observed bees and availability of bloom is becoming clear for flower-mimicking coloured pan traps (Cane et al. 2000, McIntyre and Hostetler 2001, Russell et al. 2005, Roulston et al. 2007). Our results suggest that the same concentration effect applies to trap nests placed in nesting-resource-poor areas. We also found indication for an accumulation effect: a trap nest discovered sooner allows for more cells to be built and more bee individuals to use it ($p < 0.001$, table 7.2, model E). Nest-site rather than flower availability is probably limiting *O. bicornis* in German cities as well as in the German agricultural landscape (Steffan-Dewenter and Schiele 2008).

Landscape features explained little compared to microsite attributes and none of the structural metrics had a significant influence. Our food estimation and scale of assessment were rather rough, leading to a sub-optimal resource definition for *O. bicornis*. Although the rules for land-use classification were quite specific for *O. bicornis*, we did not have detailed floral resource descriptions. Allotment areas also could have been dominated by lawns instead of abundant flowers and for exotic mass blooming shrubs such as *Forsythia x intermedia* we knew neither location nor suitability for *O. bicornis*. In some environments *O. bicornis* uses large amounts of oak (*Quercus robur*) pollen (Raw 1974), whereas we focused more on *Ranunculaceae* and *Rosaceae* as well as dandelion-rich parks as preferred urban foraging resource (Tommasi et al. 2004). Despite these concerns we think that a resource-based land-use classification is a meaningful approach. Too many land-use classes lead to zero-inflated variables when it comes to land cover around the trap nest. In a preliminary analysis, 52 urban land-cover classes were used instead of habitat suitability and none of these single classes affected *O. bicornis* significantly. As an improvement for the current method we recommend the validation of foraging habitat classification by the analysis of bee-collected pollen in the studied region. Pollen sources can then be better quantified by specific plant surveys.

7.3.2. Importance of microsite attributes

Fully sun-exposed trap nest had a higher probability of being occupied than shaded trap nests. The preference of sun exposed sites is known for many solitary bees (Osborne et al. 1991, Tscharntke and Brandl 2004) and now clearly shown experimentally (fig. 7.2.b). Sun exposure reduces the thermal constraints of bees (Willmer and Stone 2004) and may be an important criterion for nest-site selection. *O. bicornis* has a higher warm-up rate than expected (based on body mass) as adaptation to the cooler temperatures in early spring (Stone and Willmer 1989). Sun exposure may therefore be more important for *O. bicornis* than for other solitary bees, explaining the strength of this microsite attribute for the probability of trap-nest occupancy.

The importance of the object of attachment for both the probability of trap-nest occupancy and the number of cells indicates a strong preference of *O. bicornis* for certain objects. Although a preference for a micro-habitat makes sense, we can only speculate about the mechanisms that make carports, shed walls and balconies more attractive than trees or shrubs (fig. 7.2.a). Dead wood (found in carports and shed walls) may resemble natural nest sites of *O. bicornis*. The closely related mason bee *Osmia cornuta* also prefers dead wood for nesting (Bosch 1995), but dead wood alone does not guarantee a high occupancy (Gaston et al. 2005). Balconies may represent an attractive habitat where searching for nesting places is profitable. Solitary bees can find many nesting cavities at balconies such as in reed mats, chairs, flower pots and nail holes. *O. bicornis* may even nest in key holes and a folded table-cloth (Linsley 1958, Flügel 2005). It is remarkable that trap nests at the location *house* (mainly balconies) had a much higher probability of occupancy than in *backyard or park* (fig. 7.4.a), although balconies hang in Leipzig just above backyards. Microsite characteristics seem to be more important than adjacent foraging resources. Trap nests in trees and shrubs are naturally shaded by the canopy, which may explain the low occupancy. Trees (subset *tree or shrub*, n = 98) had less fully sunlit trap nests than overall (8% compared to 16%), but there was no significant interaction between *object of attachment* and *sun exposure*. Trap nests in *tree or shrub* in *backyard or park* had a lower probability of occupancy than those in *garden or allotment* (fig. 7.4.a). The young and healthy trees common to urban areas (opposed to old and dead trees with cavities) may explain the negative effect of attachment to a tree *per se*. Another experiment with *O. bicornis* also showed a low acceptance (3.4% to 35%) for trap nests hung in trees (Free and Williams 1970). This is not the case when trap nests are hung in commercial orchard trees (Bosch 1992, Steffan-Dewenter and Schiele 2008). An explanation is that bees have no alternative nesting sites in orchards leading to a stronger concentration effect of bees than in urban areas (marginally present, fig. 7.3.b).

In order to find better explanations for the strong differences at the level of *object of attachment*, we thought of several other factors influencing trap-nest attractiveness, distributed a second questionnaire and analyzed received photographs. We asked about *visibility* of the trap nest (from all directions, from most directions, from few directions, almost covered), *exposure to rain* (yes/no), *tree type* according to foraging resource availability (apple or pear, other *Rosacea*, other tree) and *height within the tree* (below 2m or higher). We tested these new explaining factors for trap nests in *tree or shrub* (largest class, n = 98) but none of these had a significant effect on the probability of trap-nest occupancy or number of cells. For trap nests on balconies (second largest class), we used height (*floor*) from the first questionnaire to see whether it requires more energy investment. *O. bicornis* was more or less equally distributed over different floors both in presence and abundance (*floor* had no effect) which may not be surprising since even smaller solitary bees can overcome a height difference of 130 meters (Zurbuchen et al. 2010a). Other suggestions include that cavity-nesting bees use scent (dead wood) rather than vision for nest-site selection, or that they may avoid nests with birds in their vicinities.

7.3.3. Citizen science with trap nests

Our study provides a good example of volunteers (the 239 participants that returned their trap-nest and questionnaire) collecting a considerable amount of ecological data and encourages the use of the citizen-science approach for future ecological research. This approach gave us valuable information about the ecology of *O. bicornis* that we could not retrieve from coarse-scale land-use data. The citizen-science approach has its limits, too. Conversations taught us that people were often unable to reliably identify the occupancy status of a nest by *O. bicornis* and assessing response variables must be quality-checked by researchers. Only few participants were able to identify more than the plant species on their own balcony. As a consequence, we had to lump plant species into very large and vague groups (*meadow flowers*, *ornamental flowers*), which proofed not useful for explaining bee habitat preferences. Among the participants the higher educated people (and therewith some of the parameters) may have been overrepresented (campaigned at a scientific institute) although many volunteers of the supporting staff (from secretaries to construction workers) participated and we sampled a high diversity of housing types and hang locations and covered most areas of Leipzig.

The information requests afterwards demonstrated that the collaboration with volunteers was fruitful for raising public awareness of wild bees. The participants were afterwards notably better informed about the biology of wild bees, their endangerment and the importance of pollination. Overall, we think this approach was efficient and, through the high level of standardization of nests and questionnaires, scientifically rewarding.

Trap nests are a widely used and valuable research tool but our results suggest that increased standardization can benefit the clarity of results. The dominant impact of *object of attachment* and *sun exposure* resulted in a spatial pattern with occupied trap nests nearby unused ones (fig. 7.1), which complicates disentanglement of local presence of an *O. bicornis* population and nest-site attractiveness. Attaching trap nests to wooden poles as proposed by Westphal et al. (2008) and placing them at sun-exposed sites would be the best way of standardizing trap-nests' sampling effort. Trap-unit factors concerning the tubes (such as the *proportion of tubes with an internode*) can be valuable as correction factor.

7.3.4. Implications for conservation

O. bicornis was present in all city regions (fig. 7.1) and does not seem to be isolated or particularly negatively affected by urban landscape features. Microsite effects were stronger than resource effects at the landscape scale. In urban environments not only wild bees but also beetles (Niemela et al. 2002), grasshoppers (Strauss and Biedermann 2006) and birds (Evans et al. 2009) respond more to microsite attributes than to landscape level features or urbanization gradients. In cities there is enough habitat heterogeneity to allow some species to survive even in cities centers. Changes in cities can work out negatively on bees when urban waste land is reclaimed or buildings are renovated (Flügel 2005), which may be true especially in formerly socialist cities such as Leipzig (Saure 1996). Similar experiments as ours in other cities could give further hints to which specific features of cities are relevant for bees.

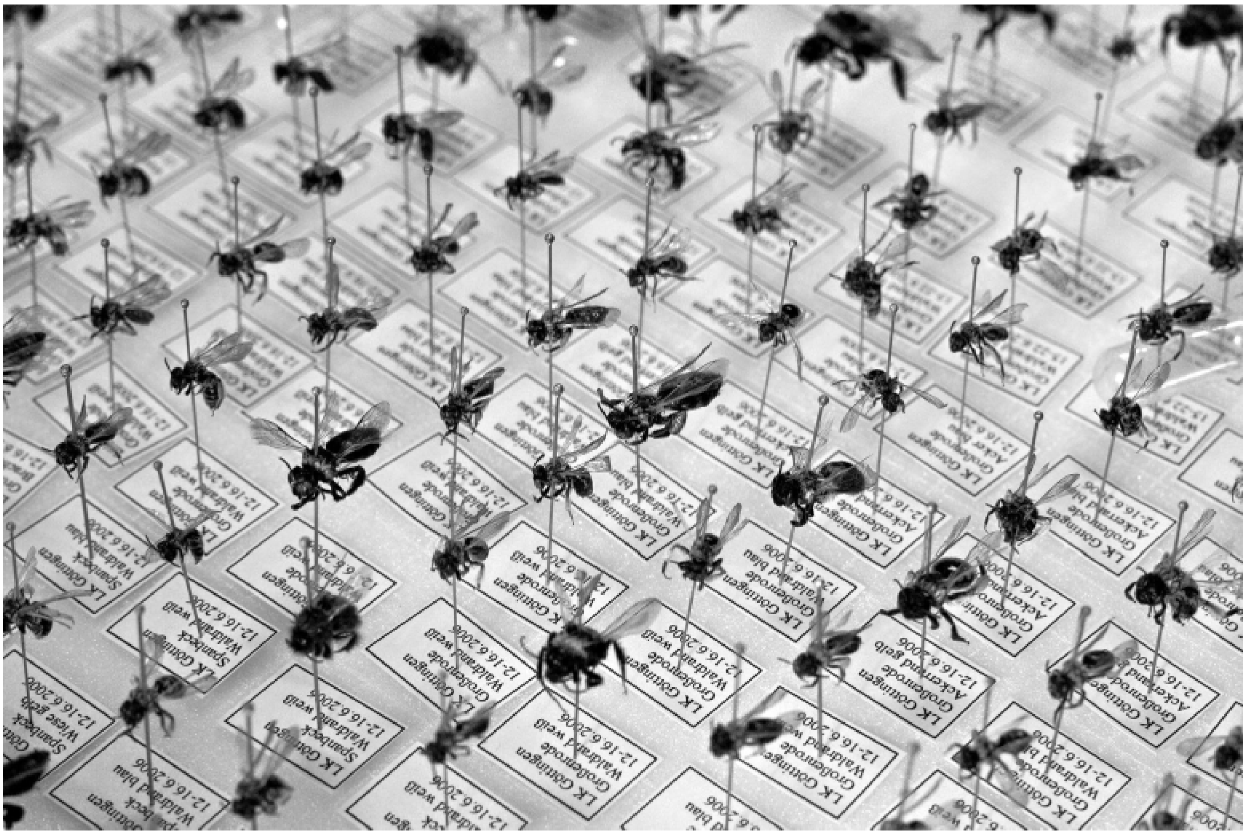
Wild bees can be promoted in cities in different ways. Planting flowers with abundant nectar and pollen and maintaining open, sun-exposed sites seems to be a universal result supported by other studies. In our study the amount of foraging resources, being present in substantial amounts, played only a marginal role in occupancy of trap nests. Therefore more attention could be given to microsite attributes such as sun exposure and ways to enhance nesting opportunities in cities, rather than to conservation and restoration of foraging resources alone. Bee communities can be supported by artificial nests at places where nesting conditions are poor. Some hang locations such as trees and parks are apparently inefficient, since bees such as *O. bicornis* will probably not use these places for nesting. Projects with wild bees can additionally help to raise public awareness of pollination issues and biodiversity conservation (Frankie et al. 2005, Matteson et al. 2008, Dearborn and Kark 2010).

7.3.5. Final conclusions

This study demonstrates the benefit that a citizen science approach can bring to descriptive science. It showed that *O. bicornis* is ubiquitous in the city of Leipzig and is positively affected by nearby urban foraging resources and sun exposed nesting sites. Microsite attributes clearly dominate nest-site selection by *O. bicornis* in urban areas. Artificial nests can promote reproduction in regions with poor nesting resources.

CHAPTER 8

Synthesis



Wild bees comprise over 500 species in Germany. They differ in many ways, including body size, nesting preference and sociality. They have in common that they require both nesting substrate and foraging resources. How do these different traits and common requirements affect their response to landscape structures?

8.1. Landscapes: resource availability for bees

8.1.1. Foraging and nesting resources

Solitary bees need two primary resources; foraging resources and nesting resources. These resources have complementary value and I have shown that both were involved in the way how bees respond to landscape structures. I found that nesting conditions (nesting preference) affected how a bee community (bees of one size) responds to foraging resource availability. Soil-nesting bees, which were allowed in the model to nest randomly in the vegetation (foraging habitat in the model) had a high availability of nest sites (fig. 5.2.B) and had a good access to local foraging resources. They hardly responded in their performance to *foraging habitat availability* (fig. 5.1, D-F). Cavity-nesting bees (wood-nesting bees in the model, nesting exclusively in field edges) showed a reduced performance compared to soil-nesting bees. They could build a lower number of brood cells for an increase in *foraging habitat availability* (fig. 5.1, A-C). The restriction to field edges reduced availability of nesting resources for wood-nesting bees (fig. 5.2.B). Note that I scaled the number of individuals to counterbalance a positive effect of the amount of foraging resources and bee size (smaller bees require less pollen and fewer flowers per bee). This revealed that the spatial restrictions of wood-nesting bees can lead to a performance reduction, even when the amount of foraging resources increases (which increases the number of bees that have to share nesting sites at field edges, fig. 5.2.C).

The case study (chapter 7) has shown that a cavity nesting solitary bee (*Osmia bicornis*) was negatively affected by the distance from *abundant foraging resources* (lower probability of trap-nest occupancy, fig. 7.2.C) and bees were increasingly using the artificial trap-nests when the proportion of *abundant nesting resources* within 500 meters was low (fig. 7.3.B). This confirmed that bees were affected by availability of both nest sites and foraging resources, not by one of both.

8.1.2. Fragmentation

I found that the effect of fragmentation was in general low compared to other variables both in the model and in the case study. Simulation experiment 2 and 4 (chapter 4) and the main simulation experiment (chapter 5) included variation of *landscape fragmentation*, which had a low explaining power and was overshadowed by much stronger parameters such as *body length*, *nesting preference* and *foraging habitat availability* (table 5.1). In the case study (chapter 7) the effect of landscape fragmentation proxies (*edge density*, *total edge length*, *mean patch fractal dimension*, *mean shape index*, *number of patches* and *mean patch size*) were too weak to be significant. While field studies may have too much noise in the data to investigate effect of weak non-significant parameters, it is the strength of a deterministic model (i.e. all input variables have a significant effect) that also small effects can be studied. I found that the effect of fragmentation differs for different bee types (see also section 8.2.2), confirming earlier research (Cane et al. 2006).

In the model the (low) effect of *landscape fragmentation* was positive, increasing the number of brood cells, attributable to enhanced edge structures. *Landscape fragmentation* increased nest habitat for wood-nesting bees (fig. 5.2.B, increased nest habitat as combined result of less foraging habitat and more fragmentation) and reduced the bee density at nest sites (fig. 5.2.C, increased density as combined result of more foraging habitat and less fragmentation). An increase in *foraging habitat availability* also implied a reduction of the amount of edge structures which was not regulated by *landscape fragmentation*. This may have weakened the effect of *landscape fragmentation* as additional parameter for generating edge structures.

During model design (chapter 3) I learned an aspect of the bee's behaviour that may be quite important for how solitary bees respond to fragmentation. I introduced a parameter *ignorance* that induced matrix crossing behaviour (see pattern oriented parameterization of the model behaviour, section 3.9). When I tried to parameterize with a realistic value (appendix B), I came to a value of 0.1 which means low matrix crossing behaviour. This parameter did not have a strong effect compared to other parameters (simulation experiment 3, chapter 4). However, this parameter was not often involved in foraging decisions by the model structure (chapter 3) and could hence not be systematically studied (without changing the model structure). Bees are flying insects for which classically matrix crossing abilities have always been considered important. my considerations based on the gathered knowledge suggest that this may not be the case.

This viewpoint finds support in the literature. Wild bees can be considered to live on islands of foraging habitat (Cane 2001), and crossing of the matrix without foraging resources may indeed be limited for wild bees (Rathcke and Jules 1993). Wild bees visit isolated fragments of foraging habitat significantly less than continuous habitat, even if the distance of isolation by a matrix is only several metres (Rusterholz and Baur 2010). Patches with a high availability of foraging resources prevent pollinators to forage elsewhere (Lander et al. 2011). When bees forage in high resource patches and mainly stay foraging in the local flower patches, factors such as the local bee density should have a high impact on foraging behaviour, as it was the case in the model (fig. 5.2.C). The model structure needs to be changed for studying effects of matrix crossing systematically. Matrix crossing behaviour could be an interesting focus for future field and modelling studies.

8.1.3. A combined measure: nesting resources relative to foraging resources

I found that the combination of nest habitat and foraging habitat in a single measure by calculating the relative availability of nest habitat to foraging habitat (their relative ratio) had practical advantages. This ratio reflects the requirements of bees in differently structured landscapes and differences in their nesting preference (habitat use). It could replace traditional measures such as *foraging habitat availability* and *landscape fragmentation* (chapter 5 and 6). Only *body length* remained as co-factor for explaining the responses (fig. 6.4). In a statistical sense it did not make much difference when one or multiple parameters explain a comparable amount of variation. However, in a practical sense it could be valuable to reduce three variables (*foraging habitat availability*, *landscape fragmentation* and *nesting preference*) to a single one. This novel landscape measure implies that soil-nesting and wood-nesting bees are on the same gradient of habitat use (fig. 5.2.D). The perspective that soil-nesting and wood-nesting bees respond fundamentally different to gradients of *foraging habitat availability* and *landscape fragmentation* (fig. 5.1) can therefore be considered premature. This illustrates that a change of perspective is essential for understanding how bees or other animals respond to different landscapes and for making differentiated conclusions.

The general observation that wild bee communities are mainly affected by foraging habitat availability (Pawlikowski 1989, Gathmann et al. 1994, Banaszak 2000, Calabuig 2000, Steffan-Dewenter et al. 2001, Steffan-Dewenter and Tscharntke 2001, Steffan-Dewenter 2002) is therefore incomplete. Bees need an appropriate ratio of nest habitat relative to foraging habitat. The hypothesis that solitary bees are most limited by nest sites (Gathmann et al. 1994, Gathmann and Tscharntke 2002, Potts and Elith 2006, Steffan-Dewenter and Schiele 2008) applies therefore only when foraging resources are abundant. The ratio of nest habitat to foraging habitat seems to be a very informative perspective for showing how wild bees interact with the landscape. As long as there are relatively enough nesting resources compared to foraging resources, solitary bees perform well.

To test the practical applicability of this ratio I tried to find in the case study a suitable proxy for the relative ratio of nest habitat to foraging habitat. I tested several different proxy ratios (mainly by improving the proxy for nest habitat availability with parameters such *edge length*) but found no significant effect. Note that I had no information about true foraging and nest habitat for bees, but only local estimates based on GIS-based biotope maps. Despite a lack of significance, the number of brood cells of *O. bicornis* seemed to increase with the ratio of the estimated nest habitat and estimated foraging habitat (fig. 8.1). The shape predicted by the model (fig. 8.1) was not obvious from the field data, but a trend in the same direction was apparent. Note here that it was quite a forced attempt with quite different methods for the model and the field study. The figure compared log-transformed brood cell numbers per trap nest from a six week foraging period with the daily performance of one bee in optimal model conditions. I performed a log-transformation to get an estimate for the performance per bee, since the up to 350 brood cells in the case study were partly so high due to accumulation effects (table 7.2, model E). It is relatively difficult to measure the daily performance of single bees in the field. Fitness measures such as the number of brood cells per trap nest are probably inappropriate to compare with simulation results.

There are opportunities to improve field studies. I used a very rough estimation of nesting resources in the case study and they could definitely be more fine-scaled. Ground truthing of nesting and foraging resources is likely to yield a more reliable and realistic measure of their availability and their ratio in the field (e.g. Williams and Kremen 2007, Knight et al. 2009). In addition, the model needs to be further explored. I used in the model only two types of foraging habitat (foraging and non-foraging habitat), while in the case study patches classified as "abundant foraging resources" contained many different flower densities. Including patches with different flower densities in the model may yield a different theoretical relationship than presented in fig. 8.1. Further, it remains to be investigated how the effect of this ratio (e.g. threshold value for foraging habitat visitation) is affected by other parameters (other than different vegetation, fig. 6.5.B).

This exercise additionally showed that it was better to use multiple landscape factors in field experiments rather than the ratio of nest habitat to foraging habitat as a replacement proxy. As many parameters as possible should always be measured or estimated and a ratio can eventually be calculated afterwards. I still think this ratio has potential for identifying patterns that remain unseen otherwise. It is e.g. tempting to consider field data unusable when an unexpected negative effect of foraging habitat availability appears. I showed with the model that such results can be explained and that such field data should not be discarded.

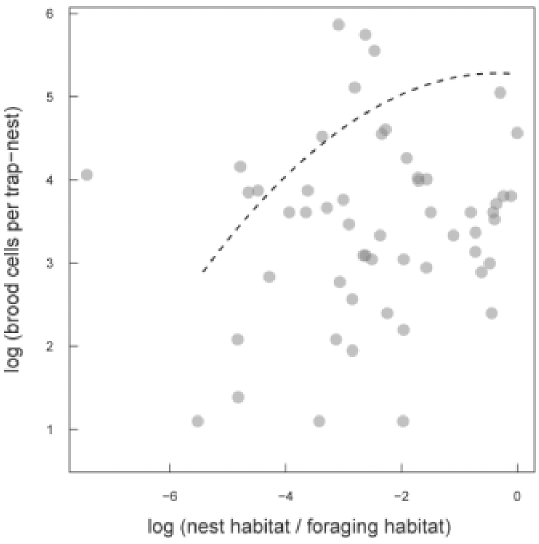


Figure 8.1. Model result and field data combined in one plot, both having a similar response (brood cells) to a similar landscape parameter (ratio of nest habitat to foraging habitat). Points represent log-transformed number of brood cells per trap-nest for the intermediate sized bee *Osmia bicornis* from the case study presented in chapter 7 (only cases with foraging habitat availability equal or higher than nest habitat availability). Correlation is not significant ($p = 0.27$). The dashed line represents the number of brood cells built per bee per day for an intermediate sized bee from the simulation model (chapter 5, fig. 5.2.D). Their comparability is discussed in the main text of this chapter.

8.1.4. Pollination services

I decided to quantify pollination services with a model from the perspective of the bee by the number of flower visits per bee and the mean distance flown per bee. Both responses showed large differences between bee types and over the gradient of *foraging habitat availability* and *landscape fragmentation* (figs. 6.1 and 6.3). The effect of *landscape fragmentation* on these pollination measures was weak, while the effect of *foraging habitat availability* was prominent. An increase in *foraging habitat availability* resulted for wood-nesting bees in slightly more flower visits (fig. 6.1) and larger mean flight distances (fig. 6.3). Further, I used the model to quantify pollination services at the landscape level with the percentage of the habitat a bee population visits in response to *foraging habitat availability* and *landscape fragmentation*. An increase in *foraging habitat availability* resulted in a much lower percentage of the total vegetation visited by bees, while *landscape fragmentation* slightly increased visitation of the foraging habitat (fig. 6.2).

The ratio of nest habitat to foraging habitat could successfully replace the effect of *foraging habitat availability*, *landscape fragmentation* and *nesting preference* as explaining variable for these three pollination proxies (fig. 6.4). This ratio was a more informative landscape measure to describe how a community of wild bees interacts with the landscape (fig. 6.4.B) than the effect of *foraging habitat availability* and *landscape fragmentation* (figs. 6.1 and 6.2) alone. Foraging habitat visitation increased with this ratio almost independent from *body length* (fig. 6.4.B), which makes it in my opinion the most robust model proxy for pollination.

Oppositely to foraging habitat visitation, the mean distance that bees fly strongly decreased with the ratio of nest habitat to foraging habitat (fig. 6.4.C). Flown distances were lower for small bees than for large bees, but this did hardly affect the percentage of foraging habitat that was visited (fig. 6.4.B). In landscapes with the highest coverage of pollination (highest ratio of nest habitat to foraging habitat), pollen was thus on average transported least far. This result highlights, that one kind of pollination service (high transportation distance) can be quite different from another one (all plants pollinated).

8.1.5. Local conditions

Bees operate at small scales. my research confirmed this in several ways. The case study showed a strong effect of microsite conditions. Local nest site conditions that were captured in the factors *object of attachment* and *hang location*, had the strongest effect on the probability of trap-nest occupancy and the number of brood cells per trap nest, followed by *sun exposure* of the nest (table 7.2), another microsite condition. The model showed small-scale effects in various ways. The majority of foraging trips were below 100 m (fig. 6.4.C). The ratio of nest habitat to foraging habitat increases by increasing edges containing nest habitat and thus also with a reduction in field size, increasing the number of brood cells. Local bee density (fig. 5.2.C) and vegetation parameters (chapter 4, simulation experiment 2 and 4), operating on more local levels rather than on the landscape level, negatively affected the number of brood cells. They additionally caused significant parameter interactions in the model (appendix C, fig. C.1.1). The model did not consider the variability of microsite conditions that appeared to be so important in the case study (such as sun exposure), but provided additional insights with other local effects that bees face.

The fact that solitary bees operate at small scales and need small-scale nest-site availability and optimal nest conditions has consequences for further research. Landscape scale studies with solitary bees should include small scale features such as nest sites and specific food availability. Question such as: "is the soil suitable to nest", "is there enough dead wood for cavity-nesting bees?" and "which flowers grow between the wheat and how dense?" should be answered by ground truthing (surveys at the site), since land-use maps provide limited information. Also sun exposure is an important local parameter that should be estimated.

Despite that local details enhance the understanding of how bees interact with the landscape, landscape-level parameters are still valuable for understanding patterns. The comparably weak effect of *landscape fragmentation* in the model (chapter 4, simulation experiment 2 and 4, table 5.1 and appendix C, tables C.1.1 and C.1.4), did still yield a clear positive effect on solitary bees (figure 5.1). The case study showed that even the very rough estimation of foraging resources and of nesting resources both had a significant effect (figs. 7.2.C and 7.3.B), although their effects were low compared to local parameters (table 7.4). In essence, parameters measured at different scales, represent different perspectives on the bee's true needs.

8.1.6. Consequences for bees and pollination services

The model shows that bees visit the foraging habitat almost completely when the ratio of nest habitat to foraging habitat rises above 0.2, almost independent from *body length* (fig. 6.5). It also means that human disturbance reducing this ratio, reduces pollination services. The ratio is reduced when nest habitat is destructed. With the assumption that food is present during the short lifetime of solitary bees, the removal or poisoning of nest habitats heavily affect this ratio and thus pollination services. In nature reserves (with semi-natural meadows) wood-nesting bees profit from woody structures to nest in and soil-nesting bees from open bare spots in the vegetation, as I have modelled it.

In addition, the findings are likely to apply to agricultural landscapes without meadows as well, since the effect of nest habitat to foraging habitat ratio on foraging habitat visitation did hardly change with vegetation type (fig. 6.5). In agricultural landscapes all bees (wood nesting and soil nesting) mainly profit from woody structures at field edges, since soil-nesting bees do not nest in agricultural fields. The finding that 25% of the landscape should remain refugee area to ensure the sustainability of a diverse bee fauna (Banaszak 2000) is in the same order of magnitude of my finding that 20% of the area (when a flowering crop is considered as foraging habitat) should be suitable nest habitat for bees to maximize reproduction (number of brood cells, fig. 5.2.D) and ensure the full potential of the flowering crop for the bee population (fig. 6.5). I expect that my results from bees foraging on meadows have a fair overlap with bees foraging on crops. In summary, this would mean that in fields that are too large (results suggest 1 ha and larger), the ratio nest habitat to foraging habitat falls below 0.2 and reduces the bee's foraging performance and pollination services.

The best way to improve pollination services to crops is thus by offering more nest habitat, since foraging resources are plentiful. One way to realise this is to protect woody and semi-natural field strips. When natural structures with nest sites fall short, nest sites can be provided artificially. There are many examples where solitary cavity-nesting bees are employed as crop pollinators, by offering artificial nests (e.g.Gruber et al. 2011, Pitts-Singer and Cane 2011). In addition, I know of one soil-nesting species (*Nomia melanderi*) that is managed as crop pollinator for which nesting beds in the soil are offered (Stephen 1960, Cane 2008). In such management practices where nest sites are managed, the right ratio of nests to foraging resources is crucial for flower visiting activity (e.g. number of released bees in proportion to crop area, see Pitts-Singer and Bosch 2010).

Additional modelling can be required to transfer the findings to specific crops. I have learned that specific conditions such as flower density and bee density can influence the modelled results. Mass flowering crops such as apples and cherries, which are pollinated by intermediate-sized cavity-nesting bees (Bilinski and Teper 2004, Gruber et al. 2011) may have a good balance between flower density and bee density. However, a crop such as oilseed rape has certainly not. I know that this crop has a much higher flower density than I modelled so far: around 11,200 flowers per m^3 (Kołtowski 2005). Wild bees clearly forage on oilseed rape but their densities remain low especially on large fields (Holzschuh et al. 2011). Further, most wild bees forage for nectar only on oilseed rape (Ali et al. 2011) possibly to refuel themselves and collect pollen somewhere else afterwards. It remains to be investigated whether wild bees collect nectar and pollen on oilseed rape for provisioning their offspring. This example shows that my model, parameterised for a meadow with bees in natural densities and foraging for pollen, may fail to cover all situations without using different parameter values and adjusted foraging rules.

Our case study suggests that human disturbance had a limited effect on wild bees in the urban area of Leipzig. There were always foraging resources within the foraging range of the bees and fragmentation proxies did not have a significant effect on their presence and brood cell number. I cannot conclude much about nest habitat limitations because I provided artificial nests. I found a positive response effect (high abundance in the trap nest) in urban regions with few nesting resources, hinting indirectly to nest-site limitations. Also an increase in distance to *abundant foraging resources* reduced the probability of trap-nest occupancy (fig. 7.2.C). This means that at the city scale nest habitat and foraging habitat were sufficiently available, but that at a smaller scales both resources were not optimally distributed. Especially a sufficient ratio of nest habitat to foraging habitat is essential for bees (fig. 8.1). Both nesting and foraging resources can be promoted at the small scale by bee-friendly management of urban area. Leipzig is a rapidly changing city that may degrade in its value for wild bees, since the many vacant buildings with undisturbed nesting sites are successively broken down and urban brown sites with flowering herbs are reclaimed for building. In the rapid changes lies also the opportunity to make Leipzig a bee friendly city. The results indicated that especially parks and backyards need improvement (fig. 7.3). Park management can be improved by shifting priorities towards offering dead wood, debris piles and unmanaged stone walls as nesting sites for bees instead of cleanliness. Private gardens and backyards could offer more pollen and nectar producing flowers and artificial nests to support wild bees, which can both be promoted by stimulating public awareness for solitary bees (Koster 2000). In this way, the city may become a better place for bees than the surrounding agriculturally dominated landscape that is often very hostile to bees (Kearns et al. 1998, Cane and Tepedino 2001).

8.2. Body size, nesting guild and solitary life style

8.2.1. Body size

Body size highly affects foraging behaviour of solitary bees, but not always as expected. In chapter 2, I reviewed the effect of body size (body length) on traits such as eye size, velocity, pollen transport capacity and flower handling time and showed that body size highly affected these traits (figs. 2.2 to 2.7), inevitably affecting most levels of foraging behaviour. I incorporated *body length* and *nesting preference* in the model as two bee traits that affect foraging behaviour. *Body length* and *nesting preference* had a stronger effect than landscape configuration (*landscape fragmentation*) and landscape composition (*foraging habitat availability*) in the model (figs. 5.1., 6.1 and 6.2). *Body length* had also a stronger effect on the investigated response variables than *nesting preference* (fig. 8.2). Only foraging habitat visitation by a bee population seemed to be hardly affected by *body length* (fig. 8.2.C). However, foraging habitat visitation did slightly increase with *body length* when the bees nest in field edges (wood-nesting bees) and had to cover larger distances (fig. 8.2.C).

I found that small bees can contribute to pollination at least as much as large bees (chapter 6). Under the simulated conditions the advantages of being large did clearly not compensate enough for the disadvantages. The better dispersal capacities of large bees did not benefit them in daily pollen foraging, leading to fewer brood cells (chapter 5). Bee traits related to dispersal ability (*return distance, velocity high*) appeared to be less important as those affecting local efficiency (*velocity medium, pollen capacity per bee, handling time per flower*, see simulation experiment 3 in chapter 4). Hence, small bees performed better than expected. I therefore agree with the presumption that small bees in small patches can in general maintain viable populations because small bees require less pollen and nectar (e.g. Cane et al. 2006) and thus need fewer flowers (figs. 6.4.A and 8.2.B).

The number of brood cells per bee for soil-nesting bees (fig. 8.2.A) and the mean distance from the nest for wood-nesting bees (fig. 8.2.B) scaled (almost) linearly with *body length*. The other responses did not (fig. 8.2). The performance of the bees was composed of multiple behavioural traits (chapter 2 and 3) which had different scaling relationships with *body length*. These traits, such as *velocity* and *handling time per flower*, affected time budgets in varying situations differently and therefore affected the response variable accordingly (simulation experiment 3 in chapter 3, and table C.1.2. in appendix C). These body-size related traits also led to shape variation for the different model responses in response to *body length* and a clear difference for bees with a different *nesting preference* (fig. 8.2). These traits and their effect on time budgets caused complex responses to body size variation.

The multiple traits related to body size had a clear ranking in their effect on brood cells (simulation experiment 3, chapter 4). *Handling time per flower* caused the largest change (high elasticity) in brood cells, followed by *pollen capacity per bee*. Hence, they are important in time allocation. These traits may have affected time allocation of large bees in a different way than small bees; otherwise they would have built the same amount of brood cells in the same amount of time (chapter 5). Open questions remain when or how much *handling time per flower* and *pollen capacity per bee* cancel each other out (see figs. 2.6 and 2.7), or whether bees require more time for flying than for pollen collecting. Additional simulation experiments would be useful for a better understanding of how body size affects different foraging tasks.

Body length interacted in the model with other parameters. The difference in number of brood cells between bees of different size decreased with larger flowers (i.e. with larger amount of *pollen per flower*, simulation experiment 2 in chapter 4). For small flowers, large bees needed to fly between many flowers in order to collect enough pollen. Larger flowers can thus optimize time budgets for large bees. Spatial effects of flower encountering also worked out differently for bees of different size. Since the number of bees in the landscape was linked to body size, large bees that occurred in low densities did only rarely encounter an empty flower, while small bees in high densities quickly depleted the flowers around the nest and often encountered empty flowers inducing increased flower visits. Small and intermediate sized bees visit more flowers in "bad" landscapes (low nest habitat to foraging habitat ratio), while this effect is absent or even opposite for large bees (fig. 6.5.A). This also means that large bees are less sensitive (moderate decrease in brood cells) to bee density than the other bees (fig. 5.2.C). As a consequence the effect of *landscape fragmentation* was weaker for large bees (fig. 5.1.C). It is an important finding that large bees and small bees interact in a different way with the landscape and is worth further exploration.

8.2.2. Nesting guild

I compared soil-nesting and wood-nesting bees. In all my simulation experiments I found a difference in their response (chapter 4, 5, 6 and fig. 8.2). However, I also found that they probably do not interact very differently with the landscape in terms of access to foraging resources. The surrogate variable ratio of nest habitat to foraging habitat (low ratio, low access) gives a clear picture (figs. 5.2 and 6.5). Soil-nesting bees had their nests in the soil evenly distributed over the meadow and therefore had a high availability of nest habitat (fig. 5.2.C) and a high ratio of nest habitat to foraging habitat (fig. 5.2.D). As a consequence, they faced little local competition and had short flight distances (fig. 5.2.A) and were always able to build more brood cells than bees of the same size that nest in the field edges (figs. 5.1 and 5.2). This means for pollination that soil-nesting bees easily cover the entire foraging habitat, while wood-nesting bees do not (fig. 8.2.C, but see gradients in fig. 6.2, A-C). The nesting guild does hardly affect the number of flowers visited during a day (fig. 8.2.B), but does affect the distance flown (fig. 8.2.D) and the number of brood cells (fig. 8.2.A).

In meadows where soil-nesting bees are not limited to nest in field edges, they hardly respond to *landscape fragmentation* (figs. 5.1, 6.1, 6.2 and 6.3). In studies with natural habitat elements, one could expect such different responses to fragmentation between soil- and wood-nesting bees (see for an example Cane et al. 2006). However, when soil-nesting bees would occupy field borders only for nesting (as wood-nesting do), bees of both nesting guilds would respond similarly. When soil-nesting bees are limited to field edges they must fly farther distances from the nest and face more local competition with bees around the nest. This is likely for crop fields. The soil disturbance in crop fields is assumed to be so high that soil-nesting bees do not survive in crop fields (Osborne et al. 1991, Banaszak 1996, Calabuig 2000) and are thus restricted to field borders. Nevertheless, there are reports that soil-nesting bees were nesting in crop fields (Minckley et al. 1994, Tanács and Benedek 2010) and nests may partly be spared by the mechanical soil disturbance since they are more than ten cm below ground for most species and for some species even more than half a metre (Cane 1991). Whether solitary bees nest also in crop fields or only in field edges, would have clear consequences for crop pollination (figs. 6.2 and 8.2.C) and remains to be investigated. A subsequent question would then be whether soil- and wood-nesting bees occur in comparable densities in field edges.

8.2.3. Solitary versus eusocial bees

The question whether large eusocial bees such as bumblebees, would respond similar in my model compared to large solitary bees cannot be answered directly. Some solitary bees can facultatively behave eusocial and build colonies. It is known from a comparison between social and solitary groups of *Xylocopa virginica* (a large bee than can facultatively live eusocial) that under similar conditions the number of brood cells they built was not significantly different and the eusocial groups were not more efficient (Richards 2011). From this perspective, some of my results for large solitary bees may apply to large eusocial wild bees. Some of my results may even apply to other pollinator groups. In a landscape level habitat study, species richness of bees and butterflies were correlated and determined by shared factors (Franzén and Nilsson 2008). However, to what extent my results are applicable to other pollinators such as butterflies and hoverflies cannot be answered with my simulation model. Differences in behaviour such as nectar vs. pollen foraging, matrix crossing behaviour and optimized foraging behaviour remain to be investigated with additional foraging rules.

In my literature review (chapter 2) I found clear trait differences for solitary and eusocial species of similar size. The body-size related traits of eusocial species clearly deviated from the expected value for their body size, such as for *homing distance* (fig. 2.4) and *flower handling time* (fig. 2.7). In the model, the *general return distance* (based on homing distance) did hardly affect the number of brood cells, while handling time was found to have a moderate elasticity (simulation experiment 3, chapter 4). Therefore, differences in body-size related traits for eusocial species may have a clear effect on the investigated time budgets and performance. The differences in behaviour between eusocial and solitary bees (chapter 1) such as a difference in pollen and nectar foraging, but also in time-budget distribution for other tasks than modelled, make a direct comparison with the model result for similarly sized eusocial bees difficult. Therefore, I can only conclude that solitary bees have a meaningful value as providers of pollination services rather than answering whether or when they provide better pollination services than eusocial bees.

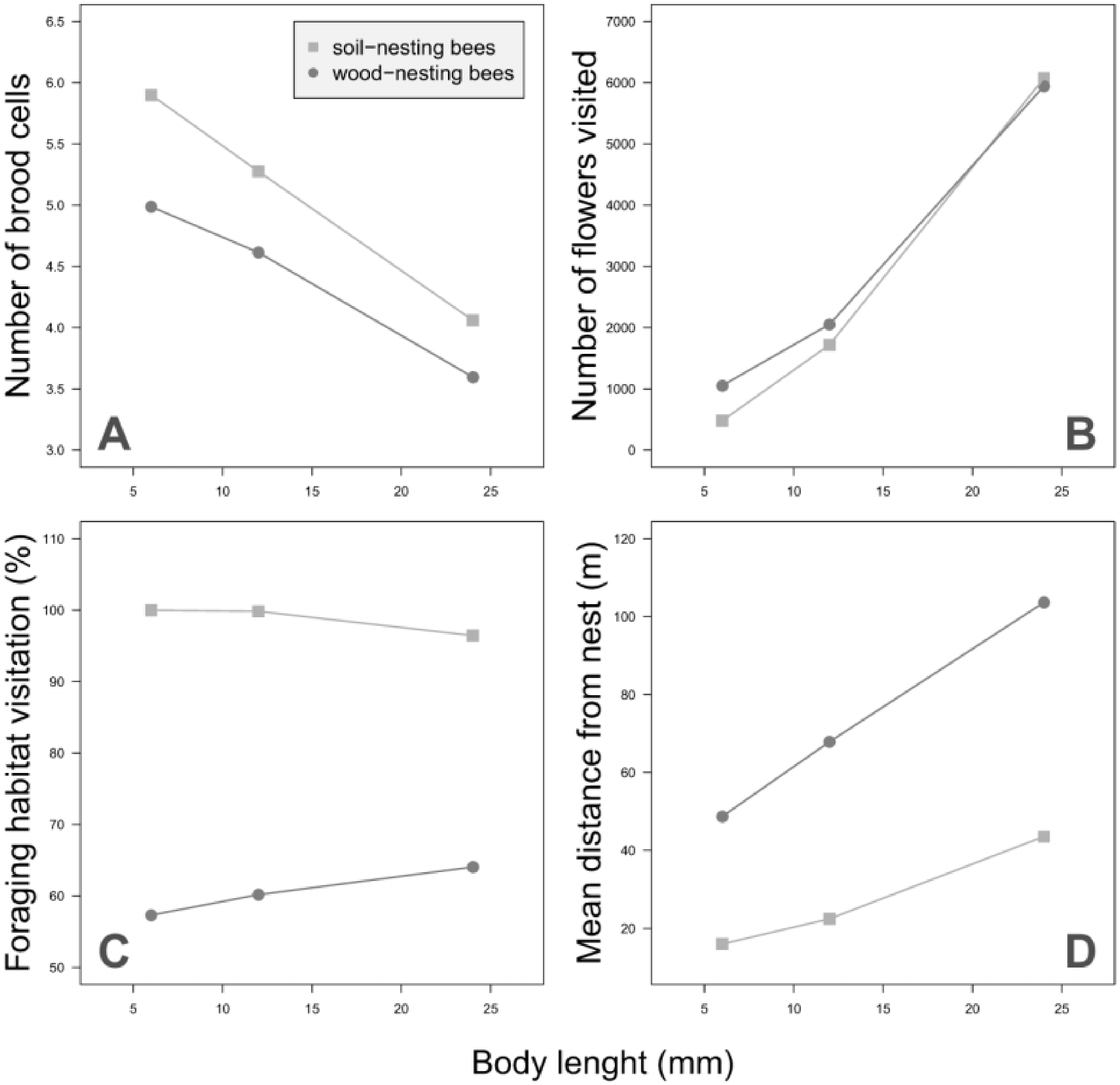


Figure 8.2. Effect of body size on the four different response variable analysed with the model, for soil- and wood-nesting bees separately. A: number of brood cells; B: number of flowers visited; C: foraging habitat visitation; D: mean distance from the nest. Values within each plot correspond with the mean value of each of the six panels presented in figs. 5.1., 6.1., 6.2 and 6.3 for plot A, B, C and D respectively.

8.3. Strengths and shortcomings of the modelling approach

8.3.1. Achievements

The decision to simulate pollen-foraging bees with a spatially-explicit individual-based model appeared to be valuable in several ways. The main strength of the model lies in the fact that it is mechanistic. A model with all essential processes and mechanisms controllable with parameters enables investigation of each parameter independently. In ecology, such models can be especially valuable, since it can rule out variance present in field experiments. In ecological field experiments it is often impossible to regulate or measure all environmental conditions. I know e.g. of no field study with wild bees that assessed different flower densities at the landscape scale (in a one by one kilometre or larger area) as covariate to explain the performance of bees. Flower densities appeared to have a strong effect in the model and improved our understanding of how bees are affected by landscape composition. The model also enabled me to study the influence of a parameter with a weak effect: landscape fragmentation. The finding that this parameter was weak in the model, explained why the effect of fragmentation in field studies is often found to be weak. Additionally, the detailed study of this parameter with a model gave the insight that fragmentation can affect different bee types (nesting preference, body length) differently and explains why fragmentation in field studies sometimes gives confusing or opposite results.

Another advantage of my model is that it has a high level of realism. All of the parameters can potentially be measured and none of the parameters has an abstract description. I therefore think that the model is usable for many applications. The model response is also very direct. It registers the direct performance of the bee in amount of pollen that can be collected in a certain amount of time, which is a relative novel approach for the ecology of bees. Most studies at the landscape scale deal with aggregated responses such as species numbers and individual numbers, while the model can study the potential offspring (brood cells) for a certain bee species in a certain landscape. Although it may be hard to assess exact values in the field for all parameters, they can be roughly estimated. Landscape parameters can be assessed from land use maps validated by field surveys and be completed with estimated flower densities for each land-use class. A more difficult measurable parameter such as pollen production per flower could be approximated by flower size. The bee's body length can be measured in the field as well and serve as proxy for behavioural foraging traits. Measuring such values in the field and use them as input for the model to simulate specific situations has a high potential for understanding observed patterns in the field.

8.3.2. Current limitations of the model

I experienced also some difficulties with my approach. More parameters give more sources of uncertainty. The review in chapter 2 revealed that most of the scaling relationships with body size are not well investigated and even after review not completely clear and evident. Especially trait estimations for very large or very small bees still have some uncertainty. I did test with my model which consequences it would have when each of the traits would be 10% higher or lower than estimated by the scaling relationship (simulation experiment 3, chapter 4) and found that a change in flower handling time was affecting the model responses most. However, I did not test which consequences altered scaling relations would have (i.e. possibly larger deviations than 10% for small or large bees). In addition to this, I ignored scaling relationships that plausibly could exist but have not been shown so far for bees or similar insects. In my model I did not scale *time at the nest* and the perceived *grain size* with body size. A body-size related preference for a certain flower size (*pollen per flower*) would even require additional foraging rules. I also assumed a body size independent time budget for pollen foraging (*flytime*). This problem can only be solved with more fundamental and descriptive ecological research on known and unknown body-size related traits.

Apart from the scaling relationships, the model uses other poorly investigated bee-related parameters (table 3.1). I have put a high effort in reducing these parameter uncertainties by extensive literature review (appendix B), effect exploration (simulation experiment 1, chapter 4) and sensitivity analysis (simulation experiment 2 and 3, chapter 4). I showed that the model produces realistic output for multiple model responses (table 4.2). However, the complexity of the model may not be in balance with the amount of data that was used for validation. The difficulty with validation data for this model is that up to date no complete set of environmental parameters is available; most experimental studies have only a fraction of the parameters measured than were used as input for the model. It was already difficult to link the number of build brood cells per day to body size, since most studies give the number of brood cells per trap-nest (undefined number of individuals) or per lifetime (undefined number of days). Although other important parameters such as flower density, plant species (pollen per flower) and activity time of the bee could be measured, no single study at the landscape level did so far. In the field it is difficult to e.g. accurately measure the local bee density in the environment. This problem is further illustrated by the finding that current trapping methods were strongly biased by attraction effects which altered bee numbers found (chapter 7). A solution is to use active sampling methods such as sweep-net transects and direct flower-visitor observations. I think that there is a good potential for further model validation, but that possibilities are restricted by financial resources due to the labour intensive nature of parameter assessment in the field.

The model design also involved many assumptions; some based on observations, some made for simplifying reasons. Examples include the assumption that: small and large bees use the same proportion of their flower visiting time for pollen collection; male and female cells are built in equal ratio (mean number of trips required per cell was applied as fixed value); bees choose to nest near their foraging resource. The latter assumption especially deserves attention, because the enhanced densities of bees on foraging resources near the nest did strongly affect the results. The case study confirmed that most bees prefer to nest in trap-nests that were close to abundant foraging resources (fig. 7.3.C). However, I have no information about which species in which situation would not nest near the foraging resource and what the consequences in the model results would be. This could be simulated in a future simulation experiment. Another consequence of my model design is that I simulated only at one scale (1 km^2). At larger scales, the foraging and nesting resources could be more spatially clumped and affect the findings. At very large scales the landscape-level ratio of nest habitat to foraging habitat may lose its value when the landscape extent exceeds maximum foraging ranges. It was not possible to explore the consequences of all these assumptions, but they could be a starting point for future work.

The number of bees in a certain landscape was calculated with the parameters *foraging habitat availability*, *flower density*, *pollen per flower*, *body length* and *landscape quality*, assuming that the bee community is in balance with the amount of foraging resources and relates to body size. A higher local bee density caused a decline in brood cells and qualitative differences between large and small bees (fig. 5.2.C). It helped explaining why wood-nesting bees responded negatively to increased *foraging habitat availability* and positively to *landscape fragmentation*. I calculated bee density independent from nesting preference so that I could compare soil- and wood-nesting bees in a fair way. However, in natural bee communities soil-nesting bees often nest in high densities while wood-nesting bees nest in lower densities (Cane 1991). As a consequence, there are often more soil-nesting bees on a meadow than wood-nesting bees (88-100% of a bee community was found to be soil-nesting on different fallow types, Steffan-Dewenter and Tscharntke 2001). A reason could be that the number of bees not only scales with foraging resources but also with nesting resources. A lower density of wood-nesting bees in the landscape would partly correct for the high local competition that they face in the model. Also the assumption that the number of bees would increase unlimited with the amount of foraging resources may be unrealistic. In natural systems the number of individuals saturates with increasing amount of natural habitat (Banaszak 2000). A better understanding of natural bees densities and the factors they are affected by, would benefit the realism of my model.

It is clear that the model needs further development and that some rule descriptions may require revision. Detailed foraging data is needed to test how realistic the foraging patterns in the model are and how strong matrix crossing behaviour is (*ignorance* parameter, fig. 3.2) and whether it differs between species. The model is flexible enough to deal with biologically meaningful alternatives to my decisions.

8.4. Outlook

8.4.1. The model

The model has many parameters and is quite flexible, which allows studying a wide range of questions. I here have selected several questions and alternative approaches which are especially meaningful to explore.

A first practical consideration is to treat bee density differently in the model. Local bee density dominated processes in the model, but was not given by a single parameter. I have learned that components of landscape-level bee density such as the bee's *body length* and *foraging habitat availability* have a major impact on how bees interact with the landscape. I have also learned that the remaining components *flower density* and flower size (*pollen per flower*) cannot be neglected in landscape studies when they affect bee densities. This method was originally chosen to set a bee population always in balance with the capacity of the landscape (amount of pollen) with a parameter (*landscape quality* for bees or bee density control). However, for further study of the model behaviour and application of the model, it can be desirable to control bee density directly with a single parameter. I were only able to systematically study the effects of the component parameters of bee density, rather than the effect of bee density itself. Unlinking bee density from body length could improve the understanding of the model. Unlinking bee density from the amount of foraging resources in the landscape enables to model spill-over effects from mass crops that were not present in the previous year. In the latter case the assumption would be that the bee community is not in balance with the amount of resources in the landscape opposing to bee communities living on semi-natural meadows.

I modelled a community of bees of one species in a landscape with two habitats (foraging and non-foraging) for the sake of simplicity. This enabled me to reduce the complexity of the model and to study the interaction of bees with the landscape under these assumptions. However, future simulation experiments could introduce even more realism in the model. One could simulate a community of solitary bees of different size foraging in the same landscape competing with each other for resources and study the effects of competing species with different hypothetical community assemblies. Or one could use a certain distribution of body sizes to mimic a realistic bee community, for which field data would be required from natural bee communities. A drawback is that the competition between honeybees and solitary bees and competition between different solitary bees is still not systematically studied in the field. Many questions about avoidance (are honeybees and bumblebees avoided by solitary bees?) and flower patch size selection (do large species prefer larger patches?) are unsolved. It is well known which bee species potentially uses which plant species. Oligolectic species (foraging on a certain plant family or genus only) could therefore have exclusive niches. The study of competition with my model without new rules for competition between species would therefore have limitations as well. Extending the two habitats to a multiple-habitat landscape would enable me to model landscapes with different crops and with other habitats offering pollen and nest sites. Does the model yield similar results with different vegetation types (different flower densities and flower sizes) in one landscape? One could also study effects of mass-crops, including spill-over effects. An extension to multiple foraging days could reveal what happens when a mass crop suddenly stops flowering and what landscape configuration is optimal to deal with these short-flowering mass-crops. An additional landscape generator would be required to control different crop proportions and the locations of nests.

Further, the model has the potential to study other topics and learn more about bee biology. What is for example the effect of different trade-offs? How do handling time, pollen requirements, number of flower visits and patch-size selection affect each other? Are there optimal strategies concerning different "giving up-times" at the flower and the patch level? Can bees of different size optimize their foraging behaviour by choosing an optimal flower size? Other questions could relate to landscape scale. Do landscapes of 100 km^2 yield the same results (e.g. Keil et al. 2011)?

8.4.2. Data collection

For mechanistic models there is still a great need for descriptive ecology, to identify and describe patterns and quantify ranges of values. I used a large amount of different data as input for the model and to validate the results, but I have also learned that the data did not suffice to describe the mechanisms and values very accurately. All scaling relationships that I identified in chapter 2 (except eye characteristics) need more data to answer open questions about the shape and accuracy of each relationship. Each of the scaling relationships could be subject of a new study. By including very small and very large bees and a systematic inclusion of other co-factors that I listed, the open questions could easily be clarified. I than would learn e.g. whether velocity increases linearly with body length or with body mass, about the difference in handling time for pollen and for nectar and to what extent handling time is influenced by plant species. Comparison between solitary and eusocial species would also be very useful.

A further need exists in extending our knowledge of foraging behaviour of solitary bees, bumblebees and honeybees and to identify pronounced differences. How do solitary bees really forage? Is it true that they perform little matrix crossing, opposing to honeybees, as some data suggest? What additional foraging rules do exist for avoiding local depletion around the nest? Do they automatically fly farther away from the nest later during the day, do they choose a different direction when leaving the nest or do they even return to the last foraging location? The current model is a fair approximation of a foraging bee community based on available data, but some mechanisms may turn out to be different.

Extension of data is needed to get to a better validation of the model. The literature review gave a good impression of the natural extent of the response variables and did overlap well with the model results. However, responses such as the number of brood cells, the number of flower visits and the mean distances flown are - in the model - a response to a variety of parameters such as flower density, basic bee density and body size. These parameters were often not available from the publications that I used for the validation of the response variables. This is a scale problem: when the number of brood cells is measured in field situations, bees have flown over larger areas. Such studies rarely estimate flower densities and almost never plant community composition to estimate pollen production in different foraging areas. It is possible to measure all of my model parameters to link input and output, which is a strength of the model. The effort and financial input would nevertheless be high to measure all parameters and indirect approaches may therefore in practice still be favoured.

A model validation on a smaller scale could become possible in the near future. Methods to track individuals are becoming available and develop fast. Recent studies used harmonic radar (Osborne et al. 1999, Reynolds et al. 2009, Menzel et al. 2010) and radio tracking (Pasquet et al. 2008, Hagen et al. 2011) for bumblebees and honeybees. The devices are considered too large to attach to most solitary bees, but the newest small transmitters were successfully applied to orchid bees and may even become smaller in the near future (Wikelski et al. 2010). Up to date these devices have been used to present the data on an aggregated level (e.g. mean foraging distance). However, they can also be used to extract detailed foraging rules and time budgets. Another newly applied technology, Radio Frequency Identification (RFID), can be used to track many individual bees at short distances e.g. close to the nest (Decourtye et al. 2011). Radio Frequency Identification was successfully applied to honeybees and bumblebees to study their behaviour under pesticide treatments (Henry et al. 2012, Schneider et al. 2012). Even low-cost low-resolution cameras appear to be able to record detailed foraging behaviour and can be used to calculate time budgets for individual bees (Lortie et al. 2011). This saves time of catching and tagging the bees, while the species or genus can still be recognized and its body size estimated (Lortie et al. 2011). All these techniques may become a new tool to study foraging behaviour of solitary bees in detail.

I further see a benefit in collecting the available data in databases. I have several suggestions for openly available databases that would be especially useful and even realisable without further experimental research. The first would be a database for the general body size of single bee species, e.g. by incorporating it in websites such as Discover Life (discoverlife.org). An automated application with a list of species as input and their body size as output would benefit many research papers working with solitary bees. A size distribution of the investigated bee community would be easily producible and would help to explaining the results and enable to compare studies with each other. Second, a crop database would help ecologists to study animals living on these crops at a new level. It would require information on common plant(ing) density and the mean number of flowers per plant. Measurements of the amount of pollen and nectar per flower (volume, mass, number) would benefit bee studies. Other data such as sowing date, flowering date, harvesting date and growth rate (crop height) would have general purposes, also serving studies with other organisms such as farmland birds. A list of possible (commonly occurring) crop-herb combinations helps to distinguish between different growing conditions of a crop. Bees can be expected to respond very differently to wheat fields with herbs in the undergrowth than to wheat fields without. Such a list would also help ecologists to define functional sub-types of crops and use them in the field for crop type identification.

The current trend in bee ecology is to sample bees at the landscape scale and use statistical models to fit the response (e.g. abundance, presence or species richness) to environmental parameters, similar as I did with colleagues in chapter 7, rather than solving more fundamental questions and identifying mechanisms. One cause is that funding agencies mainly support applied research (often directly linked to political decisions) since it yields short-term benefits for humanity. This pragmatic view overshadows the long term benefits of research that focusses on understanding the mechanisms leading to certain responses. Exact knowledge of the values and the biological mechanisms would make mechanistic models better and make them capable of predicting certain situations exactly. In comparison, statistical (habitat) models do give an impression what is important in the investigated environment, but they do often not contribute much to understanding of the driving mechanisms at lower scales, neither can they be generally applied to other environments. I therefore advocate for a better balance between applied and fundamental science. I hope that it has become evident that the abovementioned examples and research suggestions in the end will contribute to the understanding, estimation and improvement of pollination services by wild pollinators, in a similar way as my model did.

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since 2010	Scientist for farmland bird ecology and bioenergy at the Helmholtz Centre for Environmental Research
2006-2010	Scientist for wild bee ecology and pollination at the Helmholtz Centre for Environmental Research
2005-2006	Curator of the insect collection (division Coleoptera) of the Zoological Museum of the University of Amsterdam (UvA).

Education

2006-2012	Doctoral thesis in wild bee ecology and pollination at the Martin-Luther-University Halle-Wittenberg
1998-2005	Biology studies at the State University of Groningen (RUG), Master's degree with specialization degree in ecology
1995-1998	Atheneum (high school)
1991-1995	Gymnasium (high school)

Academic training and research experience

since 2010	Quantifying the impact of bioenergy crops on the abundance of farmland birds and development of mitigation strategies. With a mechanistic simulation model and data-based species-specific habitat preferences we compare different landscape scenarios.
2006-2012	Doctoral thesis: "The response of solitary bees to landscape configuration with focus on body size and nest-site preference": * Development of a spatially-explicit individual-based simulation model, in which individual bees fly according to specific flight rules in artificial landscapes where they collect pollen. I used it to analyse the impact of landscape structure (habitat loss, habitat fragmentation) on wild bees. * Review of the possible effect that body size of wild bees could have on flight and collection behaviour. * Descriptive ecological research on habitat selection of "urban bees". We used trap-nest in the city of Leipzig to investigate the relationship between the distribution of *Osmia bicornis* and a combination of land-use and local parameters.
1998-2005	Study Biology at the State University of Groningen (RUG) with specialization degree in ecology: * A research project in theoretical ecology; "Competition in a fractal landscape, and the role of scaling laws on coexistence". I developed a spatially-explicit simulation model to test a published theory about scaling laws (size relations) of herbivores. * Short thesis on "Distribution of round fungus beetles (Leiodidae) over an altitude gradient in an Andean cloud forest". I used pitfall traps and self-made Berlese Funnels to assess coleopteran diversity over an altitude gradient in an undisturbed cloud forest in Ecuador. * Essay: "Extinction vulnerability of insect orders in relation to their life history". In this essay I explored the hypothesis that later evolved taxonomic groups are more vulnerable for extinction. * Specialization subjects: vegetation dynamics, conservation biology, alpine plant diversity, landscape ecology, dynamics of biodiversity, biostatistical analysis, geology, insect biology, insect-plant interactions, modelling, chaos theory, behaviour and ecology, genetics and evolution.

Scientific publications

Everaars J., Strohbach M.W., Gruber B. and 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. Landscape and Urban Planning 103 (1): 15-23.

Gruber B., Eckel K., Everaars J. and Dormann C.F. (2011). On managing the red mason bee *(Osmia bicornis*) in apple orchards. Apidologie 42 (5): 564-576.

Training and skill development

2008	* Supervision of a Diploma Student (September 2008 - March 2009) * Preparation and supervision of the scientific part of NANO-Camp, a German television programme, in which scholars participated in research on wild bees in the city of Leipzig (http://www.3sat.de/nano/redaktion/123169/index.html) * Soft skill courses: Time Management
2007	* ALTER-Net Summer School 2007: Trends in Biodiversity: European Ecosystems and Policy * Research Stay: learning methods in pollination ecology at the Georg August University in Göttingen * Soft skill courses: Presentation Skills

Professional interests

* Scaling laws in nature
* Entomology (ecology and biodiversity of bees, butterflies and beetles)
* Nature conservation
* Spatially-explicit individual-based simulation models
* Invertebrate palaeontology and evolutionary patterns

Other skills

Languages	Native: Dutch Good: English, German Basic: French, Spanish
Software	Borland C++, R, MS Office Other: QuarkXpress, Photoshop, CorelDraw and MacIntosh experience
Other	Entomological methods (sampling, pinning, identification) Data analysis using the statistical software package "R-statistics"

Secondary activities

2006-2009	Active participation in committees: The national Yomo group (Young modellers in Ecology) and the institute's PhD-committee
1996-2004	Active participation in Netherlands youth organization of natural history (NJN): Excursion guide (insects, plants, wild mushrooms); Active participation in committees at the regional level (chairman, treasurer, organization of excursions, journal editor); Chief editor and art director of the "Amoeba", the national organization’s magazine.

Other work experience

2000-2005	Homework support institute Stavast in Haren (supervision of high school students)
1997-1998	Summer jobs (printing office and horticulture business)

Spare time interests

Nature photography; Digital image editing; Advanced origami;
Designing posters, brochures, logos; Camping and hiking

Personal characteristics

Critical and analytical thinking; Eye for detail; Curiosity driven, Creative

______________________ ______________________

Ort, Datum Unterschrift

Selbständigkeitserklärung

Hiermit erkläre ich, Jeroen Everaars, dass ich die vorliegende Arbeit selbständig und ohne fremde Hilfe verfasst, keine anderen als die angegebenen Quellen und Hilfsmittel benutzt, die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht und die Beteiligung von Koautoren (unter "Author contibutions"*) unmissverständlich spezifiziert habe.

Weiterhin erkläre ich, dass ich bisher keine weiteren Promotionsversuche unternommen habe und nicht im Besitz eines Doktrogrades bin.

Ort, Datum	Unterschrift

*Author contributions
All sections in this document, except chapter 7, concerns original research completely developed, performed and documented by me alone. Any instance of "we" refers primarily to me. "We" is chosen because the sections are in preparation for publication and refers to conceptual and methodological discussions with my supervisors and colleagues, as well to some textual corrections. All decisions were made by me. Chapter 7, as an exception, is composed of the following contributions: the experiments were conceived and designed by Carsten Dormann, Ralf Seppelt and Bernd Gruber; the experiments were performed by Jeroen Everaars (10%), Michael Strohbach (10%), Marion Pause (10%), Christian Günther (bamboo-tube splitting and counting, 20%) and many volunteers (50%); the data were prepared and analysed by Jeroen Everaars (70%) and Michael Strohbach (30%) and the paper was written by Jeroen Everaars (80%), Michael Strohbach (10%), Carsten Dormann (8%) and Bernd Gruber (2%).

SUPPLEMENTARY MATERIAL TO "THE RESPONSE OF SOLITARY BEES TO LANDSCAPE CONFIGURATION WITH FOCUS ON BODY SIZE AND NEST-SITE PREFERENCE"

Dissertation - Anhang

Zur Erlangung des akademischen Grades doctor rerum naturalium
(Dr. rer. nat.)

vorgelegt der
Naturwissenschaftliche Fakultät I - Biowissenschaften
der Martin-Luther-Universität Halle-Wittenberg

von
drs. Jeroen Everaars M.Sc.
Geboren am 11. Juli 1979 in Groningen (Niederlande)

Supplementary material to "The response of solitary bees to landscape configuration with focus on body size and nest-site preference"

PhD Dissertation (Supplementary material), Martin Luther University Halle-Wittenberg

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Supervised by:
Prof. Dr. Carsten F. Dormann,
PD Dr. Josef Settele

Contents

APPENDIX A

Supplementary material to chapter 2

A1. Regression results for body size relationships

Table A.1.1: The relation between different body size traits. The given equations with slope and intercept are based on fitted linear regression models original or transformed data. P-values and adjusted correlation coefficients adj. R^2 are given for each fitted pair. Body length and it-span are given in mm and mass in mg. Note that a fitted inverse yields a slightly different formula - including different slope - compared to just inversing the x-y equation.

Plot	x	y	Formula	*p*	adj.R^2	Data source	Origin formula
A	dry mass	it-span	$y=0.77\cdot x^{0.405}$	< 0.05	0.96	Cane 1987	Original formula
	dry mass ln	it-span ln	$y=-0.281+0.403\cdot x$	< 0.001	0.95	Cane 1987	Fitted
	dry mass	it-span	$y=0.755\cdot x^{0.403}$			Cane 1987	Back-transformed
	it-span ln	dry mass ln	$y=0.811+2.370\cdot x$	< 0.001	0.95	Cane 1987	Fitted inverse
	it-span	dry mass	$y=2.250\cdot x^{2.370}$			Cane 1987	Back-transformed
B	dry mass	fresh mass	$y=3.4\cdot 10^{-4}+2.79\cdot x$		0.98	Danforth 1989	Original formula
	fresh mass	dry mass	$y=x-3.4\cdot 10^{-4}/2.79$ $=1.219\cdot 10^{-4}+0.358\cdot x$				Inverse formula
C	dry mass ln	body length ln	$y=1.336+0.314\cdot x$	< 0.001	0.87	Cane 1987	Fitted
	dry mass	body length	$y=3.804\cdot x^{0.314}$			Cane 1987	Back-transformed
	body length ln	dry mass ln	$y=-3.300+2.779\cdot x$	< 0.001	0.87	Cane 1987	Fitted inverse
	body length	dry mass	$y=0.037\cdot x^{2.779}$			Cane 1987	Back-transformed
	dry mass ln	body length ln	$y=1.395+0.334\cdot x$	< 0.001	0.86	Müller et al. 2006	Fitted
	dry mass	body length	$y=4.035\cdot x^{0.334}$			Müller et al. 2006	Back-transformed
	body length ln	dry mass ln	$y=-3.221+2.580\cdot x$	< 0.001	0.86	Müller et al. 2006	Fitted inverse
	body length	dry mass	$y=0.040\cdot x^{2.580}$			Müller et al. 2006	Back-transformed
	dry mass ln	body length ln	$y=1.437+0.307\cdot x$	< 0.001	0.83	Cane 1987, Müller et al. 2006	Fitted
	dry mass	body length	$y=4.208\cdot x^{0.307}$			Cane 1987, Müller et al. 2006	Back-transformed
	body length ln	dry mass ln	$y=-3.423+2.717\cdot x$	< 0.001	0.83	Cane 1987, Müller et al. 2006	Fitted inverse
	body length	dry mass	$y=0.033\cdot x^{2.717}$			Cane 1987, Müller et al. 2006	Back-transformed
D	body length	it-span	$y=-0.220+0.294\cdot x$	< 0.001	0.86	Cane 1987	Fitted
	it-span	body length	$y=x+0.220/0.294$ $=0.748+3.401\cdot x$				Inverse formula
	it-span	body length	$y=2.165+2.944\cdot x$	< 0.001	0.86	Cane 1987	Fitted inverse
	body length	it-span	$y=-0.732+0.313\cdot x$	< 0.001	0.74	Greenleaf et al. 2007	Fitted
	it-span	body length	$y=x+0.732/0.313$ $=2.339+3.195\cdot x$				Inverse formula
	it-span	body length	$y=4.659+2.394\cdot x$	< 0.001	0.74	Greenleaf et al. 2007	Fitted inverse
	body length	it-span	$y=-0.504+0.303\cdot x$	< 0.001	0.78	Cane 1987, Greenleaf et al. 2007	Fitted
	it-span	body length	$y=x+0.504/0.303$ $=1.663+3.300\cdot x$				Inverse formula
	it-span	body length	$y=3.819+2.573\cdot x$	< 0.001	0.78	Cane 1987, Greenleaf et al. 2007	Fitted inverse
E	body length	thorax length	$y=-0.461+0.660\cdot x$	< 0.001	0.97	Jander and Jander 2002	Fitted for solitary diurnal species
	thorax length	body length	$y=x+0.461/0.660$ $=0.698+1.515\cdot x$				Inverse formula
	thorax length	body length	$y=1.001+1.475\cdot x$	< 0.001	0.97	Jander and Jander 2002	Fitted inverse for solitary diurnal species

Table A.1.2: The relation between eye characteristics and body size. Formulas are obtained from cited papers and rewritten for body length based on the relationship between thorax length and body length.

Plot	x	y	Formula	*p*	adj.R^2	Data source	Origin formula
2A	thorax length	Eye perimeter long	$y=0.29+0.34\cdot x$			Jander and Jander 2002	Original formula
	body length	Eye perimeter long	$y=0.13+0.22\cdot x$			Jander and Jander 2002	Transformed formula
	thorax length	Eye perimeter short	$y=0.06+0.17\cdot x$			Jander and Jander 2002	Original formula
	body length	Eye perimeter short	$y=-0.018+0.11\cdot x$			Jander and Jander 2002	Transformed formula
2B	thorax length	facet number	$y=855.3\cdot x^{1.02}$			Jander and Jander 2002	Original formula
	body length	facet number	$y=855.3\cdot 0.66\cdot x-0.46^{1.02}$			Jander and Jander 2002	Transformed formula
	body length	facet number	$y=-924.5+645.7\cdot x$	< 0.001	0.96	Jander and Jander 2002	Fitted for solitary species
2C	thorax length	facet diameter	$y=9.3\cdot x^{0.4}$			Jander and Jander 2002	Original formula
	body length	facet diameter	$y=9.3\cdot 0.66\cdot x-0.46^{0.4}$			Jander and Jander 2002	Transformed formula
2D	thorax length	interommatidial angle	$y=5.3\cdot x^{-0.5}$			Jander and Jander 2002	Original formula
	body length	interommatidial angle	$y=5.3\cdot 0.66\cdot x-0.46^{-0.5}$			Jander and Jander 2002	Transformed formula
2E	thorax length	eye parameter	$y=0.79\cdot x^{-0.08}$			Jander and Jander 2002	Original formula
	body length	eye parameter	$y=0.79\cdot 0.66\cdot x-0.46^{-0.08}$			Jander and Jander 2002	Transformed formula

Table A.1.3: The relation between flight velocities and body size of Hymenoptera.

Plot	x	y	Formula	*p*	adj.R^2	Data source	Origin formula
3	body length	velocity high speed mode	$y=0.29+0.34\cdot x$	< 0.01	0.826	mixed	Fit through origin
	body length	velocity medium speed mode	$y=0.13+0.22\cdot x$	< 0.001	0.887	mixed	Fit through origin
	body length	velocity low speed mode	$y=0.06+0.17\cdot x$	< 0.001	0.897	mixed	Fit through origin

Table A.1.4.: The relation between foraging and homing distances and body size. Some formulas were obtained from cited papers and rewritten for body length based on the relationship between it-span and body length. Distances are in m and it-span and body length given in mm when not otherwise specified.

Plot	**x**	**y**	**Formula**	***p***	**adj.R^2**	**Data source**	**Origin formula**
3A	it-span ln	homing distance ln	$y=4.348+2.551\cdot x$	< 0.001	0.714	Greenleaf et al. 2007	fitted solitary
	body length	homing distance	$y=77.324\cdot-0.504+0.303\cdot x^{2.551}$			Greenleaf et al. 2007	Back-transformed, it-span substituted
	body length ln	homing distance ln	$y=1.909+1.903\cdot x$	< 0.05	0.323	Zurbuchen et al. 2010b	fitted
	body length	homing distance	$y=6.746\cdot x^{1.903}$				Back-transformed
	body length ln	homing distance ln	$y=2.218+1.838\cdot x$	< 0.001	0.389	Greenleaf et al. 2007, Zurbuchen et al. 2010b;	Fitted solitary
	body length	homing distance	$y=1.922\cdot x^{1.838}$				Back-transformed
	body length ln	homing distance ln	$y=1.337+2.234\cdot x$	< 0.001	0.389	Greenleaf et al. 2007, Zurbuchen et al. 2010b;	Fitted all bees
	body length	homing distance	$y=3.808\cdot x^{2.234}$			Greenleaf et al. 2007, Zurbuchen et al. 2010b;	Back-transformed
	it-span log10	homing distance 90% log10, km	$y=-1.363+3.366\cdot x$	< 0.001	0.776	Greenleaf et al. 2007	Original formula
	body length	homing distance 90%	$y=43\cdot-0.504+0.303\cdot x^{3.366}$			Greenleaf et al. 2007	Back-transformed, it-span substituted
	it-span log10	homing distance 50% log10, km	$y=-1.643+3.242\cdot x$	< 0.001	0.718	Greenleaf et al. 2007	Original formula
	body length	homing distance 50%	$y=23\cdot-0.504+0.303\cdot x^{3.242}$			Greenleaf et al. 2007	Back-transformed, it-span substituted
	it-span log10	homing distance 50% log10, km	$y=3.802+2.463\cdot x$	< 0.01	0.558	Greenleaf et al. 2007	fitted solitary
	body length	homing distance 50%	$y=44.791\cdot-0.504+0.303\cdot x^{2.463}$			Greenleaf et al. 2007	Back-transformed, it-span substituted
3B	body length ln	foraging distance ln	$y=2.489+1.359*x$	< 0.01	0.332	Gathmann and Tscharntke 2002	fitted
	body length	foraging distance	$y=12.049\cdot x^{1.359}$			Gathmann and Tscharntke 2002	Back-transformed
	body length ln	foraging distance ln	$y=4.170+0.899\cdot x$	< 0.01	0.053	Zurbuchen et al. 2010b	fitted
	body length	foraging distance	$y=64.715\cdot x^{0.899}$			Zurbuchen et al. 2010b	Back-transformed
	body length ln	foraging distance ln	$y=4.058+0.851\cdot x$	< 0.01	0.073	Gathmann and Tscharntke 2002, Zurbuchen et al. 2010b	Fitted solitary
	body length	foraging distance	$y=57.858\cdot x^{0.851}$			Gathmann and Tscharntke 2002, Zurbuchen et al. 2010b	Back-transformed
	body length ln	foraging distance ln	$y=4.246+0.951\cdot x$	< 0.01	0.068	Gathmann and Tscharntke 2002, Zurbuchen et al. 2010b	Fitted all bees
	body length	foraging distance	$y=69.826\cdot x^{0.951}$			Gathmann and Tscharntke 2002, Zurbuchen et al. 2010b	Back-transformed
	it-span log10	foraging distance feeder log10, km	$y=-0.760+2.313\cdot x$	< 0.001	0.548	Greenleaf et al. 2007	Original formula
	body length	foraging distance feeder	$y=174\cdot-0.504+0.303\cdot x^{2.313}$			Greenleaf et al. 2007	Transformed formula

Table A.1.5: The relation between pollen provisions and body size.. Pollen volume is given in mm^3 and mass in mg.

Plot	**x**	**y**	**Formula**	***p***	**adj.R^2**	**Data source**	**Origin formula**
6A	body length	pollen grain number	No fit			mixed	
6B	body length	pollen volume	$y=-25.924+5.678\cdot x$	< 0.01	0.554	Müller et al. 2006	Fitted
	body length	pollen volume	$y=-52.371+8.906\cdot x$	< 0.01	0.492	mixed	Fitted
	body mass log 10	pollen volume log 10	$y=0.433+0.868\cdot x$	< 0.001	0.74	Müller et al. 2006	Müller et al. 2006
	body length	pollen volume	$y=10^{0.868\cdot c}$ $c=\log 100.433+0.040\cdot x^{2.580}$			Müller et al. 2006	Transformed formula

Table A.1.6: The relation between flower handling time and body size. Handling time is given in seconds and body length in mm.

Plot	**x**	**y**	**Formula**	***p***	**adj.R^2**	**Data source**	**Origin formula**
7A	body length ln	handling time pollen ln	$y=8.493-2.725\cdot x$	< 0.05	0.740	Strickler 1979	Fitted
	body length	handling time pollen	$y=4880.486\cdot x^{-2.725}$			Strickler 1979	Transformed
	body length ln	handling time pollen ln	$y=5.971-0.976\cdot x$	N.S.	-0.049	Chagnon et al. 1993	Fitted
	body length	handling time pollen	$y=391.897\cdot x^{-0.976}$			Chagnon et al. 1993	Transformed
	body length ln	handling time pollen ln	$y=8.646-2.722\cdot x$	NA	NA	Schlindwein et al. 2005	Fitted
	body length	handling time pollen	$y=5687.352\cdot x^{-2.722}$			Schlindwein et al. 2005	Transformed
	body length ln	handling time pollen ln	$y=3.802-0.740\cdot x$	N.S.	0.509	Javorek et al. 2002	Fitted
	body length	handling time pollen	$y=44.791\cdot x^{-0.740}$			Javorek et al. 2002	Transformed
7B	body length ln	handling time mixed ln	$y=3.751-0.786\cdot x$	< 0.05	0.303	Benedek 1973, Vicia villosa only	Fitted
	body length	handling time mixed	$y=42.564\cdot x^{-0.786}$			Benedek 1973, Vicia villosa only	Transformed
	body length ln	handling time mixed ln	$y=3.307-0.492\cdot x$	< 0.1	0.167	Benedek 1973, Medicago sativa only	Fitted
	body length	handling time mixed	$y=27.303\cdot x^{-0.492}$			Benedek 1973, Medicago sativa only	Transformed
	body length ln	handling time mixed ln	$y=0.581+0.248\cdot x$	N.S.	-0.326	Nachtigall 1994	Fitted
	body length	handling time mixed	$y=1.788\cdot x^{0.248}$			Nachtigall 1994	Transformed
	body length ln	handling time mixed ln	$y=1.873+0.043\cdot x$	N.S.	-0.071	Richards 1996, Lotus corniculatus only	Fitted
	body length	handling time mixed	$y=6.508\cdot x^{0.043}$			Richards 1996, Lotus corniculatus only	Transformed
	body length ln	handling time mixed ln	$y=5.086-1.278\cdot x$	< 0.05	0.300	Richards 1996, Astragalus cicer only	Fitted
	body length	handling time mixed	$y=161.742\cdot x^{-1.278}$			Richards 1996, Astragalus cicer only	Transformed
	body length ln	handling time mixed ln	$y=1.579+0.062\cdot x$	NA	NA	Richards 1996, Onobrychis viciaefolia only	Fitted
	body length	handling time mixed	$y=4.850\cdot x^{0.062}$			Richards 1996, Onobrychis viciaefolia only	Transformed

A2. Original data used for body size relationships

This section lists all raw data taken from the original publications. When data was neither given in the text nor in a table we used the figure with data points and a software tool "Datagrabber" from Stephen H. Roxburgh, http://www.steverox.info/software_downloads.htm to make an accurate estimation of the original data. References of all publications are given as well as a source for the body size data. Body length indications from multiple-volume publications are indicated by asterisks: Amiet * - Amiet 1996, Amiet et al. 1999, Amiet et al. 2001, 2004, 2007; Scheuchl ** - Schmid-Egger and Scheuchl 1996, Scheuchl 2000, 2006; Mitchell *** - Mitchell 1960, 1962.

Table A.2.1. Raw data used for the analysis of different body size traits.

Genus	Species	Mass	It-span	Sex	Length	Data source	Body length source	Comments
Andrena	accepta	27.99	2.89	female	11.00	Cane 1987	Mitchell***	
Calliopsis	andreniformis	7.21	1.78	female	7.00	Cane 1987	Mitchell***	
Perdita	coreopsidis	6.93	1.60	female	7.50	Cane 1987	Michener 2000	
Anthophora	urbana	41.26	3.38	female	12.50	Cane 1987	Michener 2000	
Centris	atripes	53.38	4.11	female	12.00	Cane 1987	Michener 2000	
Diadasia	olivacea	20.20	2.52	female	8.50	Cane 1987	Michener 2000	
Exomalopsis	solani	10.39	1.88	female	8.00	Cane 1987	Michener 2000	
Melissodes	agilis	32.90	3.32	female	12.00	Cane 1987	Michener 2000	
Triepeolus	verbesinae	18.76	2.09	female	NA	Cane 1987	NA	
Xylocopa	micans	151.76	5.95	female	17.00	Cane 1987	Mitchell***	
Colletes	inaequalis	42.13	3.45	female	12.50	Cane 1987	Mitchell***	
Hylaeus	rugulosus	7.79	1.65	female	NA	Cane 1987	NA	
Augochlora	pura	13.27	1.97	female	8.00	Cane 1987	Mitchell***	
Dialictus	versatus	4.91	1.42	female	6.00	Cane 1987	Mitchell***	
Dufourea	marginata	7.21	1.78	female	8.50	Cane 1987	Mitchell***	
Nomia	melanderi	37.22	2.59	female	12.00	Cane 1987	Michener 2000	
Anthidiellum	notatum	18.76	2.47	female	8.00	Cane 1987	Mitchell***	
Megachile	texana	43.29	3.74	female	12.50	Cane 1987	Mitchell***	
Hesperapis	carinata	16.45	2.82	female	11.50	Cane 1987	Michener 2000	
Protoxaea	gloriosa	98.39	4.97	female	19.50	Cane 1987	Michener 2000	
Diadasia	rinconis	30.01	3.02	female	8.50	Cane 1987	Michener 2000	
Xylocopa	violacea	188.38	5.72	female	21.50	Cane 1987	Scheuchl****	
Hylaeus	punctulatissimus	5.30	NA	mixed	7.00	Müller et al. 2006	Müller et al. 2006	
Hylaeus	signatus	6.80	NA	mixed	7.50	Müller et al. 2006	Müller et al. 2006	
Colletes	cunicularius	34.10	NA	mixed	13.00	Müller et al. 2006	Müller et al. 2006	
Colletes	daviesanus	8.90	NA	mixed	8.50	Müller et al. 2006	Müller et al. 2006	
Colletes	hederae	23.80	NA	mixed	12.00	Müller et al. 2006	Müller et al. 2006	
Andrena	ruficrus	8.50	NA	mixed	9.50	Müller et al. 2006	Müller et al. 2006	
Andrena	vaga	27.60	NA	mixed	13.50	Müller et al. 2006	Müller et al. 2006	
Chelostoma	florisomne	12.50	NA	mixed	9.50	Müller et al. 2006	Müller et al. 2006	
Chelostoma	rapunculi	8.60	NA	mixed	9.00	Müller et al. 2006	Müller et al. 2006	
Heriades	truncorum	5.50	NA	mixed	6.00	Müller et al. 2006	Müller et al. 2006	
Hoplitis	adunca	19.70	NA	mixed	12.00	Müller et al. 2006	Müller et al. 2006	
Hoplitis	mocsaryi	22.30	NA	mixed	13.00	Müller et al. 2006	Müller et al. 2006	
Hoplitis	tridentata	25.20	NA	mixed	10.00	Müller et al. 2006	Müller et al. 2006	
Hoplosmia	spinulosa	9.20	NA	mixed	7.50	Müller et al. 2006	Müller et al. 2006	
Andrena	curvungula	21.40	NA	mixed	12.50	Müller et al. 2006	Müller et al. 2006	
Andrena	hattorfiana	28.60	NA	mixed	14.50	Müller et al. 2006	Müller et al. 2006	
Andrena	marginata	8.40	NA	mixed	9.50	Müller et al. 2006	Müller et al. 2006	
Andrena	pandellei	16.10	NA	mixed	10.50	Müller et al. 2006	Müller et al. 2006	
Andrena	probata	26.10	NA	mixed	14.00	Müller et al. 2006	Müller et al. 2006	
Anthidium	manicatum	41.90	NA	mixed	14.00	Müller et al. 2006	Müller et al. 2006	
Anthidium	punctatum	18.80	NA	mixed	9.00	Müller et al. 2006	Müller et al. 2006	
Anthophora	balneorum	46.20	NA	mixed	12.50	Müller et al. 2006	Müller et al. 2006	
Chelostoma	campanularum	1.80	NA	mixed	5.00	Müller et al. 2006	Müller et al. 2006	
Chelostoma	grande	28.80	NA	mixed	13.50	Müller et al. 2006	Müller et al. 2006	
Dufourea	dentiventris	5.50	NA	mixed	7.50	Müller et al. 2006	Müller et al. 2006	
Hoplitis	anthocopoides	12.80	NA	mixed	9.50	Müller et al. 2006	Müller et al. 2006	

Hoplitis	dalmatica	42.40	NA	mixed	12.50	Müller et al. 2006	Müller et al. 2006	
Hoplitis	lepeletieri	24.10	NA	mixed	12.50	Müller et al. 2006	Müller et al. 2006	
Hoplitis	loti	14.00	NA	mixed	9.50	Müller et al. 2006	Müller et al. 2006	
Hoplitis	mitis	14.40	NA	mixed	8.00	Müller et al. 2006	Müller et al. 2006	
Hoplitis	ravouxi	10.70	NA	mixed	9.00	Müller et al. 2006	Müller et al. 2006	
Lasioglossum	clypeare	4.30	NA	mixed	6.50	Müller et al. 2006	Müller et al. 2006	
Lasioglossum	costulatum	11.90	NA	mixed	9.50	Müller et al. 2006	Müller et al. 2006	
Megachile	parietina	63.20	NA	mixed	16.00	Müller et al. 2006	Müller et al. 2006	
Melitta	dimidiata	31.30	NA	mixed	12.00	Müller et al. 2006	Müller et al. 2006	
Melitta	haemorrhoidalis	24.70	NA	mixed	12.00	Müller et al. 2006	Müller et al. 2006	
Melitta	leporina	19.70	NA	mixed	12.00	Müller et al. 2006	Müller et al. 2006	
Melitta	nigricans	16.10	NA	mixed	11.00	Müller et al. 2006	Müller et al. 2006	
Melitturga	clavicornis	40.40	NA	mixed	14.00	Müller et al. 2006	Müller et al. 2006	
Osmia	andrenoides	8.60	NA	mixed	7.00	Müller et al. 2006	Müller et al. 2006	
Osmia	brevicornis	18.80	NA	mixed	9.50	Müller et al. 2006	Müller et al. 2006	
Osmia	caerulescens	11.30	NA	mixed	9.00	Müller et al. 2006	Müller et al. 2006	
Rhophitoides	canus	5.60	NA	mixed	7.50	Müller et al. 2006	Müller et al. 2006	
Rophites	algirus	12.40	NA	mixed	9.00	Müller et al. 2006	Müller et al. 2006	
Systropha	curvicornis	13.30	NA	mixed	9.00	Müller et al. 2006	Müller et al. 2006	
Systropha	planidens	22.20	NA	mixed	10.50	Müller et al. 2006	Müller et al. 2006	
Tetraloniella	salicariae	15.10	NA	mixed	10.00	Müller et al. 2006	Müller et al. 2006	
Andrena	barbilabris	NA	2.10	mixed	10.75	Greenleaf et al. 2007	Scheuchl**	
Andrena	cineraria	NA	3.00	mixed	12.50	Greenleaf et al. 2007	Scheuchl**	
Andrena	clarkella	NA	3.10	mixed	12.25	Greenleaf et al. 2007	Scheuchl**	
Andrena	flavipes	NA	2.20	mixed	10.75	Greenleaf et al. 2007	Scheuchl**	
Andrena	vaga	NA	2.80	mixed	14.00	Greenleaf et al. 2007	Scheuchl**	
Macrotera	texana	NA	2.30	mixed	7.50	Greenleaf et al. 2007	Timberlake 1954	Perdita
Panurgus	banksianus	NA	2.20	mixed	11.00	Greenleaf et al. 2007	Scheuchl**	
Anthophora	abrupta	NA	3.90	mixed	15.13	Greenleaf et al. 2007	Mitchell***	
Anthophora	fulvitarsis	NA	4.90	mixed	17.00	Greenleaf et al. 2007	Scheuchl**	
Anthophora	linsleyi	NA	3.60	mixed	NA	Greenleaf et al. 2007	NA	
Tetraloniella	dentata	NA	3.10	mixed	12.50	Greenleaf et al. 2007	Michener 2000	
Tetraloniella	salicariae	NA	2.10	mixed	9.88	Greenleaf et al. 2007	Scheuchl**	
Xylocopa	rufa	NA	5.80	mixed	NA	Greenleaf et al. 2007	NA	
Xylocopa	violacea	NA	7.80	mixed	21.25	Greenleaf et al. 2007	Scheuchl**	
Xylocopa	virginica	NA	5.60	mixed	20.00	Greenleaf et al. 2007	Mitchell***	
Colletes	cunicularius	NA	4.00	mixed	13.00	Greenleaf et al. 2007	Amiet*	
Lasioglossum	umbripenne	NA	1.20	mixed	4.50	Greenleaf et al. 2007	Wcislo and Schatz 2003	
Lasioglossum	malachurum	NA	1.70	mixed	8.50	Greenleaf et al. 2007	Amiet*	
Lasioglossum	pauxillum	NA	1.10	mixed	5.50	Greenleaf et al. 2007	Amiet*	
Nomia	melanderi	NA	2.70	mixed	12.00	Greenleaf et al. 2007	Michener 2000	
Systropha	planidens	NA	2.10	mixed	11.00	Greenleaf et al. 2007	Amiet*	
Chelostoma	florisomne	NA	1.50	mixed	9.25	Greenleaf et al. 2007	Scheuchl**	
Chelostoma	rapunculi	NA	1.50	mixed	9.00	Greenleaf et al. 2007	Scheuchl**	Osmia
Hoplitis	anthocopoides	NA	2.40	mixed	9.50	Greenleaf et al. 2007	Scheuchl**	Osmia
Megachile	flavipes	NA	2.20	mixed	16.00	Greenleaf et al. 2007	Michener 2000	
Megachile	lapponica	NA	2.80	mixed	10.50	Greenleaf et al. 2007	Zurbuchen et al. 2010a	
Megachile	nana	NA	1.90	mixed	6.00	Greenleaf et al. 2007	Michener 2000	
Megachile	parietina	NA	4.50	mixed	15.50	Greenleaf et al. 2007	Scheuchl**	
Megachile	rotundata	NA	2.40	mixed	8.00	Greenleaf et al. 2007	Scheuchl**	
Megachile	sicula	NA	4.30	mixed	NA	Greenleaf et al. 2007	NA	
Osmia	cornifrons	NA	2.90	mixed	NA	Greenleaf et al. 2007	NA	
Osmia	lignaria_propinqua	NA	2.90	mixed	10.00	Greenleaf et al. 2007	Mitchell***	used lignaria lignaria
Osmia	maritime	NA	2.90	mixed	10.75	Greenleaf et al. 2007	Scheuchl**	
Osmia	mustelina	NA	3.50	mixed	12.25	Greenleaf et al. 2007	Scheuchl**	
Osmia	pedicornis	NA	3.30	mixed	NA	Greenleaf et al. 2007	NA	
Osmia	rufa	NA	3.30	mixed	11.25	Greenleaf et al. 2007	Scheuchl**	
Dasypoda	altercator	NA	2.90	mixed	13.75	Greenleaf et al. 2007	Scheuchl**	is hirtipes

Table A.2.2. Raw data used for the analysis of eye characteristics.

Genus	Species	Social status	Nocturnalvs.diurnal	Thorax length	Body length	Body length estimate by regression	Shortest surface perimeter	Longest surface perimeter	Number of facets	Mean facet diameter	Interomma-tidial angle	Eye para-meter	Data source	Body length source
Perdita	minima	Sol	D	1.49	2.00	2.8	0.27	0.53	1094	9.19	4.73	0.76	Jander and Jander 2002	Cane 2008
Liotrigona	madecassa	Sol	D	1.49	2.80	2.8	0.34	0.85	1591	10.16	3.88	0.69	Jander and Jander 2002	Jander and Jander 2002
Lasioglossum	inconspicuum	Sol	D	2.18	4.00	4.0	0.51	1.10	2089	13.49	3.38	0.79	Jander and Jander 2002	Mitchell***
Lasioglossum	noctivagum	Sol	N	4.29	8.75	7.4	1.04	1.82	3135	20.73	2.75	1.00	Jander and Jander 2002	McGinley 2003
Augochlora	pura	Sol	D	4.47	8.00	7.7	0.67	1.53	3209	16.27	2.72	0.77	Jander and Jander 2002	Mitchell***
Megalopta	ecuadoria	Sol	N	5.35	13.00	9.1	1.40	2.76	4006	26.67	2.44	1.14	Jander and Jander 2002	Michener 2000
Megachile	campanulae	Sol	D	5.88	9.50	10.0	1.07	2.34	7761	21.63	1.75	0.66	Jander and Jander 2002	Mitchell***
Apis	mellifera	Soc	D	5.90	12.00	10.0	0.88	2.87	5424	20.50	2.09	0.75	Jander and Jander 2002	Mitchell***
Megalopta	genalis	Sol	N	7.51	13.00	12.5	1.87	3.83	5623	26.84	2.06	0.97	Jander and Jander 2002	Michener 2000
Anthophora	occidentalis	Sol	D	8.51	14.00	14.1	1.75	3.39	8037	20.92	1.73	0.63	Jander and Jander 2002	Brooks 1983
Protoxaea	gloriosa	Sol	D	9.49	18.00	15.6	1.77	3.55	8435	23.76	1.68	0.70	Jander and Jander 2002	Rozen and Rozen 2010
Bombus	griseocollis	Soc	D	12.02	13.75	19.4	1.61	4.21	10252	22.47	1.53	0.60	Jander and Jander 2002	Mitchell***
Xylocopa	varipuncta	Sol	D	13.02	19.00	20.9	2.41	4.67	12840	25.65	1.36	0.61	Jander and Jander 2002	Essig 1926
Xylocopa	californica	Sol	D	13.61	22.00	21.8	2.01	3.76	12591	24.76	1.38	0.60	Jander and Jander 2002	Robinson 2005
Xylocopa	latipes	Sol	D	17.02	24.50	26.8	3.25	6.73	15801	30.38	1.23	0.65	Jander and Jander 2002	Robinson 2005

Table A.2.3. Raw data used for the analysis of flight velocities.

Genus	Species	Bee	Solitary bee	Body length	Velocity class	Velocity	Outlier	Data source	Body length source	Comments
Elisabethiella	baijnathi	n	n	1.40	high	0.37	n	Compton et al. 2000	NA	
Sceliphron	spirifex	n	n	22.00	high	6.00	n	Nachtigall 2001	Nachtigall 2001	
Vespa	crabro	n	n	25.00	high	5.90	n	Dean 2003	NA	
Vespa	mandarina	n	n	50.00	high	12.50	n	Piper 2007	NA	
Apis	mellifera	y	n	12.00	high	5.10	n	Nachtigall et al. 1995	Mitchell***	
Apis	mellifera	y	n	12.00	high	7.00	n	Barron and Srinivasan 2006	Mitchell***	
Bombus	terrestris	y	n	17.50	high	5.00	n	Ellington et al. 1990	NA	
Bombus	terrestris	y	n	17.50	high	7.10	n	Riley et al. 1999	NA	
Osmia	lignaria	y	y	11.50	high	5.00	n	Guédot et al. 2009	NA	
Chelostoma	rapunculi	y	y	9.00	high	1.50	n	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a	
Euglossa	sp.	y	n	14.00	high	7.00	n	Combes and Dudley 2005	Combes and Dudley 2005	
Euglossa	sp.	y	n	12.00	high	7.25	n	Combes and Dudley 2006	Combes and Dudley 2006	
Xylocopa	californica	y	y	22.00	high	7.50	n	Chappell 1982	Robinson 2005	
Anthidium	septemdentatum	y	y	15.00	high	8.00	n	Nachtigall 1997	Nachtigall 1997	speed burst
Anthidium	septemdentatum	y	y	15.00	high	5.50	n	Nachtigall 1997	Nachtigall 1997	territorial males
Anthophora	allaudi fuerteventurae	y	y	13.00	high	7.00	n	Nachtigall 1992	Nachtigall 1992	
Cerceris	arenaria	n	n	10.00	low	0.55	n	Zeil 1993	NA	
Cerceris	rybyensis	n	n	9.00	low	0.41	n	Zeil 1993	NA	
Odynerus	spinipes	n	n	10.25	low	0.44	n	Vos et al. 2002	NA	
Vespa	vulgaris	n	n	18.00	low	1.01	n	Collett and Lehrer 1993	NA	
Apis	mellifera	y	n	12.00	low	0.30	n	Srinivasan et al. 1989	Mitchell***	
Osmia	cornuta	y	y	12.75	low	0.90	n	Vicens and Bosch 2000	Amiet*	
Anthidium	septemdentatum	y	y	15.00	low	0.25	n	Nachtigall 1997	Nachtigall 1997	territorial males
Elisabethiella	baijnathi	n	n	1.40	medium	0.25	n	Ware and Compton 1994	NA	
Apis	mellifera	y	n	12.00	medium	0.90	n	Barron and Srinivasan 2006	Mitchell***	
Apis	mellifera	y	n	12.00	medium	3.30	n	Nachtigall et al. 1995	Mitchell***	
Bombus	terrestris	y	n	17.50	medium	3.00	n	Ellington et al. 1990	NA	
Anthidium	septemdentatum	y	y	15.00	medium	2.50	n	Nachtigall 1997	Nachtigall 1997	territorial males
Anthophora	allaudi fuerteventurae	y	y	13.00	medium	3.00	n	Nachtigall 1992	Nachtigall 1992	
Anthophora	plumipes	y	y	14.50	high	1.90	y	Stone et al. 1995	Amiet*	males, not foraging for pollen
Anthophora	plumipes	y	y	14.50	low	0.40	y	Stone et al. 1995	Amiet*	males, not foraging for pollen
Anthophora	plumipes	y	y	14.50	medium	1.00	y	Stone et al. 1995	Amiet*	males, not foraging for pollen
Apis	mellifera	y	n	12.00	medium	0.58	y	Kunze and Chittka 1996	NA	
Apis	mellifera	y	n	12.00	medium	1.05	y	Kunze and Chittka 1996	NA	
Bombus	pascuorum	y	n	13.50	medium	0.37	y	Kunze and Chittka 1996	NA	
Bombus	pascuorum	y	n	13.50	medium	0.50	y	Kunze and Chittka 1996	NA	

Table A.2.4. Raw data used for the analysis of foraging and homing distances.

Genus	**Species**	**Solitary**	**Distance type**	**Body length (mm)**	**Foraging distance (m)**	**Reviewed by**	**Body length source**
Andrena	barbilabris	Y	foraging distance	11.50	500	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Andrena	barbilabris	Y	foraging distance	11.50	300	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Andrena	cineraria	Y	foraging distance	14.00	300	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Andrena	clarkella	Y	foraging distance	13.00	300	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Andrena	flavipes	Y	foraging distance	12.00	260	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Andrena	vaga	Y	foraging distance	14.00	260	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Chelostoma	florisomne	Y	foraging distance	5.50	150	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Chelostoma	rapunculi	Y	foraging distance	8.50	200	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Colletes	cunicularis	Y	foraging distance	13.50	350	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Megachile	lapponica	Y	foraging distance	11.00	600	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Megachile	rotundata	Y	foraging distance	8.50	500	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Megachile	rotundata	Y	foraging distance	8.50	100	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Osmia	anthocopoides	Y	foraging distance	9.50	150	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Osmia	maritima	Y	foraging distance	11.50	150	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Osmia	mustelina	Y	foraging distance	13.50	1000	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Osmia	rufa	Y	foraging distance	11.00	600	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Panurgus	banksianus	Y	foraging distance	11.00	250	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Tetralonia	salicariae	Y	foraging distance	10.50	400	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Xylocopa	violacea	Y	foraging distance	24.00	1200	Gathmann and Tscharntke 2002	Gathmann and Tscharntke 2002
Andrena	barbilabris	Y	homing distance max	10.75	500	Greenleaf et al. 2007	length from it-span
Andrena	flavipes	Y	homing distance max	10.75	400	Greenleaf et al. 2007	length from it-span
Andrena	vaga	Y	homing distance max	14.00	500	Greenleaf et al. 2007	length from it-span
Anthophora	abrupta	Y	homing distance max	15.13	2300	Greenleaf et al. 2007	length from it-span
Bombus	terrestris	N	homing distance max	12.82	800	Greenleaf et al. 2007	length from it-span
Dasypoda	altercator	Y	homing distance max	13.75	4000	Greenleaf et al. 2007	length from it-span
Eufriesea	surinamensis	N	homing distance max	18.23	45500	Greenleaf et al. 2007	length from it-span
Lasioglossum	umbripenne	Y	homing distance max	4.50	200	Greenleaf et al. 2007	length from it-span
Megachile	flavipes	Y	homing distance max	16.00	800	Greenleaf et al. 2007	length from it-span
Megachile	nana	Y	homing distance max	6.00	600	Greenleaf et al. 2007	length from it-span
Megachile	rotundata	Y	homing distance max	8.00	700	Greenleaf et al. 2007	length from it-span
Osmia	cornifrons	Y	homing distance max	11.28	800	Greenleaf et al. 2007	length from it-span
Osmia	rufa	Y	homing distance max	11.25	900	Greenleaf et al. 2007	length from it-span
Tetraloniella	salicariae	Y	homing distance max	9.88	400	Greenleaf et al. 2007	length from it-span
Xylocopa	virginica	Y	homing distance max	20.00	13000	Greenleaf et al. 2007	length from it-span
Apis	cerana	N	feeder foraging distance max	10.77	1300	Greenleaf et al. 2007	length from it-span
Apis	cerana_indica	N	feeder foraging distance max	10.77	800	Greenleaf et al. 2007	length from it-span
Apis	cerana	N	feeder foraging distance max	10.77	800	Greenleaf et al. 2007	length from it-span
Apis	dorsata	N	feeder foraging distance max	10.77	1000	Greenleaf et al. 2007	length from it-span
Apis	florea	N	feeder foraging distance max	8.45	400	Greenleaf et al. 2007	length from it-span
Apis	mellifera	N	feeder foraging distance max	12.31	12000	Greenleaf et al. 2007	length from it-span
Apis	mellifera	N	feeder foraging distance max	12.31	12500	Greenleaf et al. 2007	length from it-span
Apis	mellifera_adansonii	N	feeder foraging distance max	12.31	2800	Greenleaf et al. 2007	length from it-span
Apis	mellifera_mellifera	N	feeder foraging distance max	12.31	2500	Greenleaf et al. 2007	length from it-span
Heterotrigona	iridipennis	N	feeder foraging distance max	6.91	100	Greenleaf et al. 2007	length from it-span
Nannotrigona	perilampoides	N	feeder foraging distance max	7.42	100	Greenleaf et al. 2007	length from it-span
Partamona	aff_cupira	N	feeder foraging distance max	8.45	500	Greenleaf et al. 2007	length from it-span
Plebeia	mosquito	N	feeder foraging distance max	6.39	500	Greenleaf et al. 2007	length from it-span
Trigona	amalthea	N	feeder foraging distance max	9.74	1000	Greenleaf et al. 2007	length from it-span
Tetragonisca	angustula	N	feeder foraging distance max	6.39	700	Greenleaf et al. 2007	length from it-span
Trigona	corvina	N	feeder foraging distance max	7.68	300	Greenleaf et al. 2007	length from it-span
Trigona	spinipes	N	feeder foraging distance max	8.45	800	Greenleaf et al. 2007	length from it-span
Osmia	adunca	Y	foraging distance	10.00	180	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Osmia	lignaria	Y	foraging distance	11.50	600	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Colletes	hederae	Y	foraging distance	11.50	1000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Chelostoma	rapunculi	Y	foraging distance	9.00	200	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a

Megachile	lapponica	Y	foraging distance	7.00	300	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Chelostoma	florisomne	Y	foraging distance	9.00	150	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Megachile	flavipes	Y	foraging distance	9.00	500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Chelostoma	florisomne	Y	foraging distance	9.00	650	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Megachile	nana	Y	foraging distance	9.00	750	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	hattorfiana	Y	flying range	14.50	130	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Osmia	maritima	Y	n.a.	10.75	150	Zurbuchen et al. 2010a	Scheuchl**
Panurgus	banksianus	Y	n.a.	11.00	250	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Colletes	cunicularis	Y	n.a.	12.50	350	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Colletes	hederae	Y	n.a.	11.50	400	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	cineraria	Y	foraging distance	12.00	300	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	clarkella	Y	foraging distance	12.00	300	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Hylaeus	punctulatissimus	Y	foraging distance	7.00	1100	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Chelostoma	rapunculi	Y	foraging distance	9.00	1275	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Hoplitis	adunca	Y	foraging distance	10.00	1400	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Lasioglossum	marginellum	Y	foraging distance	5.00	200	Zurbuchen et al. 2010a	Amiet*
Megachile	rotundata	Y	foraging distance	7.00	500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	dorsata	Y	foraging distance	9.00	650	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Lasioglossum	calceatum	Y	foraging distance	9.00	1000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	flavipes	Y	foraging distance	12.00	1150	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	carbonaria	Y	foraging distance	13.50	1250	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Lasioglossum	fulvicorne	Y	foraging distance	6.50	1250	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Megachile	rotundata	Y	foraging distance	7.00	100	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Megachile	spp.	Y	foraging distance	7.50	1000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Xylocopa	flavorufa	Y	foraging distance	25.00	6040	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Osmia	anthocopoides	Y	homing distance	9.50	150	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Megachile	femorata	Y	homing distance	13.50	500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	vaga	Y	homing distance	13.00	510	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	barbilabris	Y	homing distance	11.00	530	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	flavipes	Y	homing distance	12.00	530	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Tetralonia	salicariae	Y	homing distance	9.50	600	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Megachile	nana	Y	homing distance	NA	650	Zurbuchen et al. 2010a	NA
Megachile	flavipes	Y	homing distance	NA	800	Zurbuchen et al. 2010a	NA
Osmia	rufa	Y	homing distance	10.50	900	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Osmia	mustelina	Y	homing distance	12.00	1000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Anthidium	septemdentatum	Y	homing distance	10.50	1200	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Xylocopa	violacea	Y	homing distance	21.50	1200	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Chelostoma	florisomne	Y	homing distance	9.00	2000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Xylocopa	flavorufa	Y	homing distance	25.00	10000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Tetralonia	salicariae	Y	homing distance	9.50	400	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	barbilabris	Y	homing distance	11.00	500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	flavipes	Y	homing distance	12.00	600	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	vaga	Y	homing distance	13.00	600	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Osmia	rufa	Y	homing distance	10.50	900	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	male flight distance	21.50	9900	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	550	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	630	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	muscorum	N	foraging distance	18.00	200	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	sp.	N	foraging distance	20.00	300	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	800	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	lapidarius	N	foraging distance	21.00	1500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	1500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	1750	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	sp.	N	flying range	20.00	350	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	pascuorum	N	foraging distance	16.50	2300	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	2800	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	312.5	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	pascuorum	N	foraging distance	16.50	449	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	lapidarius	N	foraging distance	21.00	450	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	pratorum	N	foraging distance	16.00	674	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Bombus	terrestris	N	foraging distance	21.50	758	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Melipona	mandacaia	N	foraging distance	NA	2100	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Nannotrigona	testaceicornis	N	foraging distance	NA	951	Zurbuchen et al. 2010a	NA
Plebeia	poecilochroa	N	foraging distance	NA	951	Zurbuchen et al. 2010a	NA
Scaura	latitarsis	N	foraging distance	NA	951	Zurbuchen et al. 2010a	NA

Tetragonisca	angustula	N	foraging distance	NA	951	Zurbuchen et al. 2010a	NA
Frieseomelitta	varia	N	foraging distance	NA	1710	Zurbuchen et al. 2010a	NA
Geotrigona	inusitata	N	foraging distance	NA	1710	Zurbuchen et al. 2010a	NA
Partamona	cupira	N	foraging distance	NA	1710	Zurbuchen et al. 2010a	NA
Scaptotrigona	postica	N	foraging distance	NA	1710	Zurbuchen et al. 2010a	NA
Trigona	hypogea	N	foraging distance	NA	1710	Zurbuchen et al. 2010a	NA
Trigona	recursa	N	foraging distance	NA	1710	Zurbuchen et al. 2010a	NA
Melipona	bicolor	N	foraging distance	NA	2000	Zurbuchen et al. 2010a	NA
Melipona	scutellaris	N	foraging distance	NA	2000	Zurbuchen et al. 2010a	NA
Plebeia	droryana	N	foraging distance	NA	540	Zurbuchen et al. 2010a	NA
Melipona	marginata	N	foraging distance	NA	800	Zurbuchen et al. 2010a	NA
Trigona	spinipes	N	foraging distance	NA	840	Zurbuchen et al. 2010a	NA
Melipona	quadrifasciata	N	foraging distance	NA	2000	Zurbuchen et al. 2010a	NA
Melipona	compressipes	N	foraging distance	NA	2470	Zurbuchen et al. 2010a	NA
Trigona	capitata	N	homing distance	NA	1547	Zurbuchen et al. 2010a	NA
Melipona	fasciata	N	homing distance	NA	2085	Zurbuchen et al. 2010a	NA
Apis	florea	N	foraging distance	9.00	500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	915	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	1100	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	1243	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	1413	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	cerana	N	foraging distance	10.00	1900	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	7900	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	10100	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	florea	N	foraging distance	9.00	11200	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	dorsata	N	foraging distance	13.00	12000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	13500	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Apis	mellifera	N	foraging distance	12.00	14000	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Andrena	barbilabris	Y	homing distance max	10.75	100	Greenleaf et al. 2007	length from it-span
Andrena	flavipes	Y	homing distance max	10.75	200	Greenleaf et al. 2007	length from it-span
Andrena	vaga	Y	homing distance max	14.00	300	Greenleaf et al. 2007	length from it-span
Anthophora	abrupta	Y	homing distance max	15.13	500	Greenleaf et al. 2007	length from it-span
Bombus	terrestris	N	homing distance max	12.82	800	Greenleaf et al. 2007	length from it-span
Dasypoda	altercator	Y	homing distance max	13.75	1700	Greenleaf et al. 2007	length from it-span
Eufriesea	surinamensis	N	homing distance max	18.23	24000	Greenleaf et al. 2007	length from it-span
Lasioglossum	umbripenne	Y	homing distance max	4.50	100	Greenleaf et al. 2007	length from it-span
Megachile	flavipes	Y	homing distance max	16.00	500	Greenleaf et al. 2007	length from it-span
Megachile	nana	Y	homing distance max	6.00	400	Greenleaf et al. 2007	length from it-span
Megachile	rotundata	Y	homing distance max	8.00	1400	Greenleaf et al. 2007	length from it-span
Osmia	cornifrons	Y	homing distance max	11.28	600	Greenleaf et al. 2007	length from it-span
Osmia	rufa	Y	homing distance max	11.25	500	Greenleaf et al. 2007	length from it-span
Tetraloniella	salicariae	Y	homing distance max	9.88	200	Greenleaf et al. 2007	length from it-span
Xylocopa	virginica	Y	homing distance max	20.00	7500	Greenleaf et al. 2007	length from it-span

Table A.2.5. Raw data used for the analysis of pollen provisions.

Genus	Species	Body length female	Nest	Pollen per brood cell: number	Pollen per trip cell: number	Pollen per brood cell: volume	Data source	Body length source
Andrena	hattorfiana	14.5	soil	284021	31120	129.64	Larsson and Franzén 2007	Scheuchl**
Andrena	humilis	10.0	soil	3378585	876159	NA	Franzén and Larsson 2007	Franzén and Larsson 2007
Andrena	marginata	10.0	soil	116000	NA	NA	Larsson 2006	Scheuchl**
Chelostoma	rapunculi	9.0	cavity	NA	4902965	NA	Schlindwein et al. 2005	Scheuchl**
Chelostoma	rapunculi	9.0	cavity	3596300	187500	56.37	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Heriades	truncorum	6.5	cavity	2254200	NA	NA	Hamm et al. 2004	Amiet*
Hoplitis	adunca	10.0	cavity	23083000	501700	35.32	Zurbuchen et al. 2010a	Zurbuchen et al. 2010a
Mechachile	rotundata	8.5	cavity	NA	91376	NA	O'Neill and O'Neill 2011	Amiet*
Osmia	cornifrons	NA	cavity	7000000	NA	NA	Maeta 1978	NA
Osmia	cornuta	13.5	cavity	6340365	NA	NA	Bosch 1994	Amiet*
Osmia	cornuta	13.5	cavity	6700000	NA	NA	Sieg et al. 2004	Amiet*
Osmia	rufa	10.0	cavity	8300000	NA	NA	Sieg et al. 2004	Amiet*
Osmia	taurus	10.0	cavity	9000000	NA	NA	Maeta 1978	Amiet*
Dieunomia	triangulifera	14.5	soil	2847893	601388	NA	Minckley et al. 1994	Mitchell***
Hylaeus	punctulatissimus	8.0	cavity	914894	NA	4.30	Müller et al. 2006	Amiet*
Hylaeus	signatus	8.0	cavity	1275330	NA	11.58	Müller et al. 2006	Amiet*
Colletes	cunicularius	13.5	soil	NA	NA	61.86	Müller et al. 2006	Amiet*
Colletes	daviesanus	9.0	soil	3348123	NA	29.43	Müller et al. 2006	Amiet*
Colletes	hederae	11.5	soil	5144242	NA	42.44	Müller et al. 2006	Amiet*
Andrena	ruficrus	10.5	soil	NA	NA	15.92	Müller et al. 2006	Scheuchl**
Andrena	vaga	14.0	soil	NA	NA	47.60	Müller et al. 2006	Scheuchl**
Chelostoma	florisomne	9.0	cavity	2471388	NA	34.55	Müller et al. 2006	Scheuchl**
Chelostoma	rapunculi	8.5	cavity	1556619	NA	24.40	Müller et al. 2006	Scheuchl**
Heriades	truncorum	6.5	cavity	1732651	NA	15.23	Müller et al. 2006	Amiet*
Hoplitis	adunca	11.0	cavity	13816993	NA	21.14	Müller et al. 2006	Scheuchl**
Hoplitis	mocsaryi	11.5	soil	861573	NA	41.95	Müller et al. 2006	Scheuchl**
Hoplitis	tridentata	11.0	cavity	5014808	NA	50.80	Müller et al. 2006	Scheuchl**
Hoplosmia	spinulosa	7.5	cavity	3178612	NA	27.94	Müller et al. 2006	Scheuchl**

Table A.2.6. Raw data used for the analysis of flower handling time.

Genus	Species	Body length	Handling time	Handling type	Estimate by flower visits per minute	Apis vs. non-Apis	Eusocial v.s solitary	Set	Visited plant	Set of site and year	Data source	Body length source
Hoplitis	anthocopoides	9.97	5.70	pollen	n	n	n	1	Echium vulgare	NA	Strickler 1979	Strickler 1979
Megachile	relativa	10.01	10.40	pollen	n	n	n	1	Echium vulgare	NA	Strickler 1979	Strickler 1979
Osmia	coerulescens	9.52	15.70	pollen	n	n	n	1	Echium vulgare	NA	Strickler 1979	Strickler 1979
Hoplitis	producta	6.63	29.30	pollen	n	n	n	1	Echium vulgare	NA	Strickler 1979	Strickler 1979
Ceratina	calcarata	6.24	31.70	pollen	n	n	n	1	Echium vulgare	NA	Strickler 1979	Strickler 1979
Andrena	nasonii	8.00	124.90	pollen	n	n	n	2	Fragaria × ananassa	NA	Chagnon et al. 1993	Chagnon et al. 1993
Apis	mellifera	12.00	24.40	pollen	n	a	e	2	Fragaria × ananassa	NA	Chagnon et al. 1993	Chagnon et al. 1993
Halictus	confuses	7.00	43.20	pollen	n	n	n	2	Fragaria × ananassa	NA	Chagnon et al. 1993	Chagnon et al. 1993
Dialictus	lineatulus	6.00	133.20	pollen	n	n	n	2	Fragaria × ananassa	NA	Chagnon et al. 1993	Chagnon et al. 1993
Dialictus	cressonii	6.50	49.40	pollen	n	n	n	2	Fragaria × ananassa	NA	Chagnon et al. 1993	Chagnon et al. 1993
Augochlorella	striata	5.50	38.80	pollen	n	n	n	2	Fragaria × ananassa	NA	Chagnon et al. 1993	Chagnon et al. 1993
Chelostoma	rapunculi	9.50	4.60	nectar	n	n	n	3	Campanula rapunculus	NA	Schlindwein et al. 2005	Schlindwein et al. 2005
Chelostoma	campanularum	5.25	5.90	nectar	n	n	n	3	Campanula rapunculus	NA	Schlindwein et al. 2005	Schlindwein et al. 2005
Chelostoma	rapunculi	9.50	12.40	pollen	n	n	n	3	Campanula rapunculus	NA	Schlindwein et al. 2005	Schlindwein et al. 2005
Chelostoma	campanularum	5.25	62.30	pollen	n	n	n	3	Campanula rapunculus	NA	Schlindwein et al. 2005	Schlindwein et al. 2005
Bombus	hortorum	24.00	2.94	mixed	y	n	e	4	Vicia villosa	NA	Benedek et al. 1973	{Schmiedeknecht, 1907 #1893
Bombus	lapidarius	25.00	4.06	mixed	y	n	e	4	Vicia villosa	NA	Benedek et al. 1973	{Schmiedeknecht, 1907 #1893
Eucera	similis	11.50	3.78	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Eucera	interrupta	14.00	3.84	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Eucera	tuberculata	15.00	4.18	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Eucera	nitidiventris	13.00	4.58	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Eucera	pollinosa	14.50	5.40	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Tetralonia	pollinosa	13.50	4.45	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Andrena	variabilis	14.00	7.82	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Andrena	labialis	13.50	8.00	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Andrena	ovatula	10.00	11.90	mixed	y	n	n	4	Vicia villosa	NA	Benedek et al. 1973	Scheuchl**
Bombus	terrestris	26.00	3.70	mixed	y	n	e	4	Vicia villosa	NA	Benedek et al. 1973	{Schmiedeknecht, 1907 #1893
Andrena	ovatula	10.00	11.90	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Scheuchl**
Rhophitoides	canus	7.50	10.60	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Amiet*
Halictus	eurygnathus	6.50	11.63	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Amiet*
Andrena	flavipes	11.50	13.45	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Scheuchl**
Halictus	rubicundus	10.50	13.39	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Amiet*
Melitta	leporina	11.50	5.76	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Amiet*
Eucera	cinerea	10.00	7.31	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Scheuchl**
Eucera	clypeata	11.50	5.66	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Scheuchl**
Melitturga	clavicornis	14.00	3.72	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Scheuchl**
Bombus	terrestris	26.00	8.03	mixed	y	n	e	5	Medicago sativa	NA	Benedek 1973	{Schmiedeknecht, 1907 #1893
Eucera	nitidiventris	13.00	7.64	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Scheuchl**
Eucera	pollinosa	14.50	6.87	mixed	y	n	n	5	Medicago sativa	NA	Benedek 1973	Scheuchl**
Bombus	lapidarius	25.00	5.31	mixed	y	n	e	5	Medicago sativa	NA	Benedek 1973	{Schmiedeknecht, 1907 #1893
Apis	mellifera	12.00	7.50	nectar	y	a	e	6	Vaccinium angustifolium	NA	Javorek et al. 2002	Mitchell***
Mechachile	rotundata	8.50	13.95	nectar	y	n	n	6	Vaccinium angustifolium	NA	Javorek et al. 2002	Scheuchl**
Mechachile	rotundata	8.50	7.89	pollen	y	n	n	6	Vaccinium angustifolium	NA	Javorek et al. 2002	Scheuchl**
Bombus	spp	15.50	5.36	pollen	y	n	e	6	Vaccinium angustifolium	NA	Javorek et al. 2002	Michener 2000
Andrena	spp	12.00	8.33	pollen	y	n	n	6	Vaccinium angustifolium	NA	Javorek et al. 2002	Javorek et al. 2002
Halictus	spp	8.75	9.84	pollen	y	n	n	6	Vaccinium angustifolium	NA	Javorek et al. 2002	Scheuchl**
Eucera	dimidiata	12.50	1.80	mixed	n	n	n	7	Echium angustifolium	NA	Nachtigall 1994	Nachtigall 1994
Eucera	graeca	13.00	5.60	mixed	n	n	n	7	Echium angustifolium	NA	Nachtigall 1994	Nachtigall 1994
Anthophora	rutilans	16.50	2.70	mixed	n	n	n	7	Echium angustifolium	NA	Nachtigall 1994	Nachtigall 1994
Anthophora	rutilans	16.50	4.30	mixed	n	n	n	7	Echium angustifolium	NA	Nachtigall 1994	Nachtigall 1994
Apis	mellifera	13.00	4.20	mixed	n	a	e	7	Echium angustifolium	NA	Nachtigall 1994	Nachtigall 1994

Apis	mellifera	12.00	8.08	mixed	n	a	e	8	Lotus corniculatus	A1	Richards 1996	Mitchell***
Apis	mellifera	12.00	8.97	mixed	n	a	e	8	Lotus corniculatus	A2	Richards 1996	Mitchell***
Bombus	fervidus	13.25	6.76	mixed	n	n	e	8	Lotus corniculatus	A1	Richards 1996	Mitchell***
Bombus	fervidus	13.25	13.43	mixed	n	n	e	8	Lotus corniculatus	A2	Richards 1996	Mitchell***
Bombus	huntii	12.00	5.75	mixed	n	n	e	8	Lotus corniculatus	A2	Richards 1996	Mitchell***
Bombus	huntii	12.00	6.28	mixed	n	n	e	8	Lotus corniculatus	A1	Richards 1996	Mitchell***
Bombus	nevadensis	19.00	6.37	mixed	n	n	e	8	Lotus corniculatus	A1	Richards 1996	Mitchell***
Bombus	nevadensis	19.00	7.82	mixed	n	n	e	8	Lotus corniculatus	A2	Richards 1996	Mitchell***
Bombus	rufocinctus	11.75	3.67	mixed	n	n	e	8	Lotus corniculatus	A1	Richards 1996	Mitchell***
Megachile	melanopheae	13.00	7.15	mixed	n	n	n	8	Lotus corniculatus	A2	Richards 1996	Goertz 2010
Megachile	melanopheae	13.00	8.52	mixed	n	n	n	8	Lotus corniculatus	A1	Richards 1996	Goertz 2010
Megachile	perihirta	12.50	5.43	mixed	n	n	n	8	Lotus corniculatus	A1	Richards 1996	Goertz 2010
Megachile	relativa	10.50	6.80	mixed	n	n	n	8	Lotus corniculatus	A1	Richards 1996	Goertz 2010
Megachile	relativa	10.50	13.87	mixed	n	n	n	8	Lotus corniculatus	A2	Richards 1996	Goertz 2010
Megachile	rotundata	8.50	6.30	mixed	n	n	n	8	Lotus corniculatus	A2	Richards 1996	Mitchell***
Megachile	rotundata	8.50	6.88	mixed	n	n	n	8	Lotus corniculatus	A1	Richards 1996	Mitchell***
Apis	mellifera	12.00	8.60	mixed	n	a	e	9	Astragalus cicer	B1	Richards 1996	Mitchell***
Apis	mellifera	12.00	11.50	mixed	n	a	e	9	Astragalus cicer	A1	Richards 1996	Mitchell***
Apis	mellifera	12.00	15.60	mixed	n	a	e	9	Astragalus cicer	A2	Richards 1996	Mitchell***
Apis	mellifera	12.00	17.30	mixed	n	a	e	9	Astragalus cicer	B2	Richards 1996	Mitchell***
Bombus	huntii	12.00	4.90	mixed	n	n	e	9	Astragalus cicer	A1	Richards 1996	Essig 1926
Bombus	huntii	12.00	6.10	mixed	n	n	e	9	Astragalus cicer	A2	Richards 1996	Mitchell***
Bombus	huntii	12.00	6.40	mixed	n	n	e	9	Astragalus cicer	B2	Richards 1996	Mitchell***
Bombus	nevadensis	19.00	2.60	mixed	n	n	e	9	Astragalus cicer	B2	Richards 1996	Mitchell***
Bombus	nevadensis	19.00	2.70	mixed	n	n	e	9	Astragalus cicer	A2	Richards 1996	Mitchell***
Bombus	nevadensis	19.00	2.80	mixed	n	n	e	9	Astragalus cicer	A1	Richards 1996	Mitchell***
Bombus	nevadensis	19.00	4.50	mixed	n	n	e	9	Astragalus cicer	B1	Richards 1996	Mitchell***
Bombus	occidentalis	12.25	8.50	mixed	n	n	e	9	Astragalus cicer	B2	Richards 1996	Mitchell***
Bombus	rufocinctus	11.75	4.90	mixed	n	n	e	9	Astragalus cicer	A2	Richards 1996	Mitchell***
Bombus	rufocinctus	11.75	5.90	mixed	n	n	e	9	Astragalus cicer	A1	Richards 1996	Mitchell***
Bombus	rufocinctus	11.75	7.00	mixed	n	n	e	9	Astragalus cicer	B2	Richards 1996	Mitchell***
Apis	mellifera	12.00	5.66	mixed	n	a	e	10	Onobrychis viciaefolia	mixed	Richards 1996	Mitchell***
Megachile	rotundata	8.50	7.67	mixed	n	n	n	NA	Medicago sativa	A3	Richards 1996	Mitchell***
Megachile	rotundata	8.50	8.43	mixed	n	n	n	NA	Medicago sativa	A1	Richards 1996	Mitchell***
Megachile	rotundata	8.50	10.15	mixed	n	n	n	NA	Medicago sativa	A2	Richards 1996	Mitchell***
Megachile	rotundata	8.50	6.20	mixed	n	n	n	9	Astragalus cicer	A2	Richards 1996	Mitchell***
Megachile	rotundata	8.50	6.30	mixed	n	n	n	9	Astragalus cicer	B2	Richards 1996	Mitchell***
Megachile	rotundata	8.50	5.54	mixed	n	n	n	10	Onobrychis viciaefolia	mixed	Richards 1996	Mitchell***

A3. Additional guidance for measuring the body size of bees

The four different body size dimensions (it-span, dry mass, fresh mass, length) all have their own advantages and disadvantages. Intertegular span and dry mass are most reliable since they have the least variance between individuals of a species and cannot be influenced by water content. Fresh mass and length depend on water content, and length is additionally inaccurate due to taxonomic differences in ratio between length and width. Dry body mass (as well as fresh mass) can easily be "contaminated" with mass from pollen and nectar which should be removed prior to measurement. In practice, bees with empty pollen brushes are selected instead (Cane 1987, Müller et al. 2006) or loading is prevented altogether by using freshly emerged individuals (Stone 1995). It-span is the only measure based on a size-fixed chitin-containing plate and thus closest to the genotype of the bee. It is insensitive to differences in head-abdomen and length-volume ratios and one does not have to regard pollen and nectar loads. Dry body mass and it-span can accurately be measured in every laboratory. Measuring intertegular span requires a microscope with measure ocular and can be time consuming. Also bees have to be killed for both, which is undesirable from the perspective of species conservation and in many countries prohibited (many bees species are nowadays on the Red Data Lists). It should only be considered for museum or pan-trapped specimens. Many studies have used fresh mass as body size measure which is especially convenient in the field and independent of body length to width ratio. On the other hand, pollen and nectar loads can make up to one third of the total fresh mass (i.e. bees can increase half of their body mass with pollen and nectar, Stanley and Linskens 1974, Neff 2008), which may cause stronger deviations between species than a distorted length-width ratio. This methodological issue in the field has not been solved for solitary bees as far as we know. Body length can vary considerably between taxa (compared to dry mass) and it can differ for specimens of the same species depending on medium and method (fresh, dried -pinned- and alcohol-preserved specimens). Nevertheless our analysis showed that body length is a reliable dimension for body size studies and can be well approximated by independent literature references.

APPENDIX B

Supplementary material to the model SOLBEE

B1. Full rule description of the model and scheduling (including all submodels)

This section contains the full verbal description of the model rules independent of programming language. We implemented these rules in C++, but they could be implemented in any programming language. We provide here also additional details that are required to reproduce the model but are not given elsewhere. We left out some initializations, resets (back to zero), safety checks, and observer parameters to keep the structure clear. They can be reproduced by common sense of the programmer (and are hence part of good programming practice rather than part of our rule set design). In two cases a value was technically not allowed to become zero (division by zero) so that a correction was needed and they are included in the following description. Steps marked with an * are explained in more detail separately, after 'Main'.

A. Main

```
Read input value from text file
Calculate secondary input values *
Generate landscape *
Define a list of bees of one species
Assign a nest to each bee *

I. Start time loop (for each time step do:)

    Shuffle bee list randomly

II. Start individual loop

    A. When an individual's future time equals current time step (do:)

    (Initializations)

    Action according to one of following 5 behavioural states (1. FORAGE FLOWERS,
    2. NEIGHBOURING CELL, 3. FLY AROUND, 4. FLY BACK, 5. NEST REACHED):

    1. FORAGE FLOWERS (Forage flowers within a landscape grid cell)
        a. Perform only when newly entering the landscape cell:
            Set visitation mark in the landscape;
            Save position in memory (overwrite first position when memory is full).
        b. Perform always:
            aa. If minimal flowers to probe within landscape grid cell have been probed:
                Calculate leave threshold (third threshold value, uniform between upper and lower threshold);
                Calculate good fraction (success visits/flowers probed);
                Compare this fraction with remembered fraction (thus ratio present fraction/remembered
                fraction, is >1 if better than remembered);
                aaa. If ratio present-remembered < leave threshold:
                    Leave (aaaa or bbbb);
                    Set time to spend till next behaviour (1 s for assessing patch quality);
                    Add successful and unsuccessful visits from cell level to foraging bout level;
                    aaaa. If ratio present-remembered < lower threshold:
```

```
                    Set an initial direction to fly;
                    Leave; set behavioural state to FLY AROUND (3).
                bbbb.  If ratio present-remembered between lower threshold and upper threshold:
                    Leave; set behavioural state to NEIGHBOURING CELL (2).
            bbb. If ratio present-remembered > leave threshold:
                Stay, and continue with bb.
        bb. (1) If minimal # flowers has not been probed yet or (2) if it proved to be a good cell (and individual stays, coming from aa.):
            Visit a new flower:
            Calculate time to spend till next behaviour (low velocity × average flower distance);
            Calculate local floral resources (implicitly) *;
            aaa. When a successful flower visit has been made:
                add 1 to successful visits and total visits at cell level;
                add pollen to individual (foraging bout level);
                Determine time to spend till next behaviour (add handling time);
                aaaa. If loading capacity is reached:
                    Leave:
                    Add pollen to total collected pollen (equals loading capacity, at foraging day level);
                    (Determine current distance from nest and realized foraging range);
                    Add successful and unsuccessful visits from cell level to bout level;
                    Leave; set behavioural state to FLY BACK (4).
                bbbb. Loading capacity not reached:
                    Stay.
            bbb. If a unsuccessful flower visit has been made:
                Add 1 to unsuccessful visits and total visits at cell level;
                Set time to spend till next behaviour (add minimal handling time).
2. NEIGHBOURING CELL (Fly to a suitable neighbouring landscape grid cell)
    Analyze 8 neighbouring landscape grid cells *;
    Determine time to spend till next behaviour (add 1 second for decision);
    a. If a suitable cell is found:
        Move and start foraging flowers there; set behavioural state to FORAGE FLOWERS (1);
        Calculate time to spend till next behaviour (add high velocity × cell size).
    b. If no suitable cell could be found:
        Leave:
        Determine distance from nest;
        aa. If the maximum foraging range is reached:
            (Determine realized foraging range);
            Set maximum foraging distance for next foraging bout *;
            Leave; set behavioural state to FLY BACK (4).
        bb. If the maximum foraging range is not reached:
            Set an initial direction to fly;
            Leave; set behavioural state to FLY AROUND (3).
3. FLY AROUND (Fly around and look for unknown foraging areas)
    Perform a "correlated random walk" (change direction and move one step with certain length, and correct for landscape border*);
    Set visitation mark in the landscape;
    Calculate time to spend till next behaviour (high velocity × distance moved);
```

```
    a. If new landscape grid cell is foraging habitat and not remembered:
        aa. With a high probability (1-"ignorance"):
            Set behavioural state to FORAGE FLOWERS (1).
        bb. With a low probability ("ignorance"):
            Determine current distance from nest;
            aaa. If the maximum foraging range is reached:
                (Determine realized foraging range);
                Set maximum foraging distance next foraging bout *;
                (set pollen collected to non-zero (i.e. very low) if no pollen were collected);
                Leave; set behavioural state to FLY BACK (4).
            bbb. If the maximum foraging range is not reached:
                Keep flying around next time.
    b. If new cell is remembered (recently visited) or non-foraging habitat:
            Determine whether there is a grid cell with foraging habitat within sight and if so choose closest *;
            aa. If there is a landscape grid cell with foraging habitat in sight and this is not ignored (a high probability: 1-"ignorance"):
                Fly to cell with foraging habitat (perform second move);
                Calculate time to spend till next behaviour (add high velocity × distance moved);
                Set behavioural state to FORAGE FLOWERS (1).
            bb. If there is no landscape grid cell with foraging habitat in sight or foraging habitat is ignored (a low probability: "ignorance"):
                Keep flying around next time.
4. FLY BACK (Fly back to nest)
    Perform a "directed random walk" (move one step with certain length in the direction of the nest);
    Set a visitation mark in the landscape;
    Calculate time to spend till next behaviour (high velocity × distance moved);
    a. If nest reached within this step:
        Set behavioural state to NEST REACHED (5).
    b. If nest not reached within this step:
        Keep flying to nest next time.
5. NEST REACHED
    Add flowers visited and pollen collected from bout level to global level;
    Set time to spend till next behaviour (fixed time at nest);
    Determine foraging bout duration and set new time for bout start;
    Remember cell quality of last visited flower habitat cell (success visits/flowers probed) (set quality to non-zero (i.e. very low) in case it applies);
    Do several resets (including memory of visited cells);
    Add one to nest returns;
    Set behavioural state to FORAGE FLOWERS (1).

After one of the behaviours:
Set wait time (time to spend till next behaviour, minimal 1 second which is the smallest time step);
Set future time step when to do something (current time step + wait time).
```

B. If an individual's future time is higher than current time step

Proceed with next individual.

```
All individuals are checked (end of loop II)

Foraging day completed (end of loop I)

Collecting data at the end of the foraging day
Individual loop 1: collate data per individual
a. If individual is not currently at nest:
    Number of foraging bouts = nest visits+1;
    Count additional flowers visited and pollen collected.
b. If individual is currently at nest:
    Number of foraging bouts = nest visits.
Calculate average return distance and average trip duration;
Add 1 to non-returned individuals if individual never returned;
Add 1 to deaths if individual died;
Individual loop 2: average across individuals
Calculate totals and averages for all individuals;
Convert pollen collected into brood cells;
Calculate other describing statistics (e.g. mortality);
Collect landscape level data
(Calculate additional landscape and nest site statistics);
Write output files
Write all essential values to file (input values, describing landscape statistics, bee performance);
Write landscape map to two files (as graphical and textual format);
Write visitation map to two files (as graphical and textual format).
```

B. Submodels (above marked with *)

Calculate secondary input values (e.g. allometric scaling rules)

Set coarse grid dimensions and fine grid dimensions according to landscape extent and landscape element size or perceived detail by the bee;

Set size related bee characteristics (from body length and calculated weight and inter-tegular span):

pollen needed for one brood cell, maximum pollen load per foraging bout, high velocity, low velocity, flower handling time, sight distance, average flight 'step' length, border effects correction, number of individuals, curve characteristics for determining foraging range, pollen uptake per visit.

Generate landscape

Create three grids:

- a 'generator' grid with 257 × 257 cells for the landscape generator;
- a coarse grid, based on fixed landscape element detail;
- a fine grid, based on the bees perspective of the landscape;

Generate a landscape on the 'generator' grid with floating point numbers according to Saupe's midpoint displacing algorithm (with wrapping and symmetry) using the fragmentation value;

Resize (in our case up-sampling to 40 by 40 cells) this map to a coarse grid of floating point numbers "flood the valleys" (after sorting cells) using a threshold value for foraging habitat availability (convert to binary suitable and unsuitable foraging habitat);

Resize the coarse grid to a fine grid for foraging bees (in our case down-sampling to 200 by 200 cells);

Initialize each foraging habitat cell with pollen according to flower density and pollen per flower.

Assign a nest to each bee

Choose a random location and correct for landscape border (no nesting);

a. If the bees nest in woody edge habitat:

Accept location if the chosen landscape grid cell is foraging habitat and has at least one neighbouring cell unsuitable for foraging.

b. If bees nest in bare soil habitat:

Accept location if the chosen landscape grid cell is foraging habitat and if:

- grid cell is already assigned as nesting habitat (at least one individual nesting in it);
- grid cell has a neighbouring cell assigned as nesting habitat and a certain probability applies (nest clumping);
- grid cell has no neighbouring cell assigned as nesting habitat and a certain probability applies (1-nest clumping).

If location not accepted, choose a new location, until one accepted (safety break for 1 million tries).

Calculate local floral resources

Determine remaining pollen in landscape grid cell (current floral resources);

Calculate the possible number of full flowers remaining (from pollen and flower density);

Calculate the proportion of full flowers (possible number of full flowers/initial number of flowers) currently in landscape grid cell (this is the probability of visiting a flower with pollen);

Determine success or failure;

If success, deplete pollen in landscape grid cell (calculate future floral resources) according to the pollen a bee gets (as determined in function 'calculate secondary input values' *).

Analyze 8 neighbouring landscape grid cells

Consider 3 by 3 landscape grid cells around current position;
Suitable if:
- foraging habitat, AND
- not current position, AND
- not outside landscape borders, AND
- not in memory.

Choose one of the suitable cells randomly, or return "unsuitable".

Set maximum foraging distance next foraging bout

Inverse function of the Michaelis-Menten Curve, with parameters as determined in function 'calculate secondary input values';

A uniform probability (input) determines the maximum foraging distance from the nest for the next bout.

Choose closest landscape grid cell with foraging habitat

Consider the area within the sight radius (square around current position);
Correct for landscape border * (rectangular);
Analyse landscape within this area (defined by 4 outside positions);
Determine closest cells with foraging habitat that is not memorized;
Choose one of the closest cells randomly.

Correct for landscape border (when flying)

If a flight step is supposed to go over the landscape border, take the same step in opposite direction (mirror move in x or y direction);

Calculate new direction (take position outside grid as 'old position' and take corrected position as 'new location').

B2. Concept details of several submodels

Maximum distance allowed to fly on a foraging trip (distance of certain return)

First we calculated the typical (r50) and far (r90) homing distance (distance beyond which 50% and 90% of the bees were not able to return at release respectively) for a bee of a certain size based on a known allometric relationship (Greenleaf et al. 2007):

$$\text{r50} = 10^{(-1.643 + 3.242 \times \log_{10} \text{it-span}))} \tag{1}$$

$$\text{r90} = 10^{(-1.363 + 3.366 \times \log_{10} \text{it-span}))} \tag{2}$$

We use a hyperbolic Michaelis–Menten function to describe a homing probability curve. We could solve the equation with two parameters (r50 and r90) for a bee of a certain size. Since a Michaelis–Menten function normally goes through the origin and we preferred to have a range of x values (close to the nest) for which a bee would be able to return (minimal knowledge of the environment) we shifted the curve, based on the two known points on this curve (r50 and r90):

$$\text{shift} = 1.125 \times \text{r50} - 0.125 \times \text{r90} \tag{3}$$

(See also equation 5 where 50% and 90% return probability share the same shift value, resulting in (3))
The saturation constant Km changes accordingly:

$$\text{Km} = \text{r50} - \text{shift} \tag{4}$$

The return or homing probability is than described by a Michaelis–Menten function:

$$\text{P}_{\text{return}} = \frac{x - \text{shift}}{\text{Km} + x - \text{shift}}$$

(5), where x is the distance from the nest.

The response can be interpreted as the probability that an individual has reached the distance at which beyond it has no knowledge of the environment (will not be able to return home to the nest).

We know that bees fly exclusively within their homing range, which differs between individuals and within different directions. We decided to include this in the model as distance beyond which a bee is not allowed to fly and was calculated for each individual, on each foraging bout.

$$\text{distance}_{\text{return}} = \frac{\text{U} \times \text{Km}}{1 - \text{U}} + \text{shift}$$

(6), where U is drawn from a uniform distribution.

This reproduces a realistic set of distances from the nest where the bee should maximally return, never close to the nest and with a similar shape as for real foraging data (Abrol and Kapil 1994). An asymmetrical S-Curve would probably a good alternative, but we could not fit it with two known points.

Landscapes and habitat

We use 'noise' from a random number generator (*landscape stochastic factor*) and a Hurst exponent for fractional Brownian motion (*landscape fragmentation*) and a threshold (*foraging habitat availability*) to generate a landscape with the midpoint displacement algorithm (Saupe 1988). In short, this algorithm creates a three-dimensional surface, based on four initial corner points. With 'noise' from a random number generator (*landscape stochastic factor*) and a Hurst exponent for fractional Brownian motion, the additional grid points are calculated. The three-dimensional surface is converted to a two-dimensional suitable-unsuitable map by the 'valley flooding' method (in which 'water' represents the suitable habitat). This method had slightly more realistic looking landscapes than the 'mountain-cut' method. We use a modified algorithm which allows for symmetrical and wrapped landscapes (With et al. 1997). Symmetry prevents the entire suitable habitat to be in one corner, and wrapped boundaries give the landscape the appearance to be part of a larger landscape.

Boundary conditions

We implemented reflecting boundaries as follows. If the new coordinates for a move are calculated (with a change in x, a change in y and the new coordinate pair), we check whether one of the coordinates lies outside the grid. If so, we multiply the change in x, y or both with −1. This means that a line through the old coordinate pair, parallel to the border, functions as a mirror.

The correlated random walk is with this implementation not purely random anymore. In the spatial pattern of visitation marks this very small bias can become visible (if the number of individuals and the time spent on flying around are high enough) as lines parallel to the field boundary, near source habitat.

In order to prevent increased local competition at the border we apply a rule that prevents nesting at the border of the landscape. We scale this with body size: the minimal distance from the border where it is allowed to nest equals body length as being given in metres (times 1000 for body length in mm), and we rounded it to landscape grid cells. We have chosen this method after thorough experimentation with alternatives. The selected method has the best average bee performance with the least unwanted effects, but a little higher standard deviation (larger difference between individual bees) for bee performance. The field was always large enough to have most of the bees not nesting near the landscape boundary anyway.

Patch leaving rules

The probability of leaving is based on the relative habitat cell quality (fig. B.1). This is calculated by dividing current habitat quality by the remembered habitat quality. Habitat cell quality is the fraction of successful flower visits to the total flower visits (based on a minimal number of flowers, *fmem*). If the upper patch threshold (*u_plt*) is 1.0 and the current cell has at least the same quality as the last (value of 1.0 or higher), the probability of leaving is 0 (fig.B.1, right). If the relative cell quality comes below a certain threshold (*l_plt*), the probability of leaving is 1 and the bee flies up in search for a better location (behaviour FLY AROUND). A third leaving threshold is determined stochastically (for each decision) from a uniform distribution between the upper and lower patch threshold. If the relative cell quality is below this threshold, the bee will search for resources in neighbouring grid cells (behaviour NEIGBOURING CELL). In other words the separation between staying and leaving in figure B.1 is somewhere on the line between *l_plt* and *u_plt*.

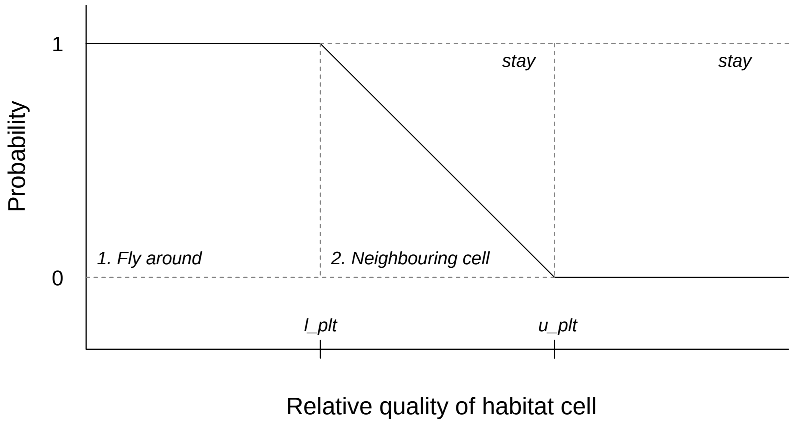


Figure B.2.1. Probability of leaving in relation to habitat cell quality.

Flower encountering

For determining the success of a flower visit we first calculated the proportion of full flowers in the habitat grid cell:

$$\text{proportion full flowers} = \frac{\text{remaining pollen volume in grid cell / pollen volume per flower}}{\text{total flowers per cell}}$$

Since we assume homogeneous vegetation, all habitat grid cells have the same amount of flowers based on *flower density*. For each landscape grid cell with foraging habitat, we track the amount of pollen left, as approximation for the amount of full flowers. We use the proportion of full flowers as probability for encountering a full flower. If a full flower is encountered, the bee takes up pollen according to its uptake capacity, and the amount of pollen in that grid cell decreases by the same amount. The bee receives a time penalty for collecting the pollen. For both full and empty flower encounters, a bee receives a time penalty for flying to the flower (based on distance and speed).

Correlated random walk

a. Turning angles

The turning angles come from a wrapped Cauchy distribution, and can be calculated from a uniform distribution with the inverse cumulative distribution function (Haefner and Crist 1994):

$$\alpha = 2 \times \operatorname{atan}\left(\frac{1-\rho}{1+\rho} \times \tan(\pi \times (U - 0.5))\right)$$

U is a randomly drawn number from a uniform distribution between 0 and 1. The equation returns a number between $-\pi$ and π, with the highest probability around 0. This is regulated by a density parameter ρ (called parameter *CRW* in our model analysis). A higher number means a higher probability around 0, and very small turning angles. We preferred an angle distribution between 0 and 2π, and added 2π for negative numbers, which results in a high probability at both sides of the range 0 - 2π. Then the previous angle is added, so that the new angle is based on the previous angle (which is the correlation in 'correlated random walk'). In some situations we used a directed walk for which we calculated a preferred angle based on a preferred location and added this preferred angle instead of the previous angle. If the result was above 2π we corrected this by subtracting 2π.

b. Step lengths

We used a normal distribution of flight unit lengths (in metres), based on the body size related flight length unit (*flightm*) and a given variance σ:

$$\text{flight lenght} = \sigma \times Z + \mathit{flightm}$$, where

$$Z = \sqrt{2 \times \log(1 - U1)} \times \cos(2\pi \times U2)$$, and

$$\sigma = 0.25 \times \mathit{flightm}$$

A normal distribution can be generated from a uniform distribution with the so-called Box-Muller method (Z). U1 and U2 are both drawn from a uniform distribution between 0 and 1. We defined σ as mean flight unit length (*flightm*) divided by 4. This means 68% of values lie in the range of mean ± 0.25% and the absolute variance thus also depends on the size of the bee. A higher variance leads to too short flight steps. The calculated flight unit length (step length) is converted into grid cell units.

c. Grid-based movement

For converting angles and step lengths into a change in x and y on the grid, one can use an "hourglass-shaped" (acute angle, shortest angle to x-axis) or the 'mill-shaped' (angle relative to the 'start-axis' in a quadrant) transformation system. We use the 'mill-shape', starting in the 'east' and reading counter-clockwise (fig. B.2). From the angle (between 0 and 2π) and step length, x and y are calculated as follows:

- 0.5π is subtracted until the angle α is between 0 and 0.5π; the according quadrant is determined
- In quadrant I and III, the change in x is cos(α) × step length, the change in x is sin(α) × step length
- In quadrant II and IV, the change in x is sin(α) × step length, the change in x is cos(α) × step length
- In quadrant II, x is negative; in quadrant III, x and y are negative; in quadrant IV, y is negative.

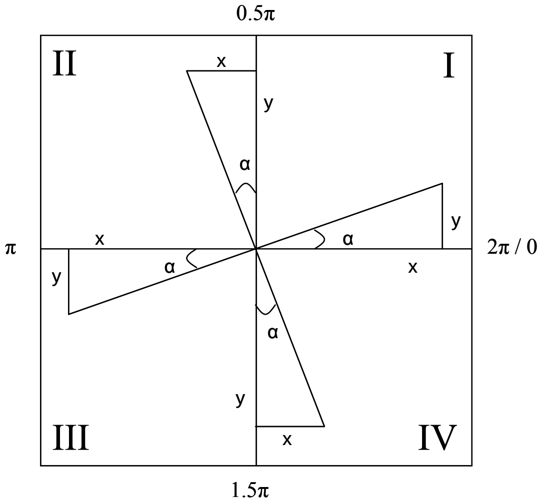


Figure B.2.2. Trigonomic translation of flight steps and turning angles on a grid.

Random number generator

We used an improved random number generator (Kirkpatrick and Stoll 1981), not the standard C random generator.

B3. Data-based parameter selection

We give in this section a short review of the known values from the literature and knowledge gaps for each parameter and describe how we selected a sensible value. We summarized the biological range for each parameter in table B.1 and thereafter we discuss each parameter separately.

Table B.3.1. Here are the variables and parameters listed that are used in the model, accompanied by the biological ranges. Definitions of the parameters are given in the main body of the paper.

	Variable	short	unit	used value	biological range
landscape	foraging habitat availability*	am		0.05 to 0.95	
	landscape fragmentation*	fr		0.05 to 0.95	
	landscape stochastic factor *	seed			
bee	body length*	size	mm	6, 12, 24	4 to 26
	nesting preference*	nest		wood, soil	
	Parameter				
landscape	landscape element size	esize	m	50	from infinitely small to infinitely large, issue of fractality of landscapes
	flower density*	fd	m^{-2}	50	1 to 11000
	pollen per flower*	ppf	mm^3	0.5	0.05 to 22
	pollen availability	plimit		0.3	<0.1 to 1.0, different per species, and relatively unknown
	landscape quality*	bdc		30	unknown
bee	pollen capacity per bee	pcap	mm^3	by size	scaling relationship (acceptable)
	pollen per brood cell	ppb	mm^3	by size	scaling relationship (good)
	velocity medium/low	vmed	$m \cdot s^{-1}$	by size	scaling relationship (acceptable)
	velocity high	vhi	$m \cdot s^{-1}$	by size	scaling relationship (acceptable)
	handling time per flower	ht	s	by size	scaling relationship (acceptable)
	perception distance*	sightm	m	by size	scaling relationship (unknown)
	length of flight units*	flightm	m	by size	scaling relationship (unknown)
	general return distance	r50	km	by size	scaling relationship (acceptable)
	flower memory*	fmem		3	1 to unknown
	habitat cell memory*	cmem		10	unknown
	ignorance	ig		0.1	unknown
	flight path tortuosity*	CRW		0.9	unknown
	lower patch leaving threshold	l_plt		0.5	unknown
	upper patch leaving threshold	u_plt		1.0	unknown
	time at the nest*	ntime	s	30	30 to 800
	flytime	tt	s	14400	4 hours to 16 hours

Landscape element size

Foraging and nesting resources for bees can probably be considered to have a fractal patch size distribution in the landscape. Even in large unsuitable regions, some smaller patches of several square metres and even single isolated flowers (down to a scale of square centimetres) can function as foraging habitat. Despite this, there are several arguments for using a coarse grain size for foraging resources. GIS-based landscape maps often use a detail of 50 square metres and we also used this as grain size for foraging resources. Landscape elements with foraging resources are usually larger than those with nesting resources. A grain size (or element size) of 50 metres as landscape detail (or somewhat smaller 0.2 ha blocks) has been used in several wild bee studies (Monsevičius 1995, Williams and Tepedino 2003, Williams and Kremen 2007). Furthermore, agriculturally dominated landscapes often have a patchy structure of large blocks that can be considered homogeneous, rather than a fractal structure with fine-scaled naturally looking patches. Artificially generated landscapes with a grain size of 30 metres were a good imitation of raster-based GIS maps in Hargis et al. (1998). The use of a grain size of 50 metres in the landscape generator provides useful maps with foraging resources. Since nesting resources for bees are finer scaled (such as linear elements with scrubs or bare spots in the vegetation) we defined nesting resources with another method.

Flower density - pollen per flower - pollen availability

Flower density is a highly variable parameter. For solitary bees the unit for visitation is the flower or flower head and not the plant and flower densities are much higher than plant densities. For a homogeneous vegetation, flower density ranges from hundreds (*Caltha palustris*) to millions (*Thalictrum aquilegiifolium, Ranunculaceae*) per square metre (Szklanowska 1995). High flower densities are often based on florets and not on flower heads (e.g. from Centaurea species: Denisow 2006). For nectar collection these are probably realistic visiting units for bees. Active pollen collection by solitary bees is nevertheless a process on the flower(-head) level. The highest density we could find for real flower units was for *Brassica napus* (oilseed rape) and counted to more than 11.000 per square meter (Kołtowski 2005). Lower densities can have any value. For clover, the flower density was counted at 50 inflorescences (flower heads) per m^2 (Diekötter et al. 2007) but Waddington reported a range of 50 to 250 flowers per square meter (Waddington 1976). Large flowers such as sunflowers are an exception and have a density below 10 per m^2. Other low flower densities reported are often a result of downscaling flower densities from heterogeneous units on a larger (hectare size) scale.

The *amount of pollen per flower* varies considerably between species. Different studies used different measures for pollen production and assessed them with different methods. There are only few examples where different plant species with a wide range of pollen production were compared. The first way to measure pollen production is by number of grains, which ranges from 1100 to 150000 (Harder 1998). A second method is by weighing the amount of pollen, which varies from 0.35 to 6.11 mg for *Ranunculacea* (Szklanowska 1995). The third method is by calculating the pollen volume for each flower, which ranges from 0.05 to 21.7 mm^3 (Müller et al. 2006). For both pollen number and pollen weight, lower values can be found (e.g. Gallardo et al. 1994 , Denisow and Bozek 2008), but we did not find higher values. Calculating the pollen volume is a relative new approach without comparable studies, but the authors put special effort in covering a wide taxonomical range. We used pollen volume, because the most qualitative information of pollen transport by bees is measured in volume (Müller et al. 2006) and therefore in the same unit.

We use an additional parameter for *pollen availability* to regulate pollen removal. Many plants release pollen in portions in order to reduce the pollen that is taken in one visit and helps the plant optimizing pollination. There are many different syndromes for doing this that are widely used in the plant kingdom (Erbar and Leins 1995) and there are no general rules for gradual release and depletion of pollen.

Our model flower does not mimic a certain flower type and we use pollen availability of 0.3 per visit, which determines the maximum amount of pollen that a bee can collect on one visit, independent of bee size. This value allows for a minimum of at least 3 to 4 visits to the flower before being empty. The value of 0.3 reflects natural flower depletion to some extent. Percentages of pollen removal at a first visit (bumble bees) vary from 20% to 80% (Harder 1990a, 1990b). Depletion rates vary from almost all pollen from all plants after 2 hours (Willis and Kevan 1995), to 60% of the pollen per flower after 3 hours (Schlindwein et al. 2005). Some pollen will never be removed (about 1%, see Schlindwein et al. 2005). We also use decision thresholds in the model (explained below) that prevent bees to spend too much time on flowers that provide little (remaining) pollen.

We tried to balance these three different flower parameters in the model. The flower density and pollen production per flower regulate the amount of pollen per square meter. Data (e.g. from Szklanowska 1995) does not reveal a direct relationship between flower density and pollen production per flower. However do plant species in this example with highest flower densities show a low pollen production (lower half of the range), indicating a resource trade-off flower number and pollen per flower.

We used 50 flowers per square meter as flower density with a rather oligolectic bee in mind that only visits flowers of a certain species that has a more scattered distribution. In contrast, polylectic bees often visit many different flowers that have a high combined density.

There is to our knowledge no evidence that the size of the flower (and hence pollen production) is correlated with the size of the flower visitor and decided to use one flower type with a certain amount of pollen visited by all bees of all size (single plant species are visited by a diverse bee fauna, e.g. Greenleaf and Kremen 2006, Hoehn et al. 2008). We decided to use relatively small flowers so that also the smallest bees have to visit several flowers before they have collected enough pollen. Therefore we used a pollen volume of 0.5 mm^3. This value is close to the mean pollen volume of 0.6426 mm^3 for one flower or flower head calculated from the data provided by Müller et al. (2006). In the analysis of the model we explore the consequences of these parameter values, with more extreme values for both *flower density* and *pollen per flower* in simulation experiment 2 and the effect of moderate changes in *pollen availability* in simulation experiment 4.

Landscape quality for bees

The number of bees in the landscape (and hence bee density) scale with body size and pollen availability in the landscape and is regulated with the parameter *landscape quality for bees*. A high value for *landscape quality for bees* (large potential number of brood cells that can be built on average per individual bee) means many resources per bee and low bee numbers, and implies a certain resource spill-over. We estimated the biological value for this parameter by reviewing reported bee densities.

Bee densities are often given in estimated number per hectare. Bee densities differ between natural habitats and crop areas. Density of *Apoidea* in natural grasslands was estimated at 256 to 1.500 individuals per ha, and at 232 to 4.700 per ha for alfalfa fields. Bee densities vary through the season with higher densities in spring (Banaszak 2000). For other habitats such as forests, woodlots, roadsides and village parks the estimates were lower, varying from 46 to 281 individuals per ha (Banaszak 1995). Note that for our model area of a square kilometre, the number of bees in the landscape needs to be divided by 100 for comparison.

The modelled parameter values for flower density and pollen per flower (table B.1) in combination with a value of 30 for landscape quality for bees yield individual numbers from 204 to 87.209 (per km^2). This span is caused by different body sizes and different amounts of foraging habitat in the landscape. A low value of 10 (maximum of 10 brood cells per bee instead of 30) in combination with high resource conditions, increases the number of individuals to 2.093.017 and 92.819 for small and large bees respectively. Scaled to 1 ha it becomes clear that these are still realistic densities. For semi-natural habitats a value of 30 yields more realistic densities (2-900) than a value of 10 (900-21.000), and is in balance with our moderate resource densities. Note that for extreme (high) values for *flower density* and *pollen per flower* (simulation experiment 2) extremely high individual numbers can occur in the model.

Pollen capacity per bee

The pollen volume that a bee requires for a brood cell relates to body size (Müller et al. 2006). However, it is not known what pollen volume bees transport per foraging trip, but it may scale in the same way with body size as the complete brood cell volume. Therefore we assumed an average of ten foraging trips per brood cell to define the capacity per bee. We assume a 1:1 sex ratio to cancel out effect of sexual dimorphism (Bosch 1994). It is not clear whether the number of foraging trips per brood cell can be used as a constant, since sexual dimorphism and other factors increase the variance. The number of flights per foraging trip varies considerably between species from 3 to 15 collection trips per brood cell (Giovanetti and Lasso 2005, Franzén and Larsson 2007). A series of other species, which differ considerably in body size, need eight to twelve trips per brood cell (Neff and Danforth 1991, Franzén and Larsson 2007, Larsson and Franzén 2007), and suggests that ten is an acceptable choice.

We made one other assumption with regard to the pollen capacity of bees and their behaviour. In rare cases (e.g. very large flowers with abundant pollen in simulation experiment 2) the smaller bees find flowers with more pollen than they can transport. Bees deal with this in different ways. From the same genus, one species visit the single flower to complete the pollen load, while another other species (of the same genus) visits several flowers regardless of pollen availability (Neff and Danforth 1991). We argue that a bee needs to visit at least two flowers to be biologically meaningful to flowers. When the pollen available per visit from a flower exceeds the transport capacity of a bee (which means that the bee would be fully loaded), we set the pollen available to half of the normal availability. As said, this rule was only invoked under extreme parameter combinations.

Velocity

We found in the literature Hymenopteran velocities from a wide taxonomic range, but almost none for solitary bees (table 2). The listed values cover a wider range of body lengths than in solitary bees and were used to provide an allomertric rule for high velocity and medium velocity.

Table B.3.2. Flight velocities of Hymenoptera. Here is the list of values that were used for calculating the relationship between body size, medium velocity and high velocity. All species belong to the Hymenoptera but not all are solitary bees. Velocities are given in metres per second. For each value references are given in brackets: 1: Kunze and Chittka (1996); 2: Barron and Srinivasan (2006); 3: Nachtigall et al. (1995); 4: Ellington et al. (1990); 5: Ware and Compton (1994); 6: Compton et al. (2000); 7: Guédot et al. (2009); 8: Nachtigall (2001); 9: Dean (2003); 10: Piper (2007).

Species	Hyme-nopteran	bee	solitary bee	body length (mm)	velocity medium	velocity high
Apis mellifera	y	y	n	12	0.58 (1) 1.05 (1) 0.9 (2) 3.3 (3)	5.1 (3) 7 (2)
Bombus pascuorum	y	y	n	13.5	0.37 (1) 0.5 (1)	
Bombus terrestris	y	y	n	17.5	3 (4)	5 (4)
Elisabethiella baijnathi	y	n	n	1.4	0.25 (5)	0.37 (6)
Osmia lignaria	y	y	y	11.5		5 (7)
Sceliphron spirifex	y	n	n	22		6 (8)
Vespa crabro	y	n	n	25		5.9 (9)
Vespa mandarinia	y	n	n	50		12.5 (10)

Flower handling time

When we searched in the literature handling times for exclusive pollen collection, we found that most studies report handling times for mixed tasks or for nectar handling. For the allometric scaling of pollen handling time with body length, we used three studies (table 3). The first (Strickler 1979) gives values for 5 solitary bees and shows that handling time decreases with body length. Solitary bees alone had a too narrow range of body sizes and we therefore included a honeybee and a bumble bee (Young and Stanton 1990, Raine and Chittka 2007). Data from another study with much longer handling times shows a similar negative relationship (Chagnon et al. 1993).

Table B.3.3. Handling times are based on three studies; 1: Strickler (1979); 2: Raine and Chittka (2007); 3: Young and Stanton(1990).

Species	Hyme-nopteran	bee	solitary bee	body length (mm)	Handling time for pollen collection (s)
Hoplitis anthocopoides	y	y	y	10.0	5.70 (1)
Megachile relativa	y	y	y	10.0	10.40 (1)
Osmia coerulescens	y	y	y	9.5	15.70 (1)
Hoplitis producta	y	y	y	6.6	29.30 (1)
Ceratina calcarata	y	y	y	6.2	31.70 (1)
Bombus terrestris	y	y	n	26.0	4.60 (2)
Apis mellifera	y	y	n	12.0	8.10 (3)

Perception distance - length of flight units

There is no direct data on the perception distance of bees, but a body of literature exist on the visual abilities of bees showing that larger bees have better visual abilities. Eye size (facet or ommatidium diameter) of wild bees scales isometrically with thorax length (Jander and Jander 2002). Bees estimate the distance with the help of their velocity. Insects experience image motion (near objects appear to move faster than distant ones), mainly in horizontal direction (Dafni and Kevan 1995). Honeybees estimate distance by holding a constant image velocity (Srinivasan et al. 1996). The spatial detail is therefore also limited by velocity (Chittka et al. 2009). Due to the close link between velocity and perception we defined the perception distance as the distance that can be flown in ten seconds (view of ten seconds forward). Since bees fly at several metres per second, the perception distance is several tens of metres. This may seem rather limited but wild bees stay mostly 1 to 3 metres above the ground when they fly over arable land (Riley et al. 1999) and do not have such a wide view of the landscape as they would have from a flight high up in the sky.

We use flight units to model flight paths of bees, since flight paths are rather erratic than straight. Such flight paths suggest that a bee would make regularly a new decision of the flight direction. We calculate a flight unit length by breaking the perception distance up into pieces and is hence also related to body size. In our implementation of movement (correlated random walk), we use slight deviations from this mean flight unit length in order to create natural looking flight paths. We did not include any odometry in the model, because odometry only plays a minor role during visual foraging (Chittka et al. 1999), mainly for recognizing similar looking landmarks (Vladusich et al. 2005).

Flight path tortuosity

The turning angle distribution determines the tortuosity (erraticness) of the flight path. A higher value for *flight path tortuosity* results in more small turning angles and straighter flight paths. Turning angle distributions differ considerably between studies (Heinrich 1979, Schmid-Hempel 1985, Cartar and Real 1997, Makino et al. 2007, Reynolds et al. 2007). We use the correlated random walk with turning angles only to cross the matrix (area with no flowers); at the foraging habitat level we use nearest neighbour selection rules (which indirectly lead to a very erratic flight path). For the matrix-crossing flight we used a high value for *flight path tortuosity* (0.9), resulting in relative straight flight paths as known for areas with almost no foraging resources (Heinrich 1979).

Flower memory - habitat cell memory - ignorance

Bees have different kinds of memory (e.g. Menzel 2001). We use *flower memory* and *habitat cell memory* in our model, since they play an important role in decision behaviour. Flower memory determines the minimal number of flowers that bees probe to assess patch quality. Bees need to assess at least several flowers to estimate the probability of finding a full flower. Patch quality is defined as the ratio of full to empty flowers and one flower (full or empty) does not suffuse. Data from solitary bees show that the decision to stay or leave (a patch) depends on the reward of least 1 to 3 visited flowers (Ne'eman et al. 2006). We used a minimum of 3 flowers for *flower memory*. Bees improve their estimation of patch quality by visiting more flowers (and thus remember the number of full and empty flowers as long as they stay within a foraging habitat grid cell). Since this kind of working memory lasts from seconds to minutes (Chittka and Raine 2006), we did not set a maximum of flowers that a bee can remember. Within minutes, the bee either found enough pollen, or left the habitat grid cell. The final ratio of full to empty flowers is remembered on entering a new habitat grid cell and act as expectation of resource quality to compare the new experience (new series of probing flowers) with.

The bee remembers ten grid cell locations (*habitat cell memory*) of the most recently visited grid cells with flowers. These are in the model 5 by 5 meter sub-locations in the larger scale patch that are remembered. It is not exactly known how bees remember this kind of information, but they have a spatial memory of their route and the landscape with landmarks (Menzel et al. 2000). We cleared this memory for each new foraging trip, leading to new exploration of flower habitat cells (including near the nest) and new foraging directions.

We introduced an 'ignore parameter' to induce matrix crossing and 'far resource exploration'. Wild bees do not prefer to cross the matrix (Powell and Powell 1987, Franzén et al. 2009). However no matrix crossing is also unrealistic since 10% of the individuals did take the risk of crossing the matrix (Franzén et al. 2009). In the model, 10% of the local optimal decisions (going to a close habitat cell) are ignored. We decided to scale the parameter with *habitat cell memory* to reduce the number of independent parameters. They are inversely related (probability of 1 divided by the *habitat cell memory*) which means that for a bee with very little memory of its environment, it is better to take more risks (inefficient decisions).

Lower patch leaving threshold - upper patch leaving threshold

For the upper patch leaving threshold we have chosen a value of 1.0, which means that a bee only stays for certain when the current habitat grid cell is at least as good as the previous one. The lower patch threshold should not be lower than 0.5, because otherwise bees would stay in a grid cell with less than half of the quality of the previous grid cell. Between both thresholds the bee stays with a uniformly distributed probability.

Time at the nest - flytime

The time spent at the nest varies from half a minute to 30 minutes (Franzén and Larsson 2007), but a time below 5 minutes has been reported more often (Tasei 1973, Danforth 1990, Neff and Danforth 1991, Teppner 1996). Time spend at the nest can be separated in time for pollen deposition (short stay) and time for egg laying and cell closure (long stay after a brood cell has enough pollen)(Danforth 1990). We do not know of an effect of body size (see e.g. data collected in Franzén and Larsson 2007) and nesting preference, but this may be knowledge gap in the literature. We use *time at the nest* as pollen deposition time and assume that larger species remove pollen more efficiently (same amount of time for depositing more pollen) and use half a minute as value unbiased by other activities. Instant pollen deposition at the nest (time zero) would lead to unrealistically high levels of local competition, and a high value would lead to a very low competition between bees, because they spend most time at the nest.

In order to keep the physical simulation time acceptable, we decided to simulate one foraging day. Foraging time (*flytime*) in the literature often is described as species activity and varies from 8 to 12 hours (Linsley 1978, Danforth 1990, Bosch and Blas 1994, Teppner 1996), but may be half of that value (4 hours) when the peak activity of the bee community is taken (Danforth 1990, Teppner 1996). Foraging time also relates to body size and climate. Large species can generate more heat needed to start earlier

(Stone 1994). However they also forage late in the day, but have less foraging activity at the middle of the day (Willmer and Stone 2004) and the effect of body size may therefore be very low. Animals often restrict their food search to the optimal time as response to the periodic nature of temporal distributions of resources (Bell 1990) and effective foraging time may be similar for different species of bees. Four to eight foraging hours would therefore be a realistic value. The combination of *time at the nest* and *flytime* determine how much pollen has been collected by the end of the day and use simulation experiment 1 to explore possible qualitative differences of different combinations.

Body length

Body lengths of wild bees normally vary in most parts of the world between 4 mm and 28 mm (Michener 2000). In the model we focussed on 6 , 12 and 24 mm body length for small, intermediate sized and large bees. We chose to model small bees of 6 mm because this covers a wide range of common bees from different genera: *Ceratina, Chelostoma, Heriades* and *Hyleaus* (wood and cavity nesting), *Dufourea*, and several bees from the genera *Halictus* and *Lasioglossum* (soil nesting). Most bumble bees, which are wild bees but not solitary bees, range from 12 to 18 mm (10 to 25 for more extreme species). However we chose a smaller group of solitary bees to represent the outer range of body sizes (24 mm). Wood-nesting bees from the genus *Xylocopa* measure 20 to 28 mm. Soil-nesting bees that are similarly large can be found in the genera *Centris, Euleama, Oxaea, Habropoda* and *Xenoglossa*. The main reason for including medium sized bees (instead of only the two extremes) is that they are the best studied group of solitary bees with the most reliable data available. Well-studied, intermediate sized bees (10 to 14 mm) are found in the genera *Osmia* and *Megachile*. Soil nesting intermediate sized bees are found in the genera *Andrena* and *Anthophora*.

B4. Diagram with interrelatedness of parameters

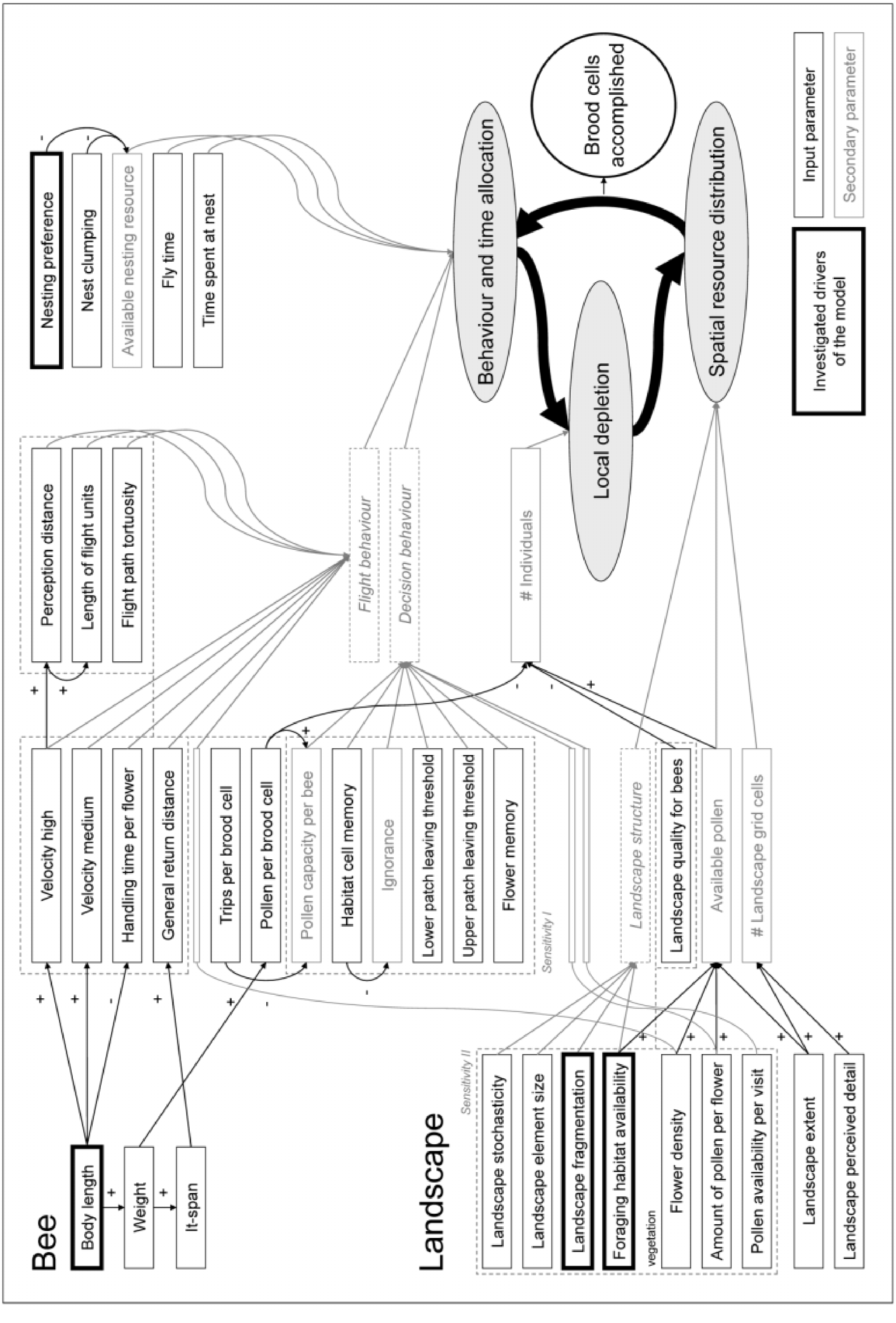


Figure B.4.1. This causal diagram connects all input parameters. Positive and negative relations are marked with a plus or minus (at black arrows). Primary input parameters are in black (solid line black boxes) and secondary parameters in grey (solid line grey boxes). Bold boxes are the focal factors of this study. Dashed boxes are non-numerical aggregations in the model flow, leading to important processes summarized in three ellipses, determining the main response; brood cells (circle). Most parameters were analyzed systematically in simulation experiments for their impact on brood cells. The parameters analyzed in simulation experiment 3 and 4 are outlined with a dashed box and captioned with Sensitivity I and II respectively.

B5. Data-based selection of foraging rules

Five behavioural modules

Resource competition in time with time penalties for different tasks is an important concept for foraging wild bees. Bumble bees spend their time performing different behaviours: they travel between nest and foraging patches, fly between flowers within a patch, handle flowers and remove nectar and pollen, and search for other rewarding patches (Westphal et al. 2006). For solitary bees, the tasks are the same. We modified these tasks to five different behavioural modules in the model:

1. Forage flowers (fly to flowers, forage flowers within a landscape grid cell, fly between flowers, handle flowers and remove pollen)
2. Neighbouring cell (fly to a suitable neighbouring landscape grid cell)
3. Fly around (fly around and look for unknown foraging areas)
4. Fly back (fly back to nest)
5. Nest reached (deposit collected pollen)

In the model these modules are performed in a loop until a certain time (*flytime*) is reached. In order to compare the bees in a fair way, all activities are stopped instantaneously. The finding that some bees perform an exclusively nectar feeding trip at the end of the day (Danforth 1990) was not included.

Subsequent loops start at the nest again and we assumed that bees first check the local resource state around the nest before investing in longer flights. The higher expected patch quality (memorized from farther away at the previous foraging trip) makes that the bee flies beyond the habitat cells near the nest. We did not assume a memory of the last visited location with abundant foraging resources for several reasons. We are not aware of any study showing this for solitary bees and even for some honeybee sub-species it is doubted that they fly to the previous rewarding patch (Couvillon et al. 2010) because they have low associative learning capabilities, behave more like individuals, fly shorter distances from the nest and probably visit different locations on different bouts (Couvillon et al. 2010), in contrast to domesticated honeybees that return to rewarding patches (Menzel 2001). Moreover, there are several indications that bees first deplete flowers in the closest patches around the nest. Solitary bees deplete all flowers under high bee densities (Neff and Danforth 1991) and some individuals keep small foraging areas (Thomson and Chittka 2001). Bumblebees forage differently compared to solitary bees by following traplines (foraging paths of considerable length that guide farther and farther away from the nest) , but solitary bees forage more primitively within a few hundred metres of their nest (Eickwort and Ginsberg 1980).

Use of memory

According to the current knowledge, five memory types can be distinguished for bees (Menzel 2001):

1. Memory of link between olfactory stimulus and reward, which lasts only seconds (flower constancy choice).
2. Short-term memory of e.g. the last visited patches, which lasts up to several minutes.
3. Mid-term memory of the last location of rewarding flowers when returning to nest, memory of sequential landmarks and time of day.
4. Long-term memory of flower cues
5. Long-term memory of nest location and according recognition cues

We represent these 5 levels of memorization in our model as follows:

(1.) Bumble bees use this memory for maintaining flower constancy, but the bees in our model forage on one kind of flower. Nevertheless the model bees memorize the numbers of empty and full flowers they have encountered and store this as an estimated ratio (current patch quality). The minimal number of flowers needed to estimate this ratio is defined in *flower memory*.

(2.) The bees in our model remember the last visited habitat grid cells. The size of this memory (number of memorized locations) is defined in *habitat cell memory*.

(3.) Honeybees return to rewarding patches (Menzel 2001) but we assumed for solitary bees that they do not (see beginning of this section, "behavioural modules"). Instead we assumed that they remember the quality of the last visited habitat grid cell (ratio of full and empty flowers encountered). We also indirectly assumed a memory of landmarks, resulting in a non-straight flight path back to the nest (directed correlated walk).

(4.) The solitary bees in our model forage on one kind of flower. Hence, recognition of the right flower (and flower cues) is assumed, not modelled.

(5.) The most basic memory of the bees in our model was their nest location to which they always return.

Within patch (grid cell) foraging behaviour (Behaviour 1: forage flowers)

We reduced the biological detail within a habitat grid cell and made very simplified assumptions about foraging behaviour. Remember that we do not use optimal flower foraging behaviour theory (as has been shown for nectar foraging bumblebees), since we model pollen collecting solitary bees foraging on homogeneous vegetation. Further we were interested in motivations of bees for moving between grid cells (landscape level), not in detailed movement within a grid cell. We implemented a 'visit nearest flower' rule with resource (flower and patch quality) analysis (see section "Concept details of several submodels").We considered the following facts for our implementation:

- Pollen-collecting solitary bees do not use scent marks as much as nectar foraging bumblebees do (Yokoi and Fujisaki 2009). Flowers normally have abundant pollen (in contrast to nectar) and marking is less useful and too costly. Pollen is also mostly easier accessible than nectar. In the model we do not use any kind of marking.
- Solitary bees are able to assess nectar reward by scent (Howell and Alarcón 2007), but scent based pollen recognition has not been shown so far. We do not use a perception rule on this scale. Our model bee flies to a flower and receives a small time penalty for assessing pollen availability.
- Flight distance of bees flying between flowers is related to plant density (Eickwort and Ginsberg 1980). We modelled the distance to the next flower as the mean distance between flowers, based on flower density.

- When bees forage on flowers they use colour contrast of multiple receptors types instead of the green contrast receptor type alone (Chittka et al. 2001, Giurfa and Lehrer 2001, Spaethe et al. 2001). In order to locate a visible flower in the third dimension bees need to adapt their velocity (Dafni and Kevan 1995)and trade off speed for accuracy (Chittka et al. 2003). We used therefore a lower velocity for within patch (within cell and between cell) movements.

Patch selection (Behaviour 2: neighbouring cell)

Honeybees cross vegetation structures very easily, but solitary bees were found to follow continuous vegetation structures (Bosch and Blas 1994). We therefore implemented a module where only neighbouring habitat cells are visited. The currently occupied cell is excluded from choice possibilities as well are recently visited habitat cells and non-foraging habitat cells. From the remaining cells, one is chosen randomly. This leads to a more or less random movement between habitat cells and a uniform distribution of turning angles with a larger-scale tendency to fly away from the nest. This movement behaviour is not in contradiction with turning angle distributions found for bumble bees in rewarding flower patches (Heinrich 1979, Goverde et al. 2002).

Nest clumping of soil-nesting bees

We used a clumping rule (see section "Full rule description of the model") for soil-nesting bees for two reasons. Not all locations within the vegetation are suitable to nest and bees thus inevitably nest clumped together. Second, clumped nest sites are better encounter sites for mating, while isolated nests are hard to find for males and even more so the chances of receptive females to emerge at that moment (Eickwort and Ginsberg 1980). Clumping of nests of ground-nesting bees varies from moderate aggregations (Neff and Danforth 1991) to very dense aggregations (Cane 1991, Julier and Roulston 2009). We used moderate clumping in our model (and did not further analyse this), since we were interested in the potential difference with wood-nesting bees and not in the effect of nest clumping (it does not change the contrast of the two nesting preferences *per se*).

B6. Literature review of response variables

We discuss here response variables that can be followed in the simulation model: number of brood cells, distance flown (mean and far distance from the nest), trip duration, number of flowers visited (per day and per trip). We discuss values for small, midsize and large bees separately to get an indication of the range of values within each group.

Number of brood cells

The number of brood cells that bees build in one day spans a large range between species and within species. Bees from the genus *Andrena* (covering probably the whole range of small to large bees) build 0.4 to 2 brood cells a day (Franzén and Larsson 2007). The small bee *Calliopsis persimilis* (< 8 mm) even builds up to 6 a day (Danforth 1990). Intermediate sized bees are relatively well studied. *Osmia cornuta* builds half a cell a day (Bosch and Vicens 2002), *Andrena humilis* builds 1.37 brood cells per day (Franzén and Larsson 2007), *Osmia lignaria* can build 2 cells a day (Williams and Tepedino 2003) and *Diadasia rincornis*, builds 2 to 3 cells a day (Neff and Danforth 1991). However, *Osmia bicornis* may build up to 7.1 cells a day in optimal conditions (Tasei 1973). A large bee, *Creightonella frontalis*, was found to build one cell a day (Willmer and Stone 1989) and another one, *Dieunomia triangulifera*, 0.2 to 3 brood cells per day (Minckley et al. 1994). This suggests in summary that small bees are able to build more brood cells in one day than large bees.

Foraging trip duration

Trip duration of different solitary bees (body length range 7 to 12 mm) lasts from 6 to 28 minutes and is positively correlated with body length (Gathmann and Tscharntke 2002). Another review found that trip duration for different species can range from 3 to 170 minutes (Franzén and Larsson 2007). Small bees show a particularly large range of trip durations. *Perdita opuntiae* needs 4.2 minutes per trip, *P. texana* 6 minutes and other *Perdita* species 15 to 30 minutes (Neff and Danforth 1991). *Calliopsis persimilis* has foraging trips of 8 minutes (Danforth 1990), *Chelostoma florisomne* has pollen collection trips of about 20 minutes (Munster-Swendsen and Calabuig 2000) and trips for *Lasioglossum figueresi* range from 7 to 46 minutes (Wcislo et al. 1993). For intermediate sized bees, the range is less extreme. *Osmia cornuta* needs for pollen collection in apple orchards 4.7 minutes per trip (Teppner 1996) in another experiment 5 to 6 minutes (Tasei 1973) and in almond orchards around 12 minutes (Bosch 1994). For *O. cornuta* and *O. rufa* it is known that they have series of longer (8 to 17minutes) and shorter flights (1 to 4 minutes) (Tasei 1973). For *Andrena humilis* foraging trips range from 2 to 35 minutes (Franzén and Larsson 2007). Large solitary bees have longer foraging trip durations. *Anthophora acervorum* needs 14 minutes per trip in apple orchards (Teppner 1996), *Xylocopa pubescens* and *X. sulcatipes* needed on average 20 to 30 minutes per trip (which was equal for pollen and nectar trips) but could range up to 78 minutes (Willmer 1988), *Creightonella frontalis* takes about 17 minutes for pollen collection (Willmer and Stone 1989) and for *Dieunomia triangulifera* the trip duration ranged from 20 to 190 minutes (Minckley et al. 1994).

Flowers visited and flowers visited per trip

Small bees visit fewer flowers than large bees (Hoehn et al. 2008) and that they visit only a few flowers per bout (Sih and Baltus 1987). It was estimated that *Osmia cornuta* (an intermediate sized bee) visits about 50 flowers per trip and about 4500-5600 flowers a day. Other estimations for *O. cornuta* range from 60 to 90 flowers per trip (Bosch 1994) which would mean about 10000 flowers a day. Large bees visit most flowers. *Anthophora acervorum* is estimated to visits about 250 flowers per trip and about 8800 flowers a day (Teppner 1996), *Creightonella frontalis* to visit 29 full flowers per trip and about 180-300 full flowers a day (Willmer and Stone 1989), *Xylocopa pubescens* and *X. sulcatipes* to visit 15 to 20 (range 4 to 65) flowers per trip (Willmer 1988) and Bumble bees to visit 20 to 150 flowers per trip (Sih and Baltus 1987).

Mean distance from nest and realized foraging range

Small bees forage near the nest. *Perdita texana* has most foraging activity within 20 m from the nest with the longer flights around 40 m from the nest (Neff and Danforth 1991). Also Calabuig found that most solitary bees, (among many small ones) forage mainly within the first 27 meters (Calabuig 2000). An experiment with fluorescent dye showed that most pollen was transferred only short distances (<15m) (Van Rossum 2009). The mean distance moved for an intermediate sized bee, *Andrena hattorfiana*, was 46 m and 76 m for two sites respectively, and the maximum ranged from 83 m to 130 m. Rare long dispersal movements (which can be assumed to come close to the homing distance) were up to 900 m (Franzén et al. 2009). In resource-rich environments, *Osmia cornuta* forages near the nest within 100 to 200 m (Vicens and Bosch 2000). Bumblebees (large bees) are in contrast to small solitary bees also frequently flying farther (100 to 200 m) from the edge (Calabuig 2000). For other bumblebees was found that 40% foraged within 100 m around the nest and 62.5% within 200 m. The mean maximum foraging distance per colony ranged from 460 to 710, and all bumblebees foraged within 800 m. The mean foraging distance ranged from 87 to 447 (Wolf and Moritz 2008). When food is abundant close to the nest, as it is e.g. in a clover field, bumble bees fly mainly even as close as 18 m from the nest (Brian).

APPENDIX C

Supplementary material to simulation experiments (chapter 4, 5 and 6)

C.1. Additional tables and figures related to model analysis (chapter 4)

Table C.1.1. ANOVA tables for four response variables (brood cells = brood cells built per bee, total flowers = total number of flower visits per bee, habitat visitation = percentage of the foraging habitat that has been visited, distance flown = mean distance flown from the nest per bee) under two scenarios (four hours foraging, eight hours foraging) from simulation experiment 2. Considered are the model parameters that are uncertain, but may have an effect under large scale perturbations. The tables of variance are based on simplified individual linear models as a result of minimising the BIC with a high threshold value (corrects for high significance of parameters in simulation models). Df stands for degrees of freedom, the sum of squares (sum sq) indicate the importance of the predictor (most important are shown *italic*) and the plus and minus in the column marked with asterisk indicates the predictor effect direction. See Table B.3.1 for predictor abbreviations.

4 hours foraging

log (brood cells)	df	sum sq	*	**log (total flowers)**	df	sum sq	*	**habitat visitation**	df	sum sq	*	**log (distance flown)**	df	sum sq	*
ppf	1	1128	+	*size*	1	2267	+	*ppf*	1	403152	+	*nest*	1	544.0	-
ntime	1	407	-	*ntime*	1	943	-	*nest*	1	306655	+	*size*	1	522.7	+
bdc	1	50	+	*ppf*	1	127	+	*bdc*	1	271602	-	*am*	1	178.1	+
nest	1	15	+	nest	1	62	-	*fd*	1	117225	+	*ntime*	1	143.1	-
size	1	10	-	am	1	38	+	ntime	1	71950	-	*bdc*	1	139.1	-
am	1	1	-	fmem	1	32	+	am	1	59859	-	ppf	1	51.5	+
ppf × *ntime*	1	135	-	bdc	1	17	-	fmem	1	17490	-	flightpar	1	33.2	-
size × *ppf*	1	22	+	flightpar	1	11	+	sightpar	1	13193	+	fmem	1	31.6	-
bdc × *ntime*	1	20	-	cmem	1	8	+	cmem	1	6828	-	sightpar	1	28.2	+
bdc × *ppf*	1	20	+	*ppf* × *ntime*	1	430	-	size	1	4891	-	fd	1	13.4	+
nest × ntime	1	8	-	size × ppf	1	75	-	flightpar	1	4152	-	cmem	1	5.0	-
nest × ppf	1	8	+	size × ntime	1	51	+	*am* × *nest*	1	88427	+	CRW	1	1.9	+
am × nest	1	4	+	size × nest	1	42	+	bdc × ppf	1	49741	+	fr	1	0.8	-
size × nest	1	3	-	am × nest	1	19	-	size × nest	1	43054	-	*am* × *nest*	1	129.9	-
am × size	1	2	+	nest × ppf	1	16	-	size × ppf	1	29134	+	ppf × ntime	1	71.3	-
size × ntime	1	1	+	nest × ntime	1	16	-	fd × ppf	1	26752	-	nest × ppf	1	14.4	-
Residuals	1983	52		bdc × size	1	15	+	fd × bdc	1	16008	+	size × ppf	1	10.7	-
				ppf × fmem	1	12	+	nest × cmem	1	13938	+	fr × nest	1	8.6	+
				am × size	1	10	-	ppf × ntime	1	13470	-	fd × size	1	7.4	-
				am × ppf	1	4	+	bdc × ntime	1	12627	-	bdc × nest	1	5.0	+
				size × fmem	1	3	-	fd × ntime	1	10419	+	CRW × cmem	1	4.0	-
				Residuals	1978	203		nest × flightpar	1	9868	+	fd × nest	1	4.0	-
								nest × sightpar	1	9676	-	size × nest	1	3.7	+
								nest × ppf	1	8805	-	Residuals	1976	159.0	
								am × size	1	7267	+				
								am × flightpar	1	5995	-				
								am × cmem	1	5267	-				
								Residuals	1972	265352					

8 hours foraging

log (brood cells)	df	sum sq	*	**log (total flowers)**	df	sum sq	*	**habitat visitation**	df	sum sq	*	**log distance (flown)**	df	sum sq	*
ppf	1	868	+	*size*	1	1928	+	*ppf*	1	273227	+	*size*	1	621.9	+
ntime	1	267	-	*ntime*	1	854	-	*bdc*	1	219624	-	*nest*	1	458.9	-
bdc	1	81	+	*ppf*	1	102	+	*nest*	1	187598	+	*am*	1	163.8	+
nest	1	19	+	nest	1	63	-	*am*	1	69951	-	*bdc*	1	156.7	-
size	1	8	-	fmem	1	49	+	fd	1	62816	+	*ntime*	1	132.5	-
am	1	2	-	am	1	44	+	ntime	1	37583	-	flightpar	1	50.7	-
ppf × *ntime*	1	63	-	flightpar	1	18	+	fmem	1	20894	-	ppf	1	49.6	+
bdc × *ppf*	1	34	+	bdc	1	18	-	sightpar	1	15378	+	sightpar	1	45.0	+
bdc × *ntime*	1	33	-	cmem	1	15	+	cmem	1	10533	-	fmem	1	39.2	-
size × *ppf*	1	26	+	*ppf* × *ntime*	1	361	-	flightpar	1	5962	-	fd	1	25.9	-
nest × ppf	1	7	+	*size* × *ppf*	1	99	-	fr	1	1023	+	cmem	1	9.8	-
am × nest	1	5	+	size × ntime	1	59	+	size	1	0	-	CRW	1	4.0	+
nest × ntime	1	4	-	size × nest	1	46	+	*am* × *nest*	1	107906	+	fr	1	0.1	-
size × nest	1	4	-	nest × ntime	1	27	-	bdc × ppf	1	69079	+	*am* × *nest*	1	94.7	-
am × size	1	4	+	am × nest	1	20	-	size × nest	1	26386	-	ppf × ntime	1	49.3	-
bdc × size	1	1	-	ppf × fmem	1	16	+	fd × ppf	1	25203	-	size × nest	1	16.9	+
Residuals	1983	64		bdc × size	1	14	+	fd × bdc	1	21051	+	nest × ntime	1	9.3	-
				nest × ppf	1	13	-	nest × cmem	1	15009	+	fd × nest	1	8.7	-
				am × size	1	10	-	size × ppf	1	11716	+	nest × ppf	1	7.4	-
				ppf × flightpar	1	10	+	am × size	1	11507	+	fr × nest	1	7.1	+
				size × fmem	1	4	-	nest × ppf	1	10383	-	CRW × cmem	1	4.4	-
				am × ppf	1	4	+	nest × sightpar	1	10293	-	Residuals	1978	155.8	
				Residuals	1977	224		nest × flightpar	1	8079	+				
								bdc × ntime	1	7196	-				
								am × flightpar	1	6520	-				
								am × cmem	1	6157	-				
								fd × ntime	1	6130	+				
								fr × nest	1	6013	-				
								bdc × size	1	4934	-				
								am × sightpar	1	4668	+				
								Residuals	1969	173398					

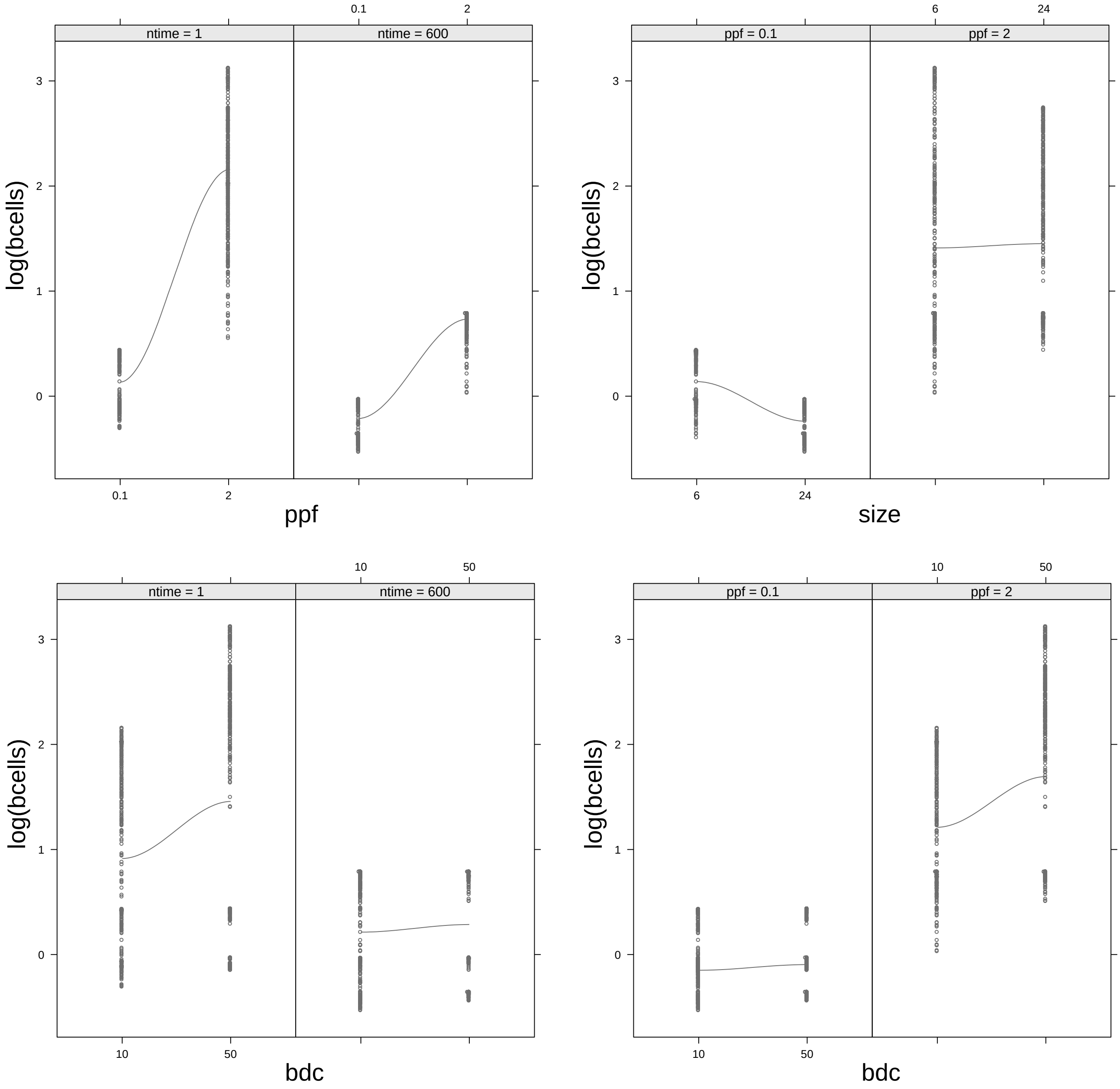


Figure C.1. The four most important parameters interactions for the response variable brood cells that were found simulation experiment 2.

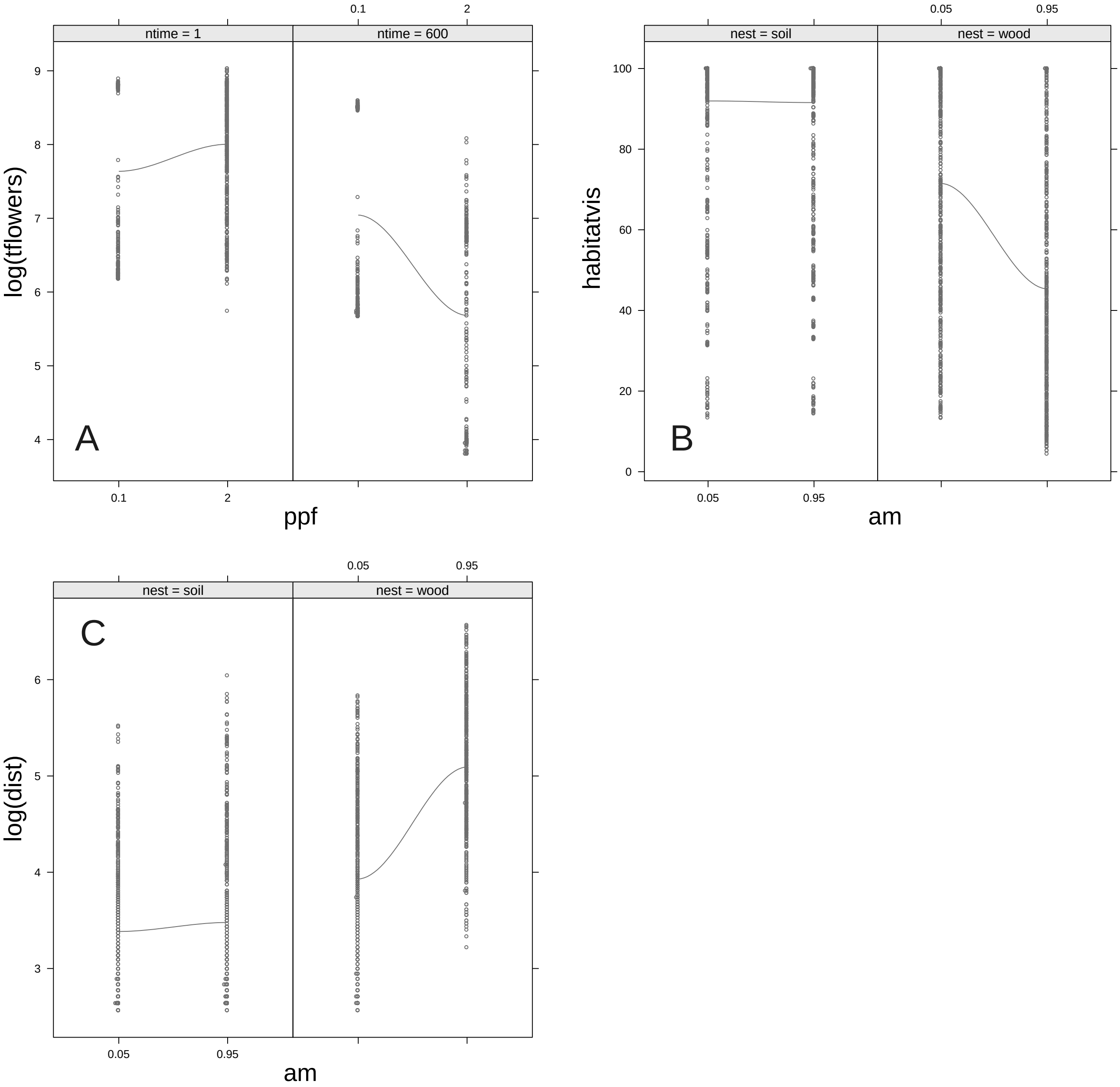


Figure C.2. The most important parameters interactions for the other response variables in simulation experiment 2: A. total number of flowers visited per bee; B. percentage of the foraging habitat visited by bees; C. the mean distance flown from the nest per bee.

Table C.1.2. ANOVA tables for four response variables (brood cells = brood cells built per bee, total flowers = total number of flower visits per bee, habitat visitation = percentage of the foraging habitat that has been visited, distance flown = mean distance flown from the nest per bee) under three scenarios (wood-nesting bees that forage for four hours, soil-nesting bees that forage for four hours and wood-nesting bees that forage for eight hours). Considered are the model parameters that determine the bees' flight and decision behaviour (simulation experiment 3). The tables of variance are based on simplified individual linear models as a result of minimising the BIC with a high threshold value (corrects for high significance of parameters in simulation models). Df stands for degrees of freedom, the sum of squares (sum sq) indicate the importance of the predictor (most important are shown *italic*) and the plus and minus in the column marked with asterisk indicates the predictor effect direction. See Table B.3.1 for predictor abbreviations.

wood nesting - 4 hours foraging

brood cells	df	sum sq	*
ht	1	69.15	-
pcap	1	2.42	+
u_plt	1	0.85	-
vhi	1	0.46	+
sightm	1	0.12	+
ht × pcap	1	0.04	-
u_plt × fmem	1	0.02	+
u_plt × ht	1	0.02	+
vhi × ht	1	0.01	-
fmem	1	0.01	-
l_plt × u_plt	1	0.01	-
l_plt	1	0.00	+
Residuals	987	0.14	

total flowers	df	sum sq	*
ht	1	24258331	-
fmem	1	1635523	+
u_plt	1	1548536	-
l_plt	1	1264559	-
flightm	1	1039777	-
pcap	1	202130	+
vhi	1	127126	+
Residuals	992	874354	

habitat visitation	df	sum sq	*
flightm	1	9519	+
l_plt	1	1302	-
ht	1	646	-
ig	1	588	+
u_plt	1	443	+
fmem	1	345	-
CRW	1	120	+
l_plt × fmem	1	78	+
Residuals	991	512	

distance flown	df	sum sq	*
sightm	1	12692	-
l_plt	1	12099	-
flightm	1	9169	+
u_plt	1	5991	+
ht	1	3209	-
fmem	1	2393	-
ig	1	608	+
pcap	1	596	+
l_plt × flightm	1	278	+
CRW	1	258	+
l_plt × fmem	1	213	+
Residuals	988	3482	

soil nesting - 4 hours foraging

brood cells	df	sum sq	*
ht	1	130.7	-
pcap	1	1.8	+
u_plt	1	0.8	-
l_plt	1	0.1	-
ht × pcap	1	0.1	-
Residuals	994	0.4	

total flowers	df	sum sq	*
ht	1	17901043	-
u_plt	1	1971046	-
pcap	1	305089	+
l_plt	1	189895	-
fmem	1	43979	+
u_plt × ht	1	16938	+
ht × pcap	1	4911	-
Residuals	992	82814	

habitat visitation	df	sum sq	*
l_plt	1	23	-
u_plt	1	21	-
fmem	1	8	-
ht	1	6	-
l_plt × u_plt	1	4	-
l_plt × fmem	1	3	+
u_plt × fmem	1	1	+
u_plt × ht	1	1	+
l_plt × ht	1	1	+
Residuals	990	17	

distance flown	df	sum sq	*
l_plt	1	3209	-
u_plt	1	1519	+
flightm	1	652	-
fmem	1	366	-
ht	1	323	-
l_plt × fmem	1	316	+
l_plt × flightm	1	158	+
Residuals	992	1669	

wood nesting - 8 hours foraging

brood cells	df	sum sq	*
ht	1	129.24	-
pcap	1	9.47	+
vhi	1	5.62	+
u_plt	1	2.27	-
sightm	1	1.35	+
ht × pcap	1	0.10	-
vhi × ht	1	0.10	-
u_plt × fmem	1	0.06	+
l_plt × flightm	1	0.04	-
u_plt × flightm	1	0.03	-
flightm × ht	1	0.03	-
fmem	1	0.03	-
l_plt	1	0.02	+
sightm × flightm	1	0.02	-
l_plt × u_plt	1	0.02	-
flightm	1	0.00	+
Residuals	983	0.26	

total flowers	df	sum sq	*
ht	1	117096730	-
fmem	1	24632794	+
flightm	1	16795671	-
u_plt	1	7357127	-
l_plt	1	7250107	-
vhi	1	1378332	+
pcap	1	596790	+
Residuals	992	9932103	

habitat visitation	df	sum sq	*
flightm	1	10597	+
l_plt	1	1283	-
ht	1	745	-
ig	1	592	+
fmem	1	489	-
u_plt	1	392	+
CRW	1	158	+
l_plt × fmem	1	49	+
Residuals	991	486	

distance flown	df	sum sq	*
sightm	1	25514	-
flightm	1	19573	+
l_plt	1	14086	-
u_plt	1	7064	+
ht	1	6051	-
fmem	1	4430	-
pcap	1	2376	+
ig	1	1571	+
CRW	1	962	+
l_plt × flightm	1	356	+
Residuals	989	3876	

Table C.1.3. Parameter elasticity for four response variables (brood cells = brood cells built per bee, total flowers = total number of flower visits per bee, habitat visitation = percentage of the foraging habitat that has been visited, distance flown = mean distance flown from the nest per bee) under three scenarios (wood-nesting bees that forage for four hours, soil-nesting bees that forage for four hours and wood-nesting bees that forage for eight hours). The higher the elasticity value is, the more sensitive is the response variable to a change in predictor variable. An elasticity value above 1.0 means that the proportion of change in the response is higher than the proportion of change in the predictor. Values above 0.5 are highlighted in **bold**. Considered are the model parameters that determine the bees' flight and decision behaviour (simulation experiment 3). Parameters 1 to 7 are based on body size and 8 to 13 are related to decision behaviour.

	wood nesting - 4 hours foraging				soil nesting - 4 hours foraging				wood nesting - 8 hours foraging			
	brood cells	total flowers	habitat visitation	distance flown	brood cells	total flowers	habitat visitation	distance flown	brood cells	total flowers	habitat visitation	distance flown
1.handling time per flower	**0.677**	**0.907**	0.170	0.395	**0.826**	**0.915**	0.010	0.344	**0.518**	**0.856**	0.156	0.360
2.length of flight units	0.004	0.142	0.407	**0.689**	0.005	0.005	0.002	0.281	0.025	0.249	0.365	**0.685**
3.perception distance	0.009	0.020	0.008	0.160	0.002	0.001	0.000	0.011	0.016	0.035	0.009	0.191
4.velocity medium/low	0.006	0.005	0.004	0.008	0.008	0.011	0.001	0.010	0.006	0.005	0.004	0.012
5.velocity high	0.047	0.055	0.012	0.041	0.008	0.011	0.001	0.011	0.073	0.118	0.023	0.066
6.general return distance	0.001	0.008	0.005	0.010	0.002	0.003	0.001	0.015	0.001	0.011	0.006	0.011
7.pollen capacity per bee	0.126	0.078	0.016	0.197	0.096	0.119	0.003	0.139	0.140	0.057	0.027	0.250
8.lower patch leaving threshold	0.008	0.116	0.126	0.386	0.006	0.036	0.009	**0.531**	0.012	0.118	0.105	0.273
9.upper patch leaving threshold	0.086	0.235	0.098	0.445	0.047	0.258	0.016	**0.715**	0.080	0.222	0.075	0.308
10.flower memory	0.008	0.221	0.129	0.329	0.003	0.038	0.012	0.393	0.013	0.374	0.127	0.293
11.habitat cell memory	0.001	0.012	0.011	0.017	0.004	0.005	0.001	0.035	0.002	0.022	0.009	0.012
12.ignorance	0.004	0.025	0.128	0.125	0.004	0.004	0.001	0.075	0.001	0.045	0.111	0.136
13.flight path tortuosity	0.000	0.001	0.080	0.109	0.002	0.001	0.000	0.003	0.002	0.002	0.076	0.135

Table C.1.4. ANOVA tables for four response variables (brood cells = brood cells built per bee, total flowers = total number of flower visits per bee, habitat visitation = percentage of the foraging habitat that has been visited, distance flown = mean distance flown from the nest per bee) under three scenarios (wood-nesting bees that forage for four hours, soil-nesting bees that forage for four hours and wood-nesting bees that forage for eight hours). Considered are the model parameters that determine the landscape structure and vegetation (simulation experiment 4). The tables of variance are based on simplified individual linear models as a result of minimising the BIC with a high threshold value (corrects for high significance of parameters in simulation models). The predictors are sorted by importance and most important ones are italic showing a pattern explained in the text. Df stands for degrees of freedom, sum of squares indicate the importance of the predictor and * indicates the direction of the predictors effect. See table B1 for predictor abbreviations.

wood nesting - 4 hours foraging

brood cells	df	sum sq	*
plimit	1	72.2	-
ppf	1	66.0	-
am	1	9.2	+
seed	1	3.4	-
bdc	1	1.9	-
ppf × plimit	1	1.4	+
fr	1	1.3	+
am × plimit	1	0.3	-
bdc × plimit	1	0.1	+
am × ppf	1	0.1	-
Residuals	989	3.6	

total flowers	df	sum sq	*
am	1	2730248	+
seed	1	1171788	+
bdc	1	680761	-
fr	1	416512	-
plimit	1	208149	+
ppf	1	173356	+
Residuals	993	400024	

habitat visitation	df	sum sq	*
am	1	31396	-
seed	1	22047	-
fr	1	6662	-
ppf	1	1414	+
bdc	1	1199	-
plimit	1	512	+
seed × am	1	354	+
esize	1	204	-
seed × fr	1	194	+
fd	1	113	+
Residuals	989	5182	

distance flown	df	sum sq	*
am	1	39965	+
seed	1	15135	+
bdc	1	8278	-
fr	1	7841	-
plimit	1	2174	+
ppf	1	1635	+
Residuals	993	8983	

soil nesting - 4 hours foraging

brood cells	df	sum sq	*
plimit	1	125	-
ppf	1	120	-
ppf × plimit	1	3	+
bdc	1	0	+
Residuals	995	2	

total flowers	df	sum sq	*
bdc	1	68878	+
ppf	1	36578	+
plimit	1	26449	+
ppf × plimit	1	3543	-
bdc × plimit	1	528	-
bdc × ppf	1	477	-
seed	1	472	-
fd	1	7	-
Residuals	991	4919	

habitat visitation	df	sum sq	*
bdc	1	6.2	-
ppf	1	5.9	-
plimit	1	1.8	+
seed	1	1.6	+
fd	1	0.7	+
am	1	0.6	+
bdc × ppf	1	0.6	+
Residuals	992	7.4	

distance flown	df	sum sq	*
bdc	1	711	-
plimit	1	194	+
ppf	1	64	+
fd	1	23	+
fd × ppf	1	7	-
Residuals	994	103	

wood nesting - 8 hours foraging

brood cells	df	sum sq	*
plimit	1	153	-
ppf	1	140	-
am	1	83	+
seed	1	43	-
bdc	1	25	+
fr	1	14	+
ppf × plimit	1	3	+
am × plimit	1	1	-
am × ppf	1	1	-
Residuals	990	25	

total flowers	df	sum sq	*
am	1	22752742	+
seed	1	12415549	+
bdc	1	8077923	-
plimit	1	4435635	+
ppf	1	3935376	+
fr	1	3642871	-
Residuals	993	5809394	

habitat visitation	df	sum sq	*
am	1	31061	-
seed	1	23491	-
fr	1	6558	-
bdc	1	1266	-
ppf	1	1106	+
plimit	1	375	+
seed × fr	1	304	+
Residuals	992	7349	

distance flown	df	sum sq	*
am	1	85250	+
seed	1	28395	+
bdc	1	19663	-
fr	1	16305	-
plimit	1	4385	+
ppf	1	3452	+
Residuals	993	13462	

Table C.1.5. Parameter elasticity for four response variables (brood cells = brood cells built per bee, total flowers = total number of flower visits per bee, habitat visitation = percentage of the foraging habitat that has been visited, distance flown = mean distance flown from the nest per bee) under three scenarios (wood-nesting bees that forage for four hours, soil-nesting bees that forage for four hours and wood-nesting bees that forage for eight hours). The higher the elasticity value is, the more sensitive is the response variable to a change in predictor variable. An elasticity value above 1.0 means that the proportion of change is higher than the proportion of change in the predictor. Values above 0.5 are highlighted in bold. Considered are the model parameters that determine the landscape structure and vegetation (simulation experiment 4). Parameters 1 to 3 describe the landscape's structure, 5 to 8 the vegetation and amount of pollen and 4 to 7 determine the number of bees in the landscape.

	wood nesting - 4 hours foraging				soil nesting - 4 hours foraging				wood nesting - 8 hours foraging			
	brood cells	total flowers	habitat visitation	distance flown	brood cells	total flowers	habitat visitation	distance flown	brood cells	total flowers	habitat visitation	distance flown
1.landscape element size	0.008	0.002	0.087	0.063	0.004	0.000	0.000	0.003	0.017	0.015	0.074	0.032
2.landscape fragmentation	0.060	0.065	0.278	0.295	0.002	0.000	0.000	0.007	0.101	0.083	0.237	0.285
3.landscape stochastic factor	0.191	0.216	**1.044**	**0.809**	0.002	0.007	0.005	0.028	0.344	0.304	**0.920**	**0.750**
4.landscape quality for bees	0.124	0.153	0.232	**0.550**	0.030	0.060	0.010	0.448	0.239	0.230	0.204	**0.570**
5.foraging habitat availability	0.126	0.158	**0.588**	**0.627**	0.002	0.000	0.001	0.014	0.212	0.200	**0.502**	**0.615**
6.flower density	0.001	0.006	0.083	0.007	0.006	0.005	0.003	0.092	0.000	0.005	0.064	0.006
7.pollen per flower	**0.700**	0.085	0.250	0.277	**0.813**	0.043	0.009	0.136	**0.572**	0.175	0.189	0.267
8.pollen availability	**0.697**	0.088	0.146	0.300	**0.807**	0.035	0.005	0.236	**0.570**	0.176	0.110	0.287

C.2. Additional tables and figures related to fragmentation analysis (chapter 5)

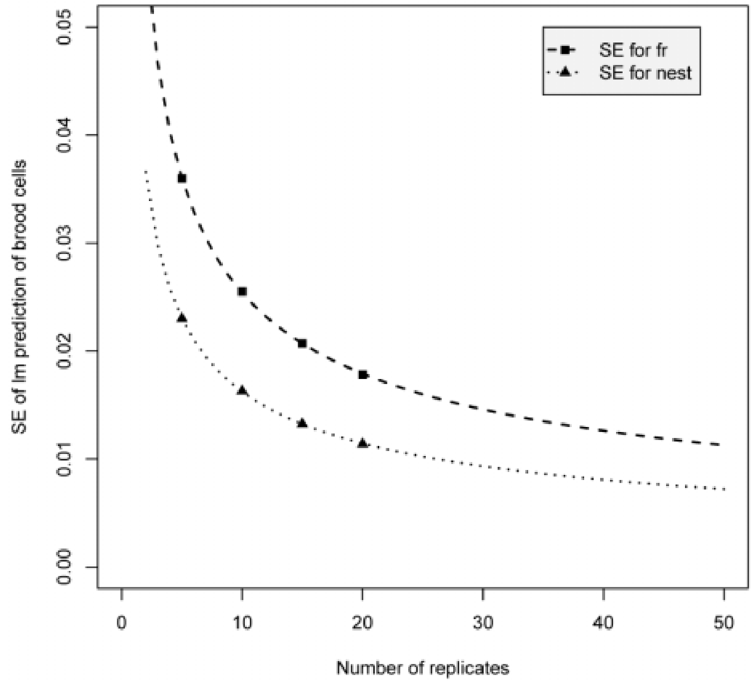
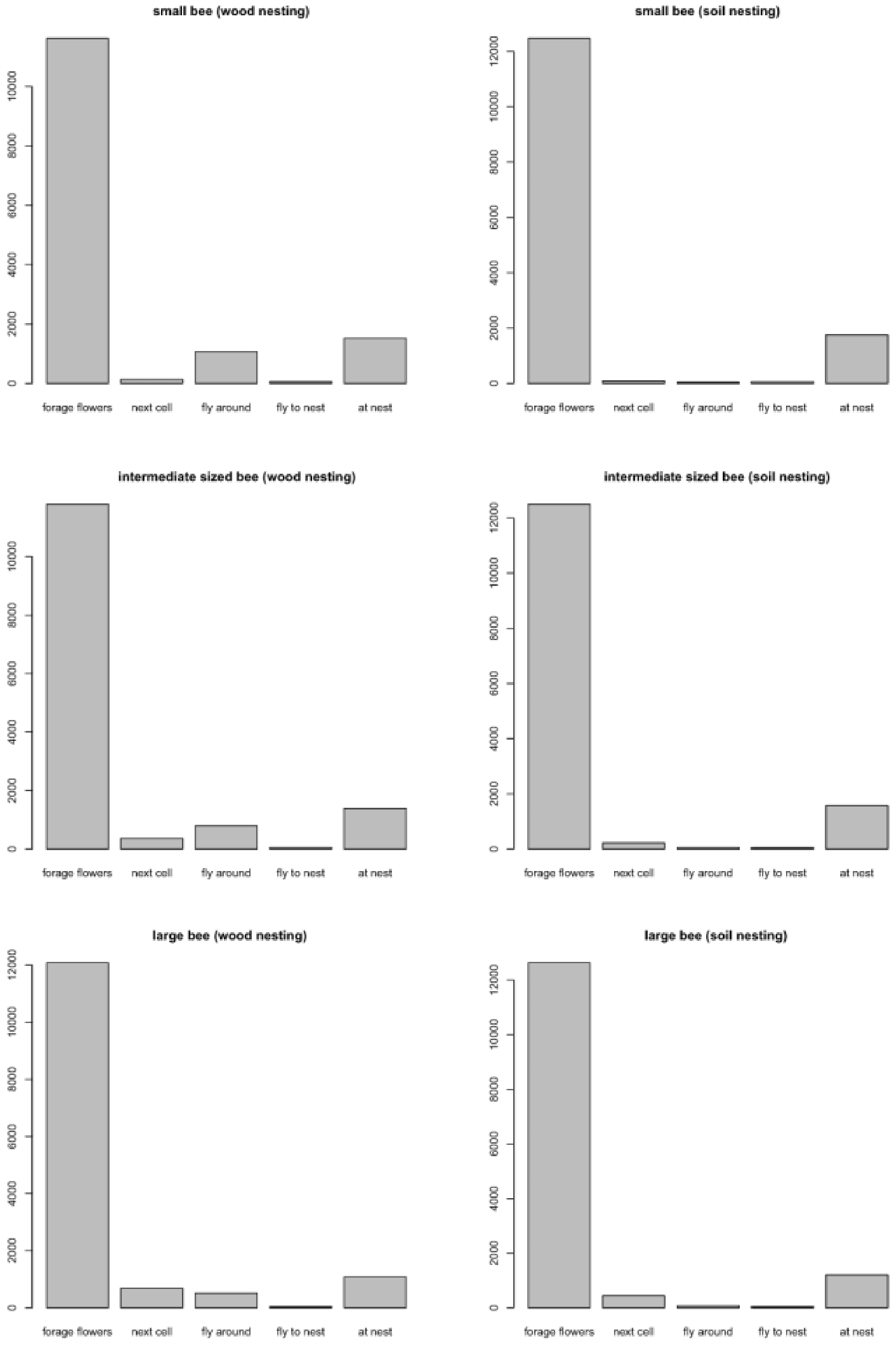


Figure C.2.1. Effect of replicate simulations. Standard error of two selected model predictors (*landscape fragmentation* and *nesting preference*) from linear regression models predicting the simulated number of brood cells, based on subsequently more stochastic replicates (steps of 5). The regression model for 20 replicates is presented in chapter 5. Note that the mean number of brood cells varied between 3 and 6.

Table C.2.1. Analysis of variance for the number of brood cells (response) for alternative predictors. Analysis is based on 20 replicates, i.e. 12000 simulations. Df stands for degrees of freedom. The sum of squares (sum sq) indicates the importance of the predictor and 'effect' indicates the direction of the effect of the predictor. The predictors are explained in the main manuscript.

Predictor	df	sum sq	effect
Model A: body size and mean foraging distance (dist)			
--------------------------------			
size	2	5473.6	−
dist	1	2163.8	−
dist^2	1	387.5	−
size×dist	2	472.4	+
size×dist^2	2	26.8	+
Residuals	11991	21.7	
adjusted r^2: 0.998			
model B: body size and nest site availability (am_nest)			
--------------------------------			
size	2	5473.6	−
log(am_nest)	1	1373.9	+
log((am_nest))^2	1	164.4	−
size×log(am_nest)	2	123.4	−
size×log((am_nest))^2	2	35.1	+
Residuals	11991	1375.4	
adjusted r^2: 0.839			
model C: body size and local density (locald)			
--------------------------------			
size	2	5473.6	−
log(locald)	1	2657.5	−
(log(locald))^2	1	114.0	−
size×log(locald)	2	196.1	+/−
size×(log(locald))^2	2	66.5	+
Residuals	11991	38.1	
adjusted r^2: 0.996			
model D: body size and nest-forage-ratio (nest-for-ratio)			
--------------------------------			
size	2	5473.6	−
log(nest-for-ratio)	1	2358.3	−
(log(nest-for-ratio))^2	1	363.1	−
size× log(nest-for-ratio)	2	226.2	+
size×(log(nest-for-ratio))^2	2	85.5	+
Residuals	11991	39.1	
adjusted r^2: 0.995			


small bee (wood nesting)

small bee (soil nesting)

intermediate sized bee (wood nesting)

intermediate sized bee (soil nesting)

large bee (wood nesting)

large bee (soil nesting)

Figure C.2.1. Time allocation for the six different bee types, emerged by interacting model rules. The six diagrams give the number of seconds spent in each of the five behavioural types. For each bee is the sum of time always 14400 seconds.

C.3. Additional tables and figures related to pollination analysis (chapter 6)

Table C.3.1. Analysis of variance for three pollination measures. Predictors are body size and the ratio of nest habitat to foraging habitat (nest-for-ratio). The analysis is based on 20 replicates, i.e. 12000 simulations. Df stands for degrees of freedom. The sum of squares (sum sq) indicates the importance of the predictor and 'effect' indicates the direction of the effect of the predictor.

Predictor	df	sum sq	effect
Model A: response is number of flowers visited			
--------------------------------			
size	2	60992000000	+
log(nest-for-ratio)	1	368770000	+
(log(nest-for-ratio))^2	1	64364000	+
size×log(nest-for-ratio)	2	467830000	−
size×(log(nest-for-ratio))^2	2	94319000	−
Residuals	11991	11053000	
adjusted r^2: 1.000			
model B: response is foraging habitat visitation			
--------------------------------			
size	2	5866	−
log(nest-for-ratio)	1	6368750	+
(log(nest-for-ratio))^2	1	172342	−
size×log(nest-for-ratio)	2	79070	−
size×(log(nest-for-ratio))^2	2	826	+
Residuals	11991	292263	
adjusted r^2: 0.958			
model C: response is mean distance from the nest			
--------------------------------			
size	2	3566155	+
log(nest-for-ratio)	1	10745524	+
(log(nest-for-ratio))^2	1	1757740	+
size×log(nest-for-ratio)	2	621446	+
size×(log(nest-for-ratio))^2	2	148269	+
Residuals	11991	116909	
adjusted r^2: 0.993			

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