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**Distance matters: impact of increasing foraging distances on
population dynamics in native bees**

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1 Summary

Insects and especially bees are the world's major pollinator group providing enormous economic and ecological benefits to flowering plants, wildlife and humans. Effective pollination services as well as the stabilisation of ecosystem services against human disturbance is highly supported by diverse pollinator assemblages. Yet, bees have suffered a considerable decline in population size and local species diversity in the last few decades. The ongoing loss, fragmentation and degradation of habitats result in a decrease of resources needed for successful bee reproduction such as nesting sites and flowering plants as pollen and nectar sources. Bees as central place foragers have to commute multiple times between nesting and foraging habitats while provisioning brood cells for offspring production. Thus, changing spatial resource availability is expected to be an important factor affecting population dynamics of bees.

A new experimental approach was applied in this PhD study to analyse spatial effects of resource distribution on foraging solitary bees. Oligolectic bee species, which exclusively collect pollen on a single plant genus to feed their larvae, were established in a host plant free area. This procedure allowed to confine bees to foraging on host plants that either occurred naturally across different landscape structures or were arranged in pots that could be moved to locations in distinct distances from bee nesting stands.

The first objective of this PhD study was to document whether hills, forests, rivers and motorways act as insurmountable barriers for foraging female bees. *Chelostoma florissomne* and *Hoplitis adunca* were tested in mark-recapture studies at a hilly, forested site and at a site with open water and a motorway, respectively. We found

that landscape structures such as hills, forests, a river and a motorway did not act as insurmountable barriers for the two bee species *C. florisomne* and *H. adunca*.

The second objective was to experimentally investigate species specific maximum foraging distances as well as average distances, at which a sizable proportion of individuals of a population was still capable of foraging. *Hylaeus punctulatissimus*, *Chelostoma rapunculi* and *H. adunca* were forced to collect pollen on potted host plants that were successively placed in increasing distance from fixed nesting stands in a structurally poor landscape. The small bee species *H. punctulatissimus*, the medium sized *C. rapunculi* and the large *H. adunca* foraged maximum distances of 1100m, 1275m and 1400m, respectively. However, half of the individuals only foraged at substantially shorter distances of 100-225m and 300m for *H. punctulatissimus* and *H. adunca*, respectively. Thus, increasing foraging distances may impose high foraging costs causing bees to discontinue nesting activity.

The third objective was to experimentally quantify the impact of increased foraging distance on the duration of foraging bouts and on the number of brood cells provisioned per time unit for *Hoplitis adunca* and *Chelostoma rapunculi*. Females nesting at different sites foraged under the same environmental conditions on a single large and movable flowering host plant patch in distinct distances from the nesting sites. Additionally, the impact of different spatial host plant arrangements on the duration of foraging bouts was investigated for *H. adunca*. Foraging costs in terms of duration of a foraging bout were found to increase with increased distances between nest and host plants in both *H. adunca* and *C. rapunculi*. The extrapolated number of brood cells provisioned per time unit by *H. adunca* was found to decrease by 23%, 31% and 26% with an increase in the foraging distance by 150m, 200m and 300m, respectively. The extrapolated number of brood cells provisioned by *C. rapunculi*

decreased by 46% and 36% with an increase in foraging distance by 500m and 600m, respectively. Contrary to expectation, a widely scattered arrangement of host plants did not result in longer mean duration of a foraging bout in *H. adunca* compared to a highly aggregated arrangement, which might be due to a reduced flight directionality combined with a high rate of revisitation of already depleted flowers in the aggregated plant arrangement or by a stronger competition and disturbance by other flower visitors.

In summary, this PhD study shows that spatial separation of nesting and foraging habitat of no more than few hundred meters seems essential for bee population persistence. Habitat diversity leading to resource availability within few hundred metres will have to be considered in future bee conservation policy with the potential to enhance not just bee species richness but biodiversity and ecosystem resilience in general.

2 Zusammenfassung

Insekten, insbesondere Bienen, übernehmen den grössten Teil der Bestäubung von Blütenpflanzen und haben einen unverzichtbaren Nutzen für die Natur und den Menschen. Artenreiche Bestäuber-Gesellschaften haben das Potential für eine effektive Bestäubung, dies auch in Ökosystemen, die vom Menschen stark beeinträchtigt sind. Allerdings haben Populationen von Bienen in den letzten Jahrzehnten Rückgänge erlitten, und die lokale Artenvielfalt ist mancherorts stark rückläufig. Durch die Fragmentierung und Zerstörung von Habitaten gehen vermehrt Nistplätze und Pollenquellen verloren. Beides sind unverzichtbare Ressourcen für die erfolgreiche Fortpflanzung von Bienen. Um eine Brutzelle mit Pollen zu versorgen, müssen Bienen mehrfach zwischen ihren Nestern und geeigneten Futterpflanzen hin und her fliegen. Zunehmende Distanzen zwischen den beiden Ressourcen könnten sich demnach negativ auf die Populationsdynamik der Bienen auswirken.

Ein neuartiges experimentelles Design wurde in dieser Arbeit gewählt, um die Auswirkung von unterschiedlichen räumlichen Verteilungen von Ressourcen auf Bienen zu untersuchen. Spezialisierte Bienenarten, die für die Versorgung von Brutzellen nur auf je einer ganz bestimmten Pflanzengattung Pollen sammeln, wurden in Gebieten untersucht, in denen die entsprechenden Wirtspflanzen fehlten. Die Bienen wurden in Nisthilfen etabliert, die so in der Landschaft platziert wurden, dass bestimmte Landschaftsstrukturen die Bienen von geeigneten Wirtspflanzenbeständen trennte. Alternativ wurden in einer strukturarmen Landschaft Topfpflanzen in ganz bestimmten Distanzen zu den Nisthilfen aufgestellt.

Eine erste Zielsetzung der vorliegenden Arbeit war es, herauszufinden, ob Hügel, Wälder, Flüsse und Autobahnen für Bienen unüberwindbare Hindernisse darstellen.

Dazu wurden Markier- und Wiederfang-Experimente mit zwei Bienenarten durchgeführt. *Chelostoma florissomne* wurde in einer Landschaft mit Hügeln und Wäldern getestet, wohingegen *Hoplitis adunca* an einem Flussufer in unmittelbarer Nähe einer Autobahn untersucht wurde. Wir konnten zeigen, dass Hügel, Wälder, ein Fluss und eine Autobahn für die zwei getesteten Bienenarten *C. florissomne* und *H. adunca* keine unüberwindbaren Hindernisse darstellen.

Eine zweite Zielsetzung war es, herauszufinden, wie weit Bienen einer Art maximal fliegen, um Pollen zu sammeln, und wie gross die durchschnittlichen Distanzen zwischen Nest und Wirtspflanzen sein dürfen, damit Wirtspflanzen noch von einer beträchtlichen Anzahl Bienen auf ihren Pollensammelflügen angefliegen werden. *Hylaeus punctulatus*, *Chelostoma rapunculi* und *H. adunca* wurden gezwungen in zunehmenden Distanzen Pollen zu sammeln, indem Wirtspflanzen in portablen Töpfen schrittweise von einem fixen Nistplatz weggerückt wurden. Die kleine Bienenart *H. punctulatus* flog maximal 1100m weit, wohingegen die Hälfte der Individuen bereits bei 100-225m ihre Pollensammelaktivität einstellte. Die grosse Bienenart *H. adunca* flog maximal 1400m weit, wohingegen die Hälfte der Individuen bereits bei 300m keine Pollensammelflüge mehr unternahm. Für die mittelgrosse Bienenart *C. rapunculi* wurde eine maximale Sammelflugdistanz von 1275m nachgewiesen. Die Zunahme der Flugdistanz zwischen den Ressourcen scheint grosse Kosten zu verursachen und zwingt die Bienen allmählich ihre Nistaktivität aufzugeben.

Eine dritte Zielsetzung war es, den Einfluss von Sammelflugdistanzen auf die Flugzeiten sowie die daraus resultierenden Fortpflanzungserfolge der beiden Bienenarten *H. adunca* und *C. rapunculi* experimentell zu quantifizieren. Dazu wurden Wirtspflanzen in portablen Töpfen an einer Stelle, in bestimmten Distanzen

zu den unterschiedlichen Niststandorten, aufgestellt. Die Weibchen verschiedener Niststandorte sammelten somit Pollen in verschiedenen Flugdistanzen, unter exakt gleichen Umweltbedingungen. Zusätzlich wurde der Einfluss von verschiedenen räumlichen Anordnungen der Wirtspflanzen auf die Flugzeiten von *H. adunca* untersucht. Wir konnten zeigen, dass der Zeitaufwand für einen Pollensammelflug mit zunehmenden Flugdistanzen grösser wird. Entsprechend kann eine Biene pro Zeiteinheit weniger Brutzellen versorgen. *H. adunca* versorgte bei einer Zunahme der Flugdistanz um 150m, 200m oder 300m rund 23%, 31% und 26% weniger Brutzellen. Ähnlich ist das Bild für die Fortpflanzungseinbusse bei *C. rapunculi* mit 46% und 36% weniger Brutzellen bei einer Zunahme der Flugdistanz um 500m beziehungsweise 600m. Wider Erwarten führte die weit verstreute Anordnung der einzelnen Wirtspflanzen, verglichen mit einer stark aggregierten Anordnung, bei *H. adunca* nicht zu längeren Sammelflugzeiten. Offenbar fliegen Bienen in der aggregierten Anordnung die einzelnen Blüten weniger zielgerichtet ab, und weisen eine höhere Rate von Zweitbesuchen auf bereits besammelten Blüten auf. Weiter könnte die stärkere Konkurrenz oder eine gegenseitige Belästigung unter Blütenbesuchern, in dicht stehenden Wirtspflanzen, einen Einfluss auf das Sammelverhalten haben.

Zusammenfassend ist festzuhalten, dass Schutzmassnahmen für Bienen zukünftig räumliche Aspekte der Ressourcenverfügbarkeit besser berücksichtigen und eine grössere Habitatsvielfalt erwirken sollten, so dass Nistplätze und geeignete Pflanzenressourcen nicht weiter als wenige hundert Meter voneinander entfernt vorkommen. Solche Massnahmen würden nicht nur Bienen, sondern die Artenvielfalt allgemein und somit auch die Widerstandsfähigkeit von Ökosystemen fördern.

3 General Introduction

3.1 Significance of pollinator diversity

Pollinating animals provide enormous economic and ecological benefits to flowering plants, wildlife and humans. Insects and especially bees are the major pollinator group (Buchmann and Ascher 2005). Their economic value to the agricultural industry was shown in numerous studies (e.g. Klein et al. 2007, Ashworth et al. 2009). However, the value to natural ecosystems is harder to quantify (Costanza et al. 1997), although much of the maintenance of terrestrial biodiversity and therefore ecosystem stability depends on pollination services.

Worldwide more than 15 000 bee species have been described (Michener 2007), and more than 1000 bee species are native to Europe. The honey bee (*Apis mellifera*) is the best known and most abundant species in Europe in terms of number of individuals. However, effective pollinating services do not just depend on honey bee abundance but also on pollinator diversity. Even crops with generalized pollination systems were shown to profit from high pollinator diversity (Kremen et al. 2002), and specialized crops can be expected to rely even more on diverse pollinator assemblages (Steffan-Dewenter et al. 2005). Indeed, pollinator diversity, not abundance, explained variation in fruit set of coffee in an agroforestry system in Indonesia (Klein et al. 2003). Furthermore, solitary bee species often show higher efficiency in depositing pollen on stigmas than honey bees (Freitas and Paxton 1998), and social bees are often completely absent when only few plants are flowering (Willmer and Stone 1989, Klein et al. 2002). Thus solitary bees provide a more efficient pollination service to sparse and irregularly distributed flowering plants (Klein et al. 2003). Where honey bees are insufficient pollinators or present in only small abundance, solitary bees as well as bumble bees are

the most important taxa providing pollination services to numerous arable crops (Walther-Hellwig and Frankl 2000b). In fact, diverse assemblages of solitary bees and bumble bees have the capacity to buffer potential declines in agricultural production due to the loss of honey bee colonies (Winfree et al. 2007). Additionally, pollinator diversity was shown to stabilize ecosystem services against human disturbance by differential response to environmental variables among species and at different scales by different species (Winfree and Kremen 2009). Even though the contribution of each solitary bee species may be small, the collective role of a species-rich bee community might turn out to be of quantitative importance for pollination services.

3.2 Pollinator crisis

The successful pollination of many crop and wild plants are assumed to be at risk with a decline of pollinators (Kearns et al. 1998, Buchmann and Ascher 2005). In fact, bees have suffered a considerable decline in population size and local species diversity in the last several decades (Biesmeijer et al. 2006, Winfree et al. 2009). Massive declines in honey bee populations were reported from the United States of America (van Engelsdorp et al. 2009), and bees other than honey bees have increasing Red Data Book entries (e.g. for 11 European countries, an average of 27.4% of the national bee fauna is listed) (Steffan-Dewenter et al. 2005).

Even though still poorly understood, parasitic attacks by *Varroa* mites, pathogen diseases, the use of pesticides or a combination of these factors are probably the major cause for declines in population size in honey bees (van Engelsdorp et al. 2009). Solitary bees can be negatively affected by the same factors. However, their decline is mainly due to the recent loss, fragmentation and degradation of their habitats (Brown

and Paxton 2009, Keitt 2009, Winfree et al. 2009), resulting in a decrease of resources needed for successful reproduction such as nesting sites, flowering plants as nectar and pollen sources and nesting materials (Westrich 1996, Klein et al. 2004).

Nesting sites, such as dead wood, stems or areas with exposed soil surface in sunny locations, are often a limiting factor as intensification in agriculture is usually accompanied by the loss of small, uncultivated field boundaries that provide the majority of nesting places (Walther-Hellwig and Frankl 2000b, Gathmann and Tschardt 2002).

Female bees provision each brood cell with pollen and nectar for larval food supply before they lay a single egg in a brood cell. Enormous pollen quantities are needed to feed enough larvae to ensure persistence of bee populations (Müller et al. 2006, Larsson and Franzen 2007). Therefore decreasing abundance and diversity of plant species might reduce floral resources to a critical level for offspring production. This seems especially true for pollen specialist bee species that collect pollen from only few suitable host plant species to feed their offspring (Larsson and Franzen 2007).

3.3 Spatial aspects of foraging in solitary bees

Bees are central place foragers: while provisioning brood cells, they have to fly frequently back and forth between nesting sites and flower resources. The number of foraging trips required to provision a single brood cell varies for different species of solitary bees from two to more than 40 (Frohlich and Parker 1983, Danforth 1990, Giovanetti and Lasso 2005). As suitable nesting habitats and foraging habitats are often spatially separated, bees have to overcome distances between their nest and floral resources. Distances between resources are expected to increase with habitat

fragmentation and degradation and bees might have to cross large areas with no reward to reach isolated fields with suitable host plants. This might be especially true for many pollen specialist species. Adult solitary bees have a relatively short reproductive lifetime of maximally four to six weeks (Westrich 1990). Throughout this period they depend on continuous pollen supply. Temporal changes in resource availability, e.g. due to the withering of a monoculture or the mowing of flower rich meadows in an otherwise highly disturbed environment, might further reduce resource abundance and therefore increase distances between nest and flower resources for both specialist and generalist bees.

If the foraging radius of an individual bee or a bee species is restricted due to internal (energy, physiology, morphology of the bee) or external factors (e.g. landscape barriers), resources outside of this radius are not available. Resources within this radius but in increasing distances from each other might only be available at higher foraging costs in terms of energy and time spent on foraging flights. For bee species with a short foraging radius or for which long distance flights impose high costs, changing spatial arrangements of resources might be an important factor affecting their population dynamics.

Studies investigating the spatial use of resources by different bee species are increasing, however, there is still significant information missing for a better understanding of how spatial resource availability can affect population dynamics of bees.

Natural or man-made landscape structures are assumed to impair movement, dispersal and colonisation of new habitats and can influence local populations and the survival of metapopulations of arthropods as shown for example for butterflies and bush crickets (Moilanen and Hanski 1998, Ricketts 2001, Hein et al. 2003, Cozzi et al. 2008). Rivers prevented movement of tortricid moths (Sciarretta and Trematerra 2006) and already minor vertical structures such as hedges, rows of poplar trees or plastic windbreaks could restrict movement of different groups of flying insects (Fry and Robson 1994, Dover and Fry 2001, Wratten et al. 2003). The knowledge of potential barrier effects of landscape structures in bees is scarce. Only very few studies directly investigated barrier effects of landscape structures on pollen-collecting bees (Bhattacharya et al. 2003, Kreyer et al. 2004), even though this knowledge is important to understand population dynamics of bees.

On the other hand, foraging distances of bees have received increasing attention in the last few years (listed in section 5.5, Table 5.1). However, most studies applied indirect methods, which may over- or underestimate foraging ranges. More detailed information of how bees within a population spatially use their resources is crucial for bee conservation managements. In contrast to species specific maximum foraging distances, threshold distances at which a sizable proportion of a bee population does forage has received hardly any attention, despite its high significance for species conservation.

Some bees might be able to forage long distances but little is known about the effect of increased foraging distances on reproduction in different bee species. There are indications that increased foraging distances negatively affect the number of progeny in *Megachile rotundata* (Peterson and Roitberg 2006b) and *Osmia lignaria* (Williams and

Kremen 2007), but more detailed and quantitative information about the costs of long compared to shorter foraging flights are needed.

3.4 Outline of the PhD study

The aim of the present PhD thesis was to gain detailed and quantitative information about the spatial use of resources by solitary bees and the consequences for bee population dynamics. Such knowledge is essential to develop strategies to conserve, protect and enhance native bee species diversity (Bronstein 1995, Osborne et al. 1999).

A new experimental approach was used in the present study to directly investigate foraging distances and their effect on foraging costs in solitary bees. Pollen specialist bee species, which exclusively collect pollen on a single plant genus to feed their larvae, were established in a host plant free area. This procedure allowed to confine bees to foraging on host plants that either occurred naturally across different landscape structures or were arranged in pots resulting in movable host plant patches.

The first objective was to investigate the ability of foraging bees to overcome landscape structures between nest and host plants. To include potential barrier effects of different structures, two landscapes were chosen to perform mark-recapture studies with two megachilid bee species. *Chelostoma florissomne* (Linné), a common spring species in Central Europe, was tested at a hilly, forested site to document whether forests and hills prevent bees from reaching their host plants and to analyze foraging distances flown by female bees. *Hoplitis adunca* (Panzer), a widespread summer species in Central Europe, was tested at a site with open water and a motorway to document whether rivers and motorways prevent bees from reaching their host plants.

The second objective was to experimentally investigate species specific maximum foraging distances and average distances at which a sizable proportion of individuals of a population is still capable to forage. As foraging distance was shown to correlate with bee body size (Gathmann and Tschardt 2002, Greenleaf et al. 2007), three differently sized solitary bee species were selected for this study: the small *Hylaeus punctulatus* (Smith 1842), the medium sized *Chelostoma rapunculi* (Lepeletier, 1841) and the large *Hoplitis adunca* (Panzer, 1798).

The third objective was to quantify the impact of foraging distance and different spatial host plant arrangements on bee reproduction. An experimental approach was chosen that allowed to simultaneously test the foraging costs of two distinct distances under the same foraging conditions. For the two bee species *Hoplitis adunca* (Panzer, 1798) and *Chelostoma rapunculi* (Lepeletier, 1841) we quantified the effect of long compared to short foraging distances on the duration of foraging bouts. The number of progeny reared by a female bee was extrapolated, i.e. the number of brood cells provisioned per time unit was calculated. *Hoplitis adunca* was further used to quantify the effect of aggregated compared to scattered arrangements of host plants on the duration of foraging bouts.

Implications of the findings for bee conservation are discussed and the importance of habitat diversity and close resource availability is reflected in a broader context of ecosystem services and functional diversity.

4 Are landscape structures insurmountable barriers for foraging bees? A mark-recapture study with two solitary pollen specialist species¹

4.1 Abstract

To investigate whether landscape structures act as insurmountable barriers for foraging bees, we conducted mark-recapture studies with two pollen-specialist solitary species. Foraging options of the bees were confined to host plant stands across different landscape structures. Differences in altitude of more than 130m were overcome and forests covering a distance of up to 480m were crossed by *Chelostoma florissomne*. A broad river and a motorway with intense traffic did not represent insurmountable barriers for *Hoplitis adunca*. For *C. florissomne*, total foraging distances of up to 650m were measured, but foraging females were recorded predominantly on host plant patches available in relatively close vicinity to their nesting site. While landscape structures might impede foraging in endangered bees, the investigated landscape structures clearly did not act as insurmountable physical barriers for the two common solitary bee species tested in our study.

4.2 Introduction

Landscapes in temperate regions are generally composed of different habitats. Natural or man-made landscape structures between or within habitats, such as forests, hills, rivers or roads, can influence local populations and the survival of metapopulations as shown for example for butterflies and bush crickets (Moilanen and Hanski 1998, Ricketts 2001, Hein et al. 2003, Cozzi et al. 2008). Landscape structures were found to act as barriers for dispersal and colonization of new habitats for several other groups of arthropods as well. Roads impaired movement of carabid beetles and spiders (Mader et

¹ Based on Zurbuchen A., C. Bachofen, A. Müller, S. Hein, and S. Dorn, 2010. *Apidologie*, in press.

al. 1990, Keller and Largiader 2003, Koivula and Vermeulen 2005) whereas rivers prevented movement of tortricid moths (Sciarretta and Trematerra 2006). Open fields and agricultural landscapes acted as severe barriers for forest-dwelling carabid beetles and ants (Niemela 2001, Kumar and O'Donnell 2009). Flying insects may be generally assumed to be less affected by landscape structures than flightless insects, as documented for coleopteran species (Driscoll and Weir 2005, Koivula et al. 2005, Driscoll 2008). However, even minor vertical structures such as hedges, rows of poplar trees or plastic windbreaks can restrict movement of different groups of flying insects (Fry and Robson 1994, Dover and Fry 2001, Wratten et al. 2003).

Landscape structures between or within suitable habitats can not only affect dispersal and habitat colonization, they might limit the foraging space of individuals as well. This is especially true for central place foragers for which nesting and foraging habitats are often spatially separated. With the exception of the cleptoparasitic species, bees are typical central place foragers, returning to their nest multiple times a day to provision their brood cells with pollen and nectar. Thus, for many bee species, the presence of natural or man-made landscape structures might reduce the access to resources, thereby adversely affecting population dynamics.

During the last few decades, bees have suffered a considerable decline in local species diversity and population size in many regions of the world (Kearns et al. 1998, Steffan-Dewenter et al. 2002, Biesmeijer et al. 2006, Brown and Paxton 2009, Murray et al. 2009). Hence, the knowledge of potential barrier effects of landscape structures is important to understand population dynamics of bees. While the knowledge of the

spatial use of landscapes by wild bees is increasing (Walther-Hellwig and Frankl 2000a, Gathmann and Tschardtke 2002, Chapman et al. 2003, Greenleaf et al. 2007, Beil et al. 2008, Pasquet et al. 2008, Wolf and Moritz 2008, Franzen et al. 2009), only very few studies directly investigated barrier effects of landscape structures on pollen-collecting bees (Bhattacharya et al. 2003, Kreyer et al. 2004).

In the present study, we investigated the ability of foraging females of two solitary bee species to overcome landscape structures such as forests, hills, rivers and motorways. At a hilly, forested site we performed a mark-recapture study with the megachilid bee *Chelostoma florissomne* (Linné), which is a common spring species in Central Europe, addressing the following questions: (1) Do forests act as insurmountable barriers preventing bees from reaching their host plants? (2) What differences in altitude are overcome by foraging females between nesting site and host plants? (3) What distance do females cover between nest and host plants? At a site with open water and a motorway, we carried out a second mark-recapture study with the megachilid bee *Hoplitis adunca* (Panzer), a widespread summer species in Central Europe, to analyse the question: (4) Do rivers and motorways act as insurmountable barriers for foraging females?

4.3 Material and Methods

4.3.1 Bee species

Chelostoma florissomne and *Hoplitis adunca* are strictly oligolectic collecting pollen on *Ranunculus* (Ranunculaceae) and *Echium* (Boraginaceae), respectively (Westrich 1990, Sedivy et al. 2008). *C. florissomne* is a medium sized species with a body length of 7-11mm and an average dry body mass of 12.5mg, whereas *H. adunca* is a larger species with a body length of 8-12mm and a body mass of 19.7mg (Müller et al. 2006). Both species naturally nest in beetle burrows in dead wood (Westrich 1990) allowing for artificial breeding in hollow bamboo sticks or in pre-drilled burrows in wooden blocks. For the present study, we collected nests of *C. florissomne* and *H. adunca* at different locations in Switzerland. These nests were transferred to artificial nesting sites in the study areas before bee emergence started.

4.3.2 Study areas

4.3.2.1 Hilly, forested site

The mark-recapture study with *Chelostoma florissomne* was conducted in an agricultural landscape intensively used for field crops in north-eastern Switzerland near Berlingen, Thurgau (47° 39' 86'' N, 9° 1' 20'' E, elevation 410-600m).

Four artificial bee nesting sites were established, two within each of two large forest clearings of 16 ha and 24 ha surface area (Fig. 4.1). These clearings were situated on a plateau above the adjacent non-forested areas.

During the whole observation period, both clearings were kept free of the bees' specific host plants by regularly mowing all flowering stands of *Ranunculus* (*R. acris* and *R. repens*). The only exception were five very small and neighbouring stands of

flowering *R. acris* and *R. bulbosus* at the north-western edge of the eastern clearing growing on species-rich and nutrient-poor meadows, which are prohibited by Swiss regulations from being mown before mid of June. This area harboured the only pollen sources that were attainable by bees without crossing forest, namely by those nesting at sites C and D (Fig. 4.1). All host plant stands were situated at lower altitudes than the four nesting sites. The difference in altitude between nesting sites and host plant stands, which mainly consisted of *R. acris*, varied between 5m and 150m.

4.3.2.2 Site with open water and a motorway

The second study with *Hoplitis adunca* was conducted in an agricultural landscape intensively used for field crops in western Switzerland near Selzach, Solothurn (47° 11' 63'' N, 7° 27' 78'' E, elevation 420m), which is crossed by the river Aare (Fig. 4.2).

One artificial bee nesting site was established at a distance of 10m from the river. The area at the near side of the river naturally lacked the specific host plants of *H. adunca*. The only host plant stand available within a radius of 1200m from the nesting site was situated at the far side of the river in a distance of 350m from the nesting site on the roof of an underpass covering half of a motorway (Fig. 4.2). It was composed of 120-150 plants of *Echium vulgare* scattered in an area of about 1.2ha.

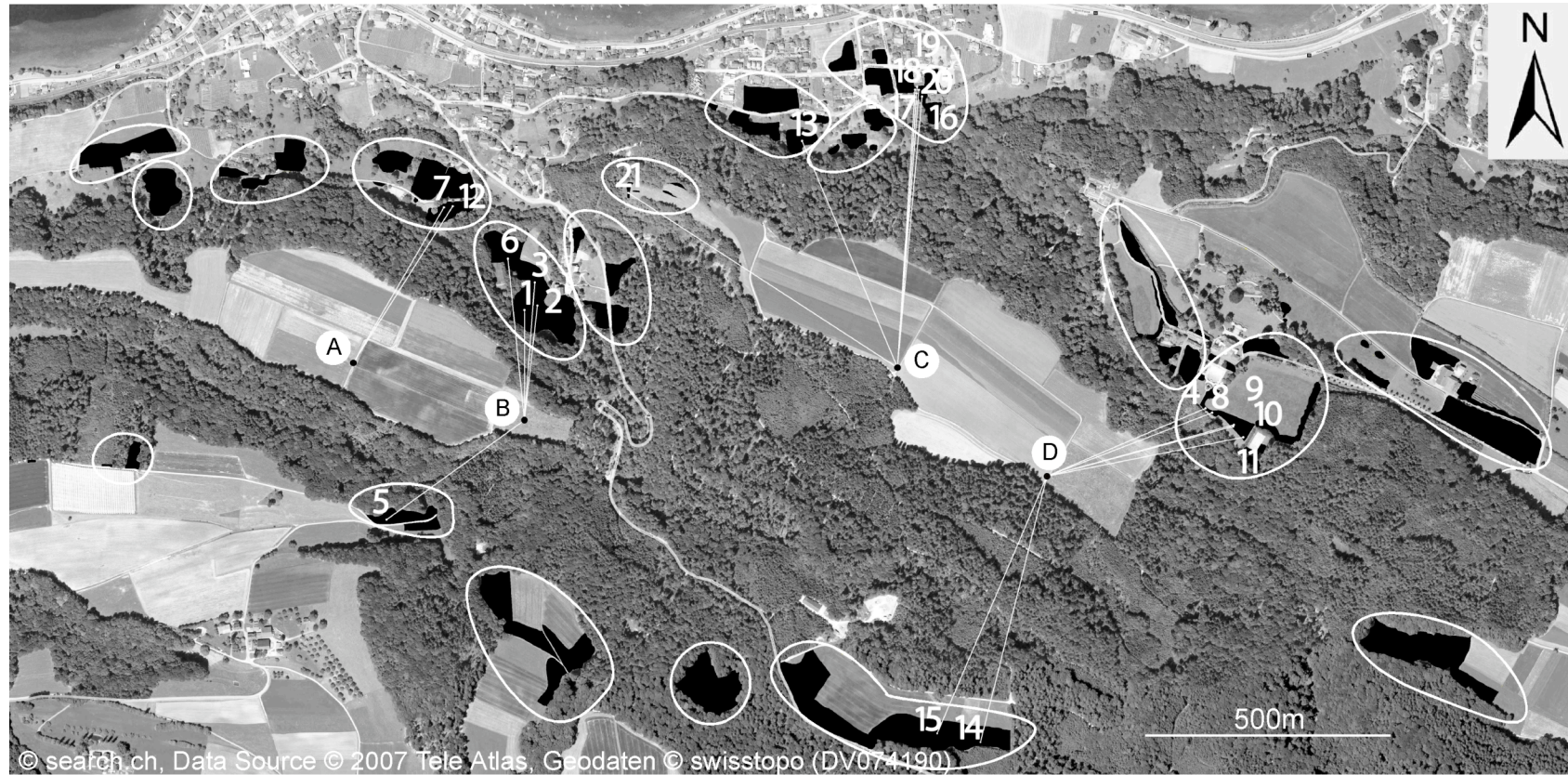


Figure 4.1 Hilly, forested area for the mark-recapture study with *Chelostoma florissomme* in north-eastern Switzerland. The four artificial nesting sites within the two forest clearings are labelled with the letters A to D. Black areas show the mapped *Ranunculus* stands which were grouped into 19 patches (white circles). White lines indicate the foraging flights of recaptured females with the numbers referring to the individual flights listed in Tab. 4.1.

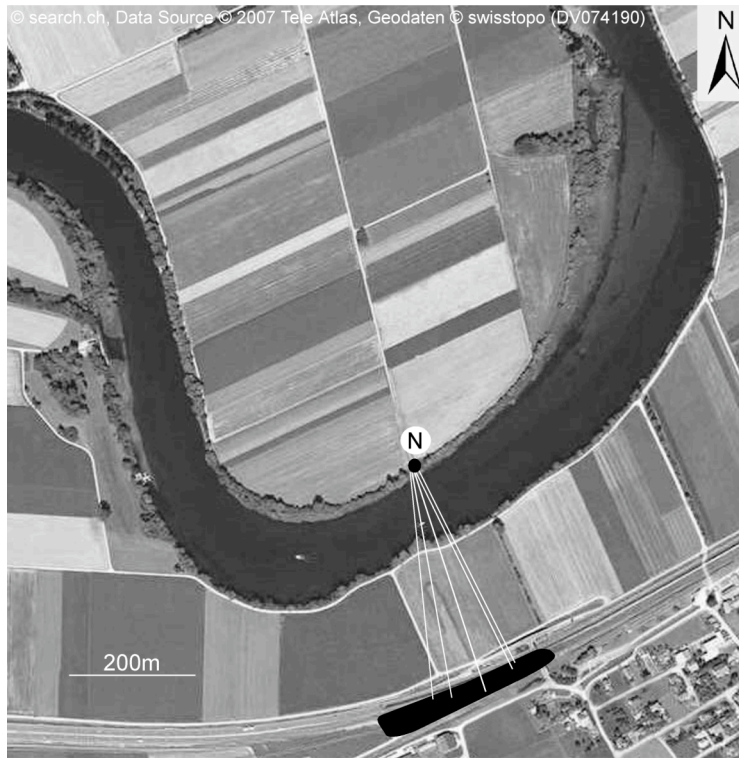


Figure 4.2 Area with open water and a motorway for the mark-recapture study with *Hoplitis adunca* in western Switzerland. The artificial nesting site close to the river is labelled with the letter N. The black area shows the *Echium vulgare* stand on the roof of an underpass covering half of the motorway. White lines indicate the foraging flights of the recaptured females.

4.3.3 Bee establishment and marking

Bees were established by transferring 100 occupied nests to each nesting site. Hollow bamboo sticks and wooden nesting blocks (150 x 150 x 400mm) with pre-drilled burrows (120mm in length, 3-5mm in diameter for *C. florissomne* and 6-9mm in diameter for *H. adunca*) were prepared as artificial nesting sites. Bamboo sticks and wooden nesting blocks were placed in a covered shelf to protect them from rain. To support initiation of nesting activity by the newly emerged females of *C. florissomne*, flowering *Ranunculus* stands were only mown shortly prior to the start of the observations. Therefore, in the initial phase, host plants were available in distances of less than 30m from the nesting sites. Similarly, to support initiation of nesting activity

by *H. adunca*, 50 potted plants of *Echium vulgare* were placed at a distance of two meters from the nesting site and plants were again removed before the onset of the observations.

Females that showed nesting behaviour were caught, immobilized at 5°C in a cool box and marked individually with fast-drying enamel paint (Revell) on the thorax (1-2 positions) and the abdomen (1 position), applying colour codes with eight different colours. A total of 351 females of *C. florissomne* were marked, ranging from 64 to 100 individuals per nesting site. A total of 20 females of *H. adunca* were marked.

4.3.4 Study design and data analysis

4.3.4.1 *Chelostoma florissomne* at a hilly, forested site

In March 2008 before flowering of *Ranunculus*, all *Ranunculus* stands around the two clearings within a radius of 700-800m from the centre of each clearing were mapped (Fig. 4.1). As we had no previous information on the flight capacity of *C. florissomne*, we fixed the position of the four nesting sites in varying distances to *Ranunculus* stands. The minimum distance from a nesting site to a *Ranunculus* stand ranged from 180m for nesting site B to 460m for nesting site D (Table 4.1).

For eleven days between May 15 and June 1, 2008, the mapped *Ranunculus* stands were searched for marked bees by at least two observers per day. The total area covered by *Ranunculus* stands that amounted to 19.7ha was divided into 63 sectors ranging from 0.01ha to 1.4ha with a median of 0.3ha. These sectors were small to medium sized *Ranunculus* stands spatially separated from other stands by unpaved roads or by large *Ranunculus*-free areas. Alternatively, they were parts of large *Ranunculus* stands, which were artificially delimited by using prominent landmarks to facilitate the systematic

search for marked females. Density of *Ranunculus* for each sector was estimated according to the following scoring system: 1 = <5 flowers/m², 2 = 5-50 flowers/m², 3 = 51-100 flowers/m², 4 = >100 flowers/m². The search time per sector was proportional to its area corrected by a factor based on the density of *Ranunculus* flowers (factor 1 for the lowest density class and 1.25, 1.5 and 1.75 for the higher density classes, respectively). The minimum time to survey a sector was set to 30min regardless of its size or host plant density as the average time of a foraging bout of *C. florisomne* in the study area was found to be approximately 10-15min. This minimum search time should allow for recapturing marked females even in very small sectors. All *Ranunculus* sectors were considered suitable foraging habitats for *C. florisomne*. Indeed, in 90% of all sectors unmarked foraging individuals of *C. florisomne* were observed. All sectors were searched for marked females twice on different days. The total time for one complete survey was 88h. *Ranunculus* stands that were mown by farmers, trampled by cattle or withered during the observation period were either omitted or assigned to a lower density class.

Marked females were caught with insect nets, individually identified and immediately set free again. The presence of each recaptured female at its artificial nesting site was verified the same day. All observations were carried out during sunny weather between 10am and 5pm with maximum daily temperatures ranging from 20.0°C to 25.5°C.

To quantify the foraging distance of recaptured females of *C. florisomne*, we calculated the *direct foraging distance* (d) using the Pythagoras formula $d = \sqrt{h^2 + a^2}$, where h being the *horizontal linear distance* between nesting site and place of recapture and a being the *difference in altitude*. If the inclination varied along an individual flight

path, d was calculated by summing up the d values of several subsequent sections each characterized by a constant inclination. Distances flown across forests were calculated analogously to the direct foraging distances between nest and place of recapture. All calculated distances were rounded to the nearest 10m.

To analyze the bees' favoured choice for host plant stands in respect of (1) the difference in altitude between nest and host plants and (2) the distance to the available *Ranunculus* stands, the 63 *Ranunculus* sectors were grouped into 19 *Ranunculus* patches (Fig. 4.1) representing contiguous foraging habitats in contrast to the sectors that were artificially delimited for methodological reasons. A patch consisted of several *Ranunculus* sectors that were at equal altitude and connected or close to each other where foraging bees were likely to switch easily from one *Ranunculus* sector to another. As differences in altitude and the direct minimum distances from the nesting site to *Ranunculus* patches varied considerably between the four nesting sites, the 19 patches were ranked (1) according to their difference in altitude, the patch with the lowest rank representing the patch with the least difference in altitude to the nesting site, and (2) according to their direct minimum distance to the nesting site, the patch with the lowest rank representing the closest host plant patch. Direct minimum distance was calculated with the Pythagoras formula analogously to the direct foraging distances (see above), using the shortest horizontal linear distance between the nesting site and the edge of the according *Ranunculus* patch. Patch ranking was made individually for each of the four nesting sites. The recorded foraging flights were assigned to the ranked patches separately for each nesting site, e.g. the foraging flight of a bee from site C recaptured in the sixth closest patch from its nest was assigned to rank 6. The total number of foraging flights for each rank was determined by summing up the results from all four

nesting sites. Statistical analysis of patch ranking was not feasible due to the low number of recorded foraging flights.

To test whether wind conditions influenced the direction of the foraging flights, wind directions at the time of recapture of the individual bees were correlated with the individual bees' foraging directions using the software R (version 2.8.0). Weather data were recorded by a field weather station (CR10 Measurement and Control Module, Campbell Scientific Ltd., Shepshed Leicestershire, England).

4.3.4.2 *Hoplitis adunca* at a site with open water and a motorway

To test whether bees are able to cross open water and paved roads, the host plant stand across the river was searched for marked females during two hours each on July 27 and July 31, 2007 during sunny weather between 12am and 5pm with maximum daily temperatures ranging from 24.2°C to 26.0°C. The presence of each recaptured female at the artificial nesting site was verified the same day it was observed at the host plant stand.

4.4 Results

4.4.1 *Chelostoma florissomne* at a hilly, forested site

Of the 351 marked females, 19 (5.4%) were recaptured in the *Ranunculus* stands on and around the forest clearings (Fig. 4.1). Three of these females were recaptured twice in the same sector. All recaptured females were observed to collect pollen, as could be judged by their filled abdominal scopa, and all but one recaptured bees were observed to provision brood cells at one of the four nesting sites the same day they were recaptured. The single female that was not observed at any of the nesting sites after being

recaptured was discarded from analysis. In total, 21 foraging flights of 18 individual bees (Table 4.1) were included in the analysis below.

Table 4.1 Distance values for the recorded foraging flights of *Chelostoma florissomne*. The direct minimum distance represents the distance to the closest host plant stand from each nesting site. The direct foraging distance (d) was calculated from the horizontal linear distance (h) between nesting site and place of recapture and the difference in altitude (a) applying the formula of Pythagoras (see text). The direct distance across forest represents the distance a bee had to fly over or through forest. All distance values are given in meters. Foraging flights no. 9 and 10, no. 16 and 20, as well as no. 18 and 19 were by one female each.

Foraging flight	Nesting site	Direct minimum distance	Horizontal linear distance (h)	Difference in altitude (a)	Direct foraging distance (d)	Direct distance across forest
1	B	180	250	55	260	170
2	B	180	260	55	270	200
3	B	180	300	55	310	170
4	D	340	360	10	360	150
5	B	180	370	5	370	270
6	B	180	360	65	370	200
7	A	310	360	80	380	140
8	D	340	390	10	390	160
9	D	340	390	10	390	160
10	D	340	390	10	390	160
11	D	340	390	10	390	150
12	A	310	390	80	410	140
13	C	460	500	110	510	210
14	D	340	560	45	560	450
15	D	340	570	45	570	480
16	C	460	560	135	580	290
17	C	460	560	135	580	290
18	C	460	560	135	580	290
19	C	460	560	135	580	290
20	C	460	560	135	580	290
21	C	460	650	30	650	0

All but one recaptured bee flew across forest to reach the host plant stands (Table 4.1). The calculated direct distances these females had to fly over or through forest ranged from 140m to 480m with a median of 200m (Table 4.1).

Differences in altitude overcome by foraging females ranged from 5m to 135m with a median of 55m (Table 4.1). Frequency of recaptures did not reveal a distinct pattern with respect to the differences in altitude overcome by the recaptured females between nesting site and host plant patch (Fig. 4.3A).

The calculated direct foraging distances (d) between nesting site and place of recapture ranged from 260m to 650m with a median of 390m (Table 4.1). Nine bees flew more than 500m to reach the host plant patch. Frequency of recaptures was high at host plant patches close to the nesting sites (Fig. 4.3B) and low at more distant places with a single recapture in a plant patch not belonging to the four closest host plant patches from the respective nesting site.

Wind direction did not correlate with the direction of the foraging flights ($R_{\text{Spearman}} = -0.1785$, $p = 0.439$).

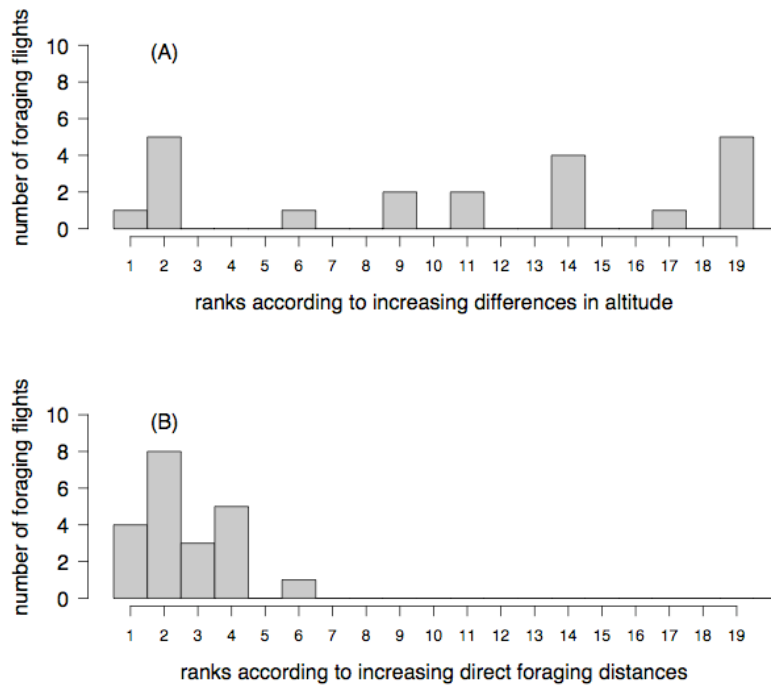


Figure 4.3 Total number of foraging flights of *Chelostoma florissomne* per rank with respect to (A) the difference in altitude from each nesting site and (B) the minimum direct distance to each nesting site. Rank 1 represents the *Ranunculus* patches with the least difference in altitude from each of the four nesting sites and the closest patches from each of the four nesting sites, respectively.

4.4.2 *Hoplitis adunca* at a site with open water and a motorway

Of the 20 marked females, three (15%) were recaptured in the *Echium* stand across the river in a distance of 360m to 400m from the artificial nesting site (Fig. 4.2). To reach their host plants, the bees had to fly at least 100m over open water and 12m over two lanes of a motorway. Two of the three females were observed on both observation days, yielding a total of five recorded foraging flights. All females collected pollen and provisioned brood cells at the day of recapture.

4.5 Discussion

Considerable differences in altitude between nest and foraging habitat as well as dense forests with tall trees were overcome by pollen-foraging females of the specialist solitary bee *Chelostoma florissomne*. Further, a broad river and a motorway with intense traffic did not prevent females of the specialist solitary bee *Hoplitis adunca* from pollen foraging on its host plant. Thus, the landscape structures tested in our study clearly did not act as insurmountable barriers for foraging females of the two solitary bee species.

While recapture rates found in the present study are well within the range of recaptures measured for species of other insect groups in search of their key resources (Toepfer et al. 1999, 2000, Haddad et al. 2008), they are lower than those reported in other studies with pollen specialist bee species (Bischoff 2003, Franzen et al. 2009).

The limited number of recaptured females of *C. florissomne* and *H. adunca* was undoubtedly due to the low probability of finding marked bees in the vast host plant stands. However, surpassing landscape structures appears to be a widespread behaviour of foraging *C. florissomne* and *H. adunca* females in the study areas. At least 30 to 50 females of *C. florissomne* were constantly provisioning brood cells at each of the four nesting sites during the whole observation period. As the forest clearings were devoid of *Ranunculus* flowers with the single exception mentioned above, the great majority of these females must have overcome similar differences in altitude and similar distances across forests as the recaptured females. We can not quantify the percentage of non-recaptured marked females that might have discontinued provisioning a nest at our nesting sites in favour of a nesting site with easier access to host plants. Such nesting sites were supposed to be plentiful along the forest edges. Among the recaptured marked females, however, this percentage remained below 10% as only one recaptured

bee out of 19 was never observed at our nesting sites again, either because it had left the site or died after recapture. Similar considerations apply to surmounting of landscape structures by *H. adunca*. Most marked individuals that were not recaptured were observed to provision brood cells at the nesting site, and to arrive from and leave in the direction of the *Echium* plant stand that was the only host plant stand within a radius of 1200m from the nesting site. These observations indicate that many foraging *H. adunca* females indeed crossed the river and the motorway.

Our study design allowed the bees first to establish a nest, before the bees' foraging options were confined to host plant stands across a landscape structure. It is yet unknown to which degree the bees would have left these nesting sites after emergence without the initial flower supply in close vicinity to their nests.

4.5.1 Differences in altitude

Pollen-collecting females of *C. florissomne* overcame differences in altitude of up to 135m, which is close to the maximal difference in altitude of 150m of the study area. This finding is remarkable for two reasons. First, the bees had to transport the full pollen load uphill back to their nest. Second, the females overcame the differences in altitude 10-15 times per day, with each foraging flight lasting 10-15min (A. Zurbuchen, unpubl. data). Therefore, the topography of the study area does not appear to act as an insurmountable barrier for the foraging *Chelostoma* bees. This conclusion is in line with our finding that the frequency distribution of recaptured females did not show a clear pattern in favour for those host plant patches with the lowest difference in altitude to the nest.

4.5.2 Forests

Foraging females of *C. florissomne* crossed forest areas over distances of up to 480m when trees were already completely foliated. While it remains open whether the bees flew through or over the forest, we observed several females, which, after leaving their nest, flew in a straight line at a height of about 1.5m towards the forest border suggesting that they flew through rather than over the forest. A study with bumblebees showed that *Bombus terrestris* crossed forests above the canopy, while *B. pascuorum* was assumed to fly below it (Kreyer et al. 2004). Foraging workers of these two species were found to occasionally cross woodland over a distance of 600m between mass floral resources. Similarly, workers of the bumblebee species *Bombus affinis* and *B. impatiens* were able to cross forests over a distance of up to 130m (Bhattacharya et al. 2003). However, workers of all four bumblebee species were reluctant to do so as long as there was an ample supply of flowers available. These studies as well as several studies on butterflies (Fry and Robson 1994, Sutcliffe and Thomas 1996, Haddad 1999b, a, Haddad and Baum 1999, Townsend and Levey 2005) clearly show that the reluctance to cross a landscape structure does not necessarily indicate an insuperable barrier effect of that structure, but rather indicates an adaptive behaviour during periods when resources are plentiful. It is possible that a large percentage of the females of *C. florissomne* provisioning brood cells at our nesting sites would have refrained from crossing forests if flower rich *Ranunculus* stands were available on the two forest clearings at similar distances from the nesting site.

4.5.3 Open water

The present study documents the phenomenon that pollen-collecting females of *Hoplitis adunca* can successfully cross a large distance (100m) of open water to reach the closest available host-plant patch. The capability to cross open water has been documented so far for one solitary bee species and the honeybee indicating that this behaviour might be more widespread among bees. The solitary bee *Dasypoda altercator* was found to fly over water in homing experiments (Chmurzynski et al. 1998), and honeybees could be trained to use feeders positioned on lakes in distances of up to 300m from the shore (Tautz et al. 2004, Wray et al. 2008).

4.5.4 Roads

In the present study, females of *Hoplitis adunca* flew over a motorway with intense traffic to collect pollen. Likewise, females of two bumblebee species were reported to fly over roads to reach suitable foraging places (Bhattacharya et al. 2003). However, these bumblebees crossed roads mainly when floral resources were declining. Similarly, only a small percentage of females of the rare solitary bee *Andrena hattorfiana* crossed unpaved roads (Franzen et al. 2009).

4.5.5 Distance between nest and pollen source

As a medium sized bee species, *C. florisomne* is predicted to have a maximum foraging distance of about 200-400m (Gathmann and Tscharntke 2002). In contrast, the current study documents a flight distance of 500-650m for several females of *C. florisomne*, indicating that the foraging capacity of this species is higher than expected. In spite of these long foraging distances, recaptured *Chelostoma* bees were found on available host

plant stands situated at minimum distances to their nest. As many as 20 out of 21 foraging bees were noted on one of the four closest host plant patches. As individual insects within a population may vary in their capacity for long flights (Keil et al. 2001), the proportion of individuals that successfully reaches distant resources is in many instances relatively low (Dorn et al. 1999, Gu et al. 2006, Pasquet et al. 2008). Conversely, a relatively high proportion of individuals can successfully cover short distances (Keil et al. 2001, Sarvary et al. 2008), coinciding with the large number of bees recaptured in the current study at the shortest possible distance categories from the nest. On the other hand, by foraging on host plant patches in the vicinity of the nest, the females of *C. florisomne* may reduce foraging time and energy expenditure, thereby maximizing the number of brood cells they can build within their short lifetime as adult insects. Indeed, foraging expenditure in terms of energy and time were shown to affect reproduction in bees (Feuerbacher et al. 2003, Peterson and Roitberg 2006b, Williams and Kremen 2007) and travel costs were assumed to render distant patches less profitable to foragers than closer ones (Williams and Tepedino 2003).

4.5.6 Conclusions

Landscape structures such as forests, hills, rivers and motorways do not act as insuperable barriers for the bee species and the spatial scales tested in our study. These findings lead to consecutive questions, referring to possible costs for crossing landscape structures, and to females' preferences when given the choice to forage with or without crossing landscape structures. Further, as both bee species investigated in the present study are widespread and common in central Europe, the impact of the same landscape structures

on foraging behaviour of rare and endangered bee species should be the subject of future investigations.

5 Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances²

5.1 Abstract

To preserve populations of endangered bee species, sound knowledge of their maximum foraging distance between nest and host plants is crucial. Previous investigations predicted maximum foraging distances of 100-200m for small bee species and up to 1100m for very large species based on mainly indirect methods. The present study applied a new and direct approach to experimentally investigate maximum foraging distances in solitary bees. One endangered and two common species of different body sizes, all of which restrict pollen foraging to a single plant genus, were established in a landscape lacking their specific host plants. Females were forced to collect pollen on potted host plants that were successively placed in increasing distance from fixed nesting stands. The maximum foraging distance recorded for the small *Hylaeus punctulatissimus* was 1100m, for the medium sized *Chelostoma rapunculi* 1275m and for the large *Hoplitis adunca* 1400m, indicating that maximum foraging distances at species level have been underestimated. However, the capability to use resources on such a large spatial scale applied only to a small percentage of individuals as 50% of the females of *H. punctulatissimus* and *H. adunca* did not forage at distances longer than 100-225m and 300m, respectively. This finding suggests that a close neighbourhood of nesting and foraging habitat within few hundred meters is crucial to maintain populations of these species, and that threshold distances at which half of the population discontinues foraging are a more meaningful parameter for conservation practice than the species specific maximum foraging distances.

² Based on Zurbuchen A., L. Landert, J. Klaiher, A. Müller, S. Hein, and S. Dorn, 2010. Biological Conservation, in press.

5.2 Introduction

Pollinating animals provide enormous ecological and economic benefits to flowering plants, wildlife and humans (Buchmann and Ascher 2005). Bees are among the world's most important pollinators (Allen-Wardell et al. 1998, Buchmann and Ascher 2005, Klein et al. 2007). However, bees have suffered a substantial decline in local species diversity and population size during the last few decades (Kearns et al. 1998, Biesmeijer et al. 2006, Grixti et al. 2009). In Western and Central Europe, 25% to 65% of the bee species are listed in national and regional Red Data Books (Else and Spooner 1987, Amiet 1994, Westrich et al. 1998, Westrich et al. 2000, Mandery et al. 2003, Burger et al. 2004, Steffan-Dewenter et al. 2005, Westrich et al. 2008). Modern agricultural practices, landscape fragmentation and habitat degradation have been negatively affecting bee populations by the elimination of resources needed for successful reproduction such as nesting sites and pollen and nectar sources (Westrich 1996, Klein et al. 2004). Increased spatial separation of nest and plant resources may result from a decrease of both suitable nesting habitats (Westrich 1996, Klein et al. 2004) and host plants (Müller et al. 2006, Larsson and Franzen 2007) with increasing fragmentation and isolation of suitable habitats. Such spatial separation might adversely affect bee population dynamics, as female bees require a substantial number of foraging bouts between nest and pollen source to provision their brood cells. As the flight radius of an individual bee or a bee species is restricted due to internal (e.g. physiology, morphology) or external factors (e.g. landscape barriers), resources outside of this radius are not available rendering colonization or exploitation of otherwise suitable habitats impossible. In fact, the distance between crop fields and natural or semi-natural habitats containing suitable nesting sites was found to be negatively correlated with

species richness and abundance of crop pollinators in America (Kremen et al. 2004, Ricketts et al. 2004), Asia (Klein et al. 2003) and Europe (Free 1993). Furthermore, bees might to a certain extent be able to adjust to changes in the spatial arrangement of nest and plant resources and forage increasing distances, which might involve a substantial fitness cost however. Higher energy and time investments spent on longer foraging distances are assumed to negatively affect the number of progeny that can be produced during a bee's reproductive life span (Peterson and Roitberg 2006b, Zurbuchen et al., submitted).

Sound knowledge of foraging ranges is crucial in management practices to conserve populations of bees. In the last few years, maximum bee foraging ranges, which describe the maximum distance a bee species can cover between nest and host plants, have received increased attention (Table 5.1). However, most of these investigations applied indirect methods, which may over- or underestimate maximum foraging distances. Foraging distances deduced from translocation experiments (e.g. Abrol 1988, Gathmann and Tschardt 2002, Pasquet et al. 2008), which measure the percentage of bees returning to their nest from a release point, are likely to overestimate maximum foraging ranges. On the other hand, maximum foraging distances inferred from mark-recapture experiments (e.g. Abrol 1988, Walther-Hellwig and Frankl 2000a, Wolf and Moritz 2008, Zurbuchen et al., 2010), the use of harmonic radar (e.g. Carreck et al. 1999, Osborne et al. 1999) or pollen analysis (e.g. Tepedino 1983, Westrich 2006, Beil et al. 2008) might represent optimized foraging distances based on local floral resource supply and distribution (Beekman and Ratnieks 2000, Ricketts 2001), and thereby underestimate maximum foraging distances. The same may hold true for the use of trap

nest colonization (e.g. Gathmann and Tschardt 2002) to deduce maximum foraging distances as bees are expected to optimize distances between the nesting sites and available host plant stands.

In contrast to the maximum foraging distance at the species level, the distance reached by a sizable proportion of the population (such as 50%, defined here as average distance) has received hardly any attention so far, despite its high significance for species conservation. In the present study, we used a new and direct approach to experimentally investigate both maximum and average foraging distances in solitary bees. We forced three pollen specialist bee species of different body sizes to forage on host plant patches at distinct distances from their nests in an otherwise unsuitable foraging habitat, addressing the following research question: what are maximum and average foraging distances of these three species? We discuss the implications of our findings for bee preservation.

5.3 Material and Methods

5.3.1 Bee species

Hylaeus punctulatus (Smith, 1842) (Colletidae), *Chelostoma rapunculi* (Lepeletier, 1841) (Megachilidae) and *Hoplitis adunca* (Panzer, 1798) (Megachilidae) are pollen-specialist (oligolectic) solitary bee species, which exclusively collect pollen from a single plant genus (Westrich 1990, Sedivy et al. 2008): *H. punctulatus* collects solely from *Allium* (Alliaceae), *C. rapunculi* from *Campanula* (Campanulaceae) and *H. adunca* from *Echium* (Boraginaceae). In the first species, pollen is transported back to the nest in the crop, while the latter two species transport pollen in a hair brush

(scopa) on the ventral side of the abdomen. All three bee species have their reproductive period in summer (June-August). They naturally nest in beetle burrows in dead wood or hollow stems (Westrich 1990) allowing for artificial breeding in hollow bamboo sticks or pre-drilled burrows in wooden blocks. *H. punctulatissimus* is a small sized species with an average dry body mass of 5.3mg and a body length of 6-8mm, *C. rapunculi* is medium sized with an average dry body mass of 8.6mg and a body length of 8-10mm, and *H. adunca* is a large species with an average dry body mass of 19.7mg and a body length of 11-13mm (Müller et al. 2006). Both *C. rapunculi* and *H. adunca* are widespread and common in many regions of Central Europe, whereas *H. punctulatissimus* is a rare species listed in the Red Data Books of both Germany and Switzerland (Amiet 1994, Westrich et al. 2008). For the present study, we collected nests of the three bee species at different locations in Switzerland in hollow bamboo sticks that had been offered the preceding year as artificial nesting sites. These nests were transferred to artificial nesting stands in the study area before bee emergence started.

5.3.2 Plant material

Host plants of the three bee species tested in this study were planted in pots (diameter: 20cm, volume: 3520cm³). *Allium cepa* was used as the main host plant for *H. punctulatissimus*, complemented later in the season by *A. sphaerocephalon*, *A. carinatum* and *A. senescens*. *Campanula rapunculus* was used as host plant for *C. rapunculi* and *Echium vulgare* for *H. adunca*. To ensure a stable quantity and quality of pollen until the end of the experiments, flowering was phased by repeatedly trimming shoots before flowering (except for *Allium*) and by cooling plants in a greenhouse

chamber ($15 \pm 2^\circ\text{C}$, $70 \pm 5\%$ RH, 16L:8D light regime). The host plant stock was kept outdoors under an insect net to prevent flowers from being exploited by insects prior to the experiments.

5.3.3 Experimental agricultural landscape

The experimental area was an agricultural landscape intensively used for field crops in western Switzerland near Selzach, Solothurn ($7^\circ 27' 78''$ E, $47^\circ 11' 63''$ N, elevation 420m), situated in a plain devoid of potential landscape barriers such as forests or wide roads. Experiments were conducted along three straight, unpaved and parallel tracks (sites A, B and C) in a north-south direction. Distances between the tracks were 1780m (A-B), 1100m (B-C) and 2880m (A-C). An artificial nesting stand was placed adjacent to the south end of each of the three tracks. Preliminary investigations showed that the area within a radius of 1200m from each of the nesting stands lacked the specific host plants of the three bee species tested. To further assure that the bees had no pollen sources other than the potted plants at their disposal, we repeatedly checked the experimental landscape for plants of the genus *Allium*, *Campanula* and *Echium*, and in one case had to eliminate a small patch of *Echium vulgare*.

5.3.4 Bee establishment and marking

Hollow bamboo sticks and wooden nesting blocks (150 x 150 x 400mm) with pre-drilled burrows (120mm in length, 3-4mm in diameter for *H. punctulatissimus*, 4-6mm for *C. rapunculi* and 6-9mm for *H. adunca*) were prepared as artificial nests and placed in a covered shelf to protect them from rain. Bees were established by transferring 100 occupied nests per species to sites A and C (*H. punctulatissimus* and *H. adunca*) and to

site B (*C. rapunculi*). To support initiation of nesting activity by the newly emerged females, flowering host plants in pots (50 plants of *Allium cepa* and *Echium vulgare*, 100 plants of *Campanula rapunculus*) were placed at a distance of less than one meter from the nesting stands.

Females that started to nest were caught, immobilized by placing them for two to three minutes in a cool box at 5°C and marked individually with fast-drying enamel paint (Revell) on the thorax (1-2 positions) and the abdomen (1 position), applying colour codes with eight different colours. All females per nesting stand were marked prior to the initiation of the experiments.

5.3.5 Experimental design for *Hylaeus punctulatissimus* and *Hoplitis adunca*

To identify maximum foraging distances at which female bees discontinued pollen harvesting, a host plant patch consisting of 50 flowering plants, which covered an area of 2m², was consecutively moved along the tracks to a new position in increasing distance from the fixed artificial nesting stands. Prior to data collection, bees were led to the new position of the host plant patch by a trail lined up with potted flowering host plants placed at 10m intervals. This trail, designed to minimize the time needed by the bees to find the new position of the host plant patch, was provided for 6 hours while bees were active. Thereafter, these plants were incorporated into the previously moved host plant patch. At the same time, 10-20% of the host plants of a plant patch were replaced by new plant material from the host plant stock to assure abundant pollen and nectar supply.

The presence of marked females on the host plant patch was recorded by a first observer during two hours. This observation period was kept constant for all distances

tested. Flight duration of females to reach two subsequent positions of the plant patch (50m to 400m apart from each other) was considered only marginally different. Furthermore, the probability was considered high to find any marked female during the two hour observation period, as a bee flying at a velocity of 2m/sec needs only 8min to reach a plant patch at a distance of 1000m from the nest. Simultaneously with the first observer, a second observer checked the nesting stand for marked females during three hours for *H. punctulatissimus* and during two hours for *H. adunca*. The extra hour allocated for *H. punctulatissimus* should compensate for the long absence of this species from the nest due to its long foraging time (on average 80min per foraging bout compared to 30min in *H. adunca*). A marked female was considered to forage at a given distance when observed both actively collecting pollen on the plant patch and provisioning brood cells at the artificial nesting stand. Individual bees that were not monitored at a given distance but were recorded to forage at a longer distance later on in the experiment were assumed to have foraged also at the shorter distance. The experiment was discontinued when marked females nesting at the artificial nesting stand could no longer be observed foraging on the plant patch during two consecutive observation periods on two different days.

The experiments with *H. punctulatissimus* were conducted between June and August during the two field seasons 2007 and 2008. In the first season, we tested 15 distinct distances at site A (<1m, 50m, 100m, 150m, 225m, 300m, 380m, 450m, 525m, 600m, 675m, 750m, 825m, 900m, 975m) and in parallel five distances at site C (<1m, 225m, 525m, 675m, 825m). In the second season we tested nine distances at site A (<1m, 100m, 200m, 300m, 400m, 500m, 600m, 700m, 800m) and in parallel six distances at

site C (<1m, 380m, 750m, 900m, 1100m, 1270m). Each distance was tested once per season and site.

The experiments with *H. adunca* were conducted between June and August 2008. Twelve distances were tested at site A (<1m, 75m, 200m, 300m, 400m, 500m, 600m, 700m, 800m, 900m, 1000m, 1100m) and in parallel seven distances at site C (<1m, 300m, 700m, 1000m, 1270m, 1400m, 1600m). Each distance was tested once per site.

Weather data were recorded by a field weather station (CR10 Measurement and Control Module, Campbell Scientific Ltd., Shepshed Leicestershire, England). All observations were carried out on sunny days with maximum daily temperatures ranging from 23.2°C to 30.7°C between 10am and 6pm when bee activity was high. The prevailing wind direction was from the west, i.e. perpendicular to the north-south alignment of artificial nesting stand and host plant patch. Therefore, the marked females were not expected to face direct headwind nor direct downwind to reach the host plant patch. Wind was generally absent or only weak during the experiments.

5.3.6 Experimental design for *Chelostoma rapunculi*

Following the observation that some *C. rapunculi* females nesting at the artificial nesting stand collected yellow pollen from unknown Campanulaceae species that were not available within a radius of 1200m from their nests, we did not apply the same experimental design for *C. rapunculi* as described above for *H. punctulatus* and *H. adunca*. Instead, we placed a large host plant patch of 300 *Campanula rapunculus* plants covering an area of 5m² at a distance of 1000m from the artificial nesting stand at site B. Marked females were simultaneously observed by two observers for pollen collecting activity on the host plant patch and for brood cell provisioning at the nesting

stand during two hours each on eight days between end of June and beginning of July 2008. In addition, we identified the unknown *Campanula* species to species level by microscopic analysis of the yellow pollen, and mapped stands of *Campanula* species possessing yellow pollen outside the study area in the neighbouring villages.

5.4 Results

5.4.1 Hylaeus punctulatissimus

In the first year, a total of 28 females of *H. punctulatissimus* were marked (21 at site A, 7 at site C). In the second year, a total of 57 females were marked (28 at site A, 29 at site C). The observation period covered 51 days (June 30 – August 19) in year 1 and 32 days (July 10 – August 10) in year 2.

There was a clear decrease in the number of marked females foraging on the host plant patch with increasing foraging distance to the nest (Fig. 5.1). Maximum distances at which individual females were last observed to collect pollen while still provisioning brood cells at the artificial nesting stand ranged from <50m up to 900m in year 1 and from <100m to 1100m in year 2. When data from sites A and C were pooled, 50% of the marked females had discontinued foraging at 225m in year 1 and at <100m in year 2, and 75% had discontinued foraging at 380m in year 1 and at 400m in year 2.

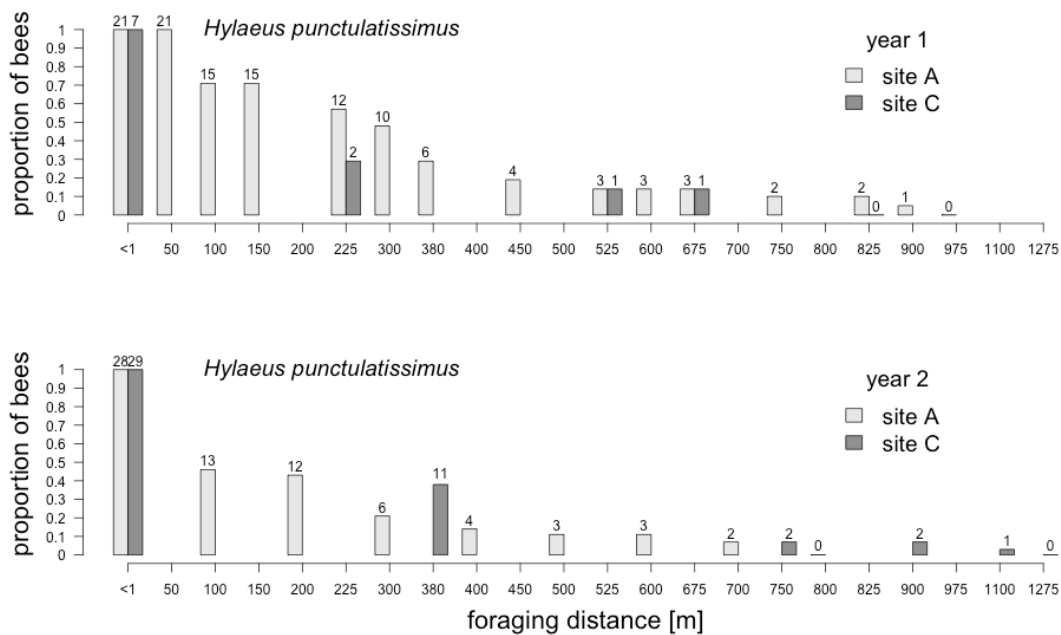


Figure 5.1 Proportion of initially marked females of the small bee species *Hylaeus punctulatissimus* observed on potted host plants that were successively placed in increasing distances from a fixed nesting stand. In year 1, fifteen distinct distances were tested at site A and five at site C; in year 2, nine distances were tested at site A and six at site C. Experiments were performed during a time period of 51 days in year 1 and 32 days in year 2. Numbers above bars indicate the number of females observed.

5.4.2 *Hoplitis adunca*

A total of 39 females of *H. adunca* were marked (15 at site A, 24 at site C). The observation period covered 45 days (June 27 – August 10) in year 2.

There was a clear decrease in the number of marked females foraging on the host plant patch with increasing distance (Fig. 5.2). Maximum foraging distances of individual females ranged from 75m to 1400m. When data from sites A and C were pooled, 50% of the marked females had discontinued foraging at a distance of 300m and 75% had discontinued foraging at a distance of 700m.

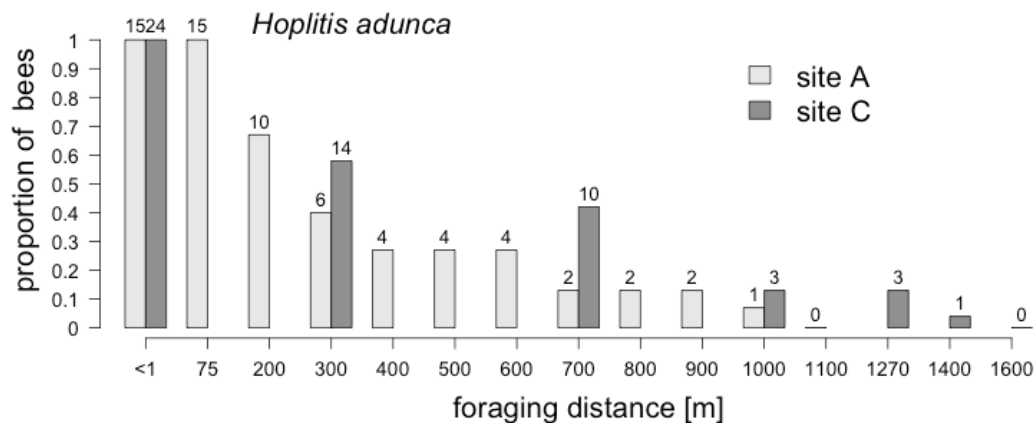


Figure 5.2 Proportion of initially marked females of the large bee species *Hoplitis adunca* observed on potted host plants that were successively placed in increasing distances from a fixed nesting stand. Twelve distances were tested at site A and seven distances at site C. Experiments were performed during a time period of 45 days in year 2, overlapping with that of *H. punctulatissimus*. Numbers above bars indicate the number of females observed.

5.4.3 *Chelostoma rapunculi*

Seven out of 35 marked females were recorded to collect pollen on the *Campanula rapunculus* patch, set at a distance of 1000m from the artificial nesting stand. Two of these females were observed on the plant patch on five out of eight observation days, two were recorded on three days and another two on two days. These six females provisioned brood cells at the artificial nesting stand with white pollen over a time period of at least 14 days (June 26 – July 7) until the end of the experiment. One marked female was observed to collect pollen on the plant patch and to provision brood cells at the nesting stand on one day only and then apparently left its initial nest but continued to forage on the patch.

The remaining 28 marked females were never observed on the *Campanula rapunculus* patch. However, 24 of them repeatedly arrived at the nesting stand carrying full loads of yellow pollen, identified microscopically as originating from *Campanula*

medium and *Platycodon grandiflorum*. Both of these Campanulaceae species are exclusively grown in home gardens and parks. The closest stands of Campanulaceae with yellow pollen were found in a home garden at a distance of 1275m from the nesting stand.

5.5 Discussion

Our direct approach investigating bee foraging distances revealed that all three bee species tested flew substantially longer maximum foraging distances at the species level than would have been expected from a regression model based on bee body size (Gathmann and Tscharrntke 2002). We observed that the small bee species *H. punctulatissimus* collected pollen at a maximum distance of 1100m from the nest, whereas its expected maximum foraging distance was only 100-250m. The medium sized *C. rapunculi* regularly foraged at a maximum distance of 1275m, which is substantially longer than the expected 300-400m. Finally, the large *H. adunca*, of which the maximum foraging distance was expected to be in the range of 400-600m, exploited host plant patches at a maximum distance of 1400m from the nest. We do not assume that these observed long distance flights are an artefact due to our experimental design, which forced the bees to fly long distances. Instead, we expect these same females to have covered similarly long distances under more natural conditions, if for example all meadows containing the specific pollen hosts had been mowed in a radius of several hundred meters around the nests. The trail of flowers that guided our bees to the new position of the host plant patch might have resulted in a decrease of time and energy spent to locate the floral resources. Thus, we can not exclude that the capability of

individual bees to reach distant host plant patches would be lowered if they had to randomly search the landscape for suitable host plants.

The results of our study indicate that maximum bee foraging distances at the species level might have been underestimated so far. This conclusion is in line with an increasing number of observations of long maximum foraging distances in solitary bees (including social sweat bees), bumblebees, stingless bees and honeybees (Table 5.1). Single individuals of small to medium sized species of the genera *Andrena*, *Chelostoma*, *Lasioglossum* and *Megachile* were found to forage at maximum distances of 500m up to 1250m from their nests as revealed indirectly by pollen analyses and mark-recapture experiments (Beil et al. 2008). The closest host plant stand of the large pollen specialist species *Colletes hederæ* was located at a distance of 1000m from a nest aggregation (Westrich 1996). The maximum foraging distance documented for a female of the medium sized species *Colletes daviesanus* was 2225m (Esser 2005) and one female of the giant *Xylocopa flavorufa* was radio-tracked at a distance of 6040m from its nest (Pasquet et al. 2008). Bumblebees were shown to forage at maximum distances of 800-1750m from their nest in mark-recapture experiments (Walther-Hellwig and Frankl 2000a, Osborne et al. 2008) and were calculated to fly 2300-2800m based on models of nest densities (Chapman et al. 2003). Similarly, stingless bees were repeatedly found to forage at distances of 1000-2500m from their hive (Araujo et al. 2004, Kuhn-Neto et al. 2009, Roubik and Aluja 1983), and analysis of waggle dances of the honeybee revealed foraging distances ranging from 1250m to 14 000m (von Frisch 1967, Visscher and Seeley 1982, Dyer and Seeley 1991, Waddington et al. 1994, Beekman and Ratnieks 2000).

Table 5.1 Literature data on maximum foraging distances in bees. *Foraging distance* refers to the distance between a bees' nest and the flower resources exploited for pollen and nectar. *Homing distance* refers to the distance between the location to which a bee was transferred and its nest. n.a. = not available, - = method used without testing individual bees. Within each of the four bee guilds the entries are sorted according to (1) the method used and (2) the distances flown.

bee species	size [mm]	distances flown [m]	distance type	method	n	references
solitary bees/social sweat bees						
<i>Osmia adunca</i>	8-12	180	foraging distance	closest host plant patch	n.a.	Hembach (1993)
<i>Osmia lignaria</i>	11-12	600	foraging distance	closest host plant patch	n.a.	Rust (1990)
<i>Colletes hederæ</i>	7-16	1000	foraging distance	closest host plant patch	n.a.	Westrich (1996)
<i>Chelostoma rapunculi</i>	8-10	200	foraging distance	trap nest colonisation, statistical modelling	n.a.	Gathmann and Tscharntke (2002)
<i>Megachile lapponica</i>	6-8	300	foraging distance	trap nest colonisation, statistical modelling	n.a.	Gathmann and Tscharntke (2002)
<i>Chelostoma florissomne</i>	7-11	150	foraging distance	mark-recapture	n.a.	Käpylä (1978)
<i>Megachile flavipes</i>	8-10	500	foraging distance	mark-recapture	n.a.	Abrol (1988)
<i>Chelostoma florissomne</i>	7-11	650	foraging distance	mark-recapture	18	Zurbuchen et al. (2010a)
<i>Megachile nana</i>	8-10	750	foraging distance	mark-recapture	n.a.	Abrol (1988)
<i>Colletes daviesanus</i>	7-9	2225	foraging distance	mark-recapture	74	Esser (2005)
<i>Andrena hattorfiana</i>	13-16	130	flying range	mark-recapture (marked while foraging)	270	Franzen et al. (2009)
<i>Osmia maritima</i>	n.a.	150	n.a.	n.a.	n.a.	Haeseler (1982)
<i>Panurgus banksianus</i>	10-12	250	n.a.	n.a.	n.a.	Münster-Swendsen (1968)
<i>Colletes cunicularis</i>	11-14	350	n.a.	n.a.	n.a.	Wesslering (1996)
<i>Colletes hederæ</i>	7-16	400	n.a.	n.a.	n.a.	Schmid-Egger et al. (1995)
<i>Andrena cineraria</i>	10-14	300	foraging distance	observation on host plants	n.a.	Gebhardt and Röhr (1987)
<i>Andrena clarkella</i>	11-13	300	foraging distance	observation on host plants	n.a.	Gebhardt and Röhr (1987)
<i>Hylaeus punctulatus</i>	6-8	1100	foraging distance	oligolectic bees, host plants in distinct distances	85	this study
<i>Chelostoma rapunculi</i>	8-10	1275	foraging distance	oligolectic bees, host plants in distinct distances	35	this study
<i>Hoplitis adunca</i>	8-12	1400	foraging distance	oligolectic bees, host plants in distinct distances	39	this study
<i>Lasioglossum marginellum</i>	n.a.	200	foraging distance	pollen analysis	8	Westrich (2006)
<i>Megachile rotundata</i>	6-8	500	foraging distance	pollen analysis, closest host plants	n.a.	Tepedino (1983)
<i>Andrena dorsata</i>	8-10	650	foraging distance	pollen analysis, closest host plants	1	Beil et al. (2008)
<i>Lasioglossum calceatum</i>	8-10	1000	foraging distance	pollen analysis, closest host plants	4	Beil et al. (2008)
<i>Andrena flavipes</i>	10-14	1150	foraging distance	pollen analysis, closest host plants	3	Beil et al. (2008)
<i>Andrena carbonaria</i> agg.	n.a.	1250	foraging distance	pollen analysis, closest host plants	1	Beil et al. (2008)
<i>Lasioglossum fulvicorne</i>	6-7	1250	foraging distance	pollen analysis, closest host plants	1	Beil et al. (2008)
<i>Megachile rotundata</i>	6-8	100	foraging distance	pollination rates within a radius from nesting site	-	Tasei and Delaude (1984)
<i>Megachile spp.</i>	6-9	1000	foraging distance	pollination, dispersal of pollen	-	Amand et al. (2000)
<i>Xylocopa flavorufa</i>	24-26	6040	foraging distance	radio-transmitter	135	Pasquet et al. (2008)
<i>Osmia anthocoides</i>	8-11	150	homing distance	translocation exp.	n.a.	Molitor (1937)
<i>Megachile femorata</i>	13-14	500	homing distance	translocation exp.	10	Abrol (1986)
<i>Andrena vaga</i>	11-15	510	homing distance	translocation exp.	42	Gathmann and Tscharntke (2002)
<i>Andrena barbilabris</i>	10-12	530	homing distance	translocation exp.	38	Gathmann and Tscharntke (2002)
<i>Andrena flavipes</i>	10-14	530	homing distance	translocation exp.	36	Gathmann and Tscharntke (2002)
<i>Tetralonia salicariae</i>	9-10	600	homing distance	translocation exp.	40	Gathmann and Tscharntke (2002)
<i>Megachile nana</i>	n.a.	650	homing distance	translocation exp.	20	Abrol (1988)
<i>Megachile flavipes</i>	n.a.	800	homing distance	translocation exp.	20	Abrol (1988)
<i>Osmia rufa</i>	8-13	900	homing distance	translocation exp.	25	Gathmann and Tscharntke (2002)
<i>Osmia mustelina</i>	10-14	1000	homing distance	translocation exp.	n.a.	Molitor (1937)
<i>Anthidium septemdentatum</i>	9-12	1200	homing distance	translocation exp.	n.a.	Molitor (1937)
<i>Xylocopa violacea</i>	20-23	1200	homing distance	translocation exp.	n.a.	Molitor (1937)
<i>Chelostoma florissomne</i>	7-11	2000	homing distance	translocation exp.	6	Herrmann (1999)
<i>Xylocopa flavorufa</i>	24-26	10000	homing distance	translocation exp.	22	Pasquet et al. (2008)
<i>Anthophora abrupta</i>	14-17	12'500	homing distance	translocation exp.	66	Rau (1929)
<i>Tetralonia salicariae</i>	9-10	400	homing distance	translocation, logistic regression	n.a.	Wesslering and Tscharntke (1995)
<i>Andrena barbilabris</i>	10-12	500	homing distance	translocation, logistic regression	n.a.	Wesslering and Tscharntke (1995)
<i>Andrena flavipes</i>	10-14	600	homing distance	translocation, logistic regression	n.a.	Wesslering and Tscharntke (1995)
<i>Andrena vaga</i>	11-15	600	homing distance	translocation, logistic regression	n.a.	Wesslering and Tscharntke (1995)
<i>Osmia rufa</i>	8-13	900	homing distance	translocation, logistic regression	n.a.	Gathmann and Tscharntke (2002)
bumblebees						
<i>Bombus terrestris</i>	20-23	9900	male flight distance	density of worker- and/or drone-producing colonies	-	Kraus et al. (2009)
<i>Bombus terrestris</i>	20-23	550	foraging distance	harmonic radar	21	Carreck et al. (1999)
<i>Bombus terrestris</i>	20-23	630	foraging distance	harmonic radar	21	Osborne et al. (1999)
<i>Bombus muscorum</i>	17-19	200	foraging distance	mark-recapture	13	Walther-Hellwig and Frankl (2000a)
<i>Bombus sp.</i>	17-23	300	foraging distance	mark-recapture	1	Dramstad (1996)
<i>Bombus terrestris</i>	20-23	800	foraging distance	mark-recapture	126	Wolf and Moritz (2008)
<i>Bombus lapidarius</i>	20-22	1500	foraging distance	mark-recapture	22	Walther-Hellwig and Frankl (2000a)
<i>Bombus terrestris</i>	20-23	1500	foraging distance	mark-recapture	297	Osborne et al. (2008)
<i>Bombus terrestris</i>	20-23	1750	foraging distance	mark-recapture	28	Walther-Hellwig and Frankl (2000a)
<i>Bombus sp.</i>	17-23	350	flying range	mark-recapture (marked while foraging)	36	Saville et al. (1997)
<i>Bombus pascuorum</i>	15-18	2300	foraging distance	model based on estimation of nest density	-	Chapman et al. (2003)
<i>Bombus terrestris</i>	20-23	2800	foraging distance	model based on estimation of nest density	-	Chapman et al. (2003)
<i>Bombus terrestris</i>	20-23	312.5	foraging distance	molecular analysis - sister-pairs	-	Darvill et al. (2004)
<i>Bombus pascuorum</i>	15-18	449	foraging distance	molecular analysis - sister-pairs	-	Knight et al. (2005)
<i>Bombus lapidarius</i>	20-22	450	foraging distance	molecular analysis - sister-pairs	-	Knight et al. (2005)
<i>Bombus pratorum</i>	15-17	674	foraging distance	molecular analysis - sister-pairs	-	Knight et al. (2005)
<i>Bombus terrestris</i>	20-23	758	foraging distance	molecular analysis - sister-pairs	-	Knight et al. (2005)

(continued on next page)

Table 5.1 (continued)

bee species	size [mm]	distances flown [m]	distance type	method	n	references
stingless bees						
<i>Melipona mandacaja</i>	n.a.	2100	foraging distance	feeder training	n.a.	Kuhn-Neto et al. (2009)
<i>Nannotrigona testaceicornis</i>	n.a.	951	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Plebeia poecilochroa</i>	n.a.	951	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Scaura latitarsis</i>	n.a.	951	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Tetragonisca angustula</i>	n.a.	951	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Frieseomelitta varia</i>	n.a.	1710	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Geotrigona inusitata</i>	n.a.	1710	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Partamona cupira</i>	n.a.	1710	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Scaptotrigona postica</i>	n.a.	1710	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Trigona hypogea</i>	n.a.	1710	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Trigona recurva</i>	n.a.	1710	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Melipona bicolor</i>	n.a.	2000	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Melipona scutellaris</i>	n.a.	2000	foraging distance	linear regression	-	Araujo et al. (2004)
<i>Plebeia droryana</i>	n.a.	540	foraging distance	mark-recapture	n.a.	Araujo et al. (2004)
<i>Melipona marginata</i>	n.a.	800	foraging distance	mark-recapture	n.a.	Araujo et al. (2004)
<i>Trigona spinipes</i>	n.a.	840	foraging distance	mark-recapture	n.a.	Araujo et al. (2004)
<i>Melipona quadrifasciata</i>	n.a.	2000	foraging distance	mark-recapture	n.a.	Araujo et al. (2004)
<i>Melipona compressipes</i>	n.a.	2470	foraging distance	mark-recapture	n.a.	Araujo et al. (2004)
<i>Trigona capitata</i>	n.a.	1547	homing distance	translocation exp.	16	Roubik and Aluja (1983)
<i>Melipona fasciata</i>	n.a.	2085	homing distance	translocation exp.	45	Roubik and Aluja (1983)
honeybees						
<i>Apis florea</i>	8-10	500	foraging distance	mark-recapture	n.a.	Abrol (1988)
<i>Apis mellifera</i>	11-13	915	foraging distance	mark-recapture	131	Gary et al. (1972)
<i>Apis mellifera</i>	11-13	1100	foraging distance	mark-recapture	613	Gary et al. (1981)
<i>Apis mellifera</i>	11-13	1243	foraging distance	waggle dance	n.a.	Schneider and Hall (1997)
<i>Apis mellifera</i>	11-13	1413	foraging distance	waggle dance	5	Waddington et al. (1994)
<i>Apis cerana</i>	9-11	1900	foraging distance	waggle dance	18	Dyer and Seeley (1991)
<i>Apis mellifera</i>	11-13	7900	foraging distance	waggle dance	37	Dyer and Seeley (1991)
<i>Apis mellifera</i>	11-13	10100	foraging distance	waggle dance	n.a.	Visscher and Seeley (1982)
<i>Apis florea</i>	8-10	11200	foraging distance	waggle dance	8	Dyer and Seeley (1991)
<i>Apis dorsata</i>	12-14	12000	foraging distance	waggle dance	11	Dyer and Seeley (1991)
<i>Apis mellifera</i>	11-13	13500	foraging distance	waggle dance	n.a.	von Frisch (1967)
<i>Apis mellifera</i>	11-13	14000	foraging distance	waggle dance	n.a.	Beekman and Ratnieks (2000)

The unexpectedly long maximum foraging distances in *H. punctulatissimus* and *H. adunca* concerned only single females. In fact, the number of nesting females decreased rapidly with increasing foraging distance in both species. Only 50% of the females of the small *H. punctulatissimus* and the large *H. adunca* foraged at distances longer than 100m-225m and 300m, respectively, and 75% had discontinued foraging at a distance of 380m-400m and 700m, respectively, which is still considerably less than the maximum foraging distance recorded for the small and the large species (1100m and 1400m, respectively). For the medium sized species *C. rapunculi*, as many as 90% of the marked females were foraging at distances of 1000m or more. This comparatively high proportion of females foraging long distances might have resulted in part from a relatively short observation period (14 days) at the beginning of the nesting season compared to much longer observation periods (32-51 days) in the other two bee species. As longer distances were tested relatively late in the nesting season of both

H. punctulatus and *H. adunca*, increased natural mortality might also have contributed to the rapid decrease of foraging females with increasing distance. Thus, we can not exclude that more individuals of these two species would have managed to forage long distances if tested early in the nesting season. However, mortality alone can not fully explain the rapid decrease of foraging individuals. In fact, many females of both species discontinued foraging but were still present at the original nesting stand. Other females might have dispersed by routine movement (Van Dyck and Baguette 2005) to alternative nesting habitats outside the radius of the host plant free space. Both behaviours are expected to be a consequence of increasing foraging costs with increasing distances.

Studies in the context of dispersal showed that individual insects within a population may vary in their capacity for long flights (Keil et al. 2001). The proportion of individuals that successfully reaches distant resources is in many cases relatively low (Dorn et al. 1999, Gu et al. 2006, Pasquet et al. 2008), whereas a relatively high proportion of individuals can successfully cover short distances (Hughes and Dorn 2002, Keil et al. 2001; Sarvary et al. 2008). This is in line with our finding that only few individuals of *H. punctulatus* and *H. adunca* foraged at a distance of more than 1000m, which indicates that populations of these bee species are negatively affected by increasing foraging distance already at a considerably smaller spatial scale than maximum foraging distances would suggest.

The finding that threshold distances at which 50% of the females discontinued foraging were substantially shorter than the species specific maximum foraging distances indicate that a close neighbourhood of suitable nesting sites and flower rich

foraging habitats may be crucial for maintaining populations of bees. In the two bee species investigated, only half of the tested individuals managed to overcome distances of more than 100-225m and 300m, respectively, suggesting that a spatial separation of nesting and foraging habitat of less than few hundred meters might be fundamental for population persistence in these two species. In addition to threshold and maximum foraging distances, conservation strategies for endangered bee species also have to consider the costs of foraging flights. Indeed, there are indications that foraging flights may impose high costs on solitary bees. Females of *Osmia lignaria* produced enough offspring to guarantee population maintenance when their nesting site was surrounded by natural habitat offering suitable flower resources, whereas the number of offspring generated by females nesting at sites more distant from natural habitats was too low for population persistence (Williams and Kremen 2007). Similarly, the mean number of brood cells completed during one season was 75% lower in females of *Megachile rotundata*, which foraged in plant patches 150m away from their nests, compared to females foraging at plant patches directly adjacent to the nests (Peterson and Roitberg, 2006b).

In conclusion, the maximum foraging distances of solitary bees at the species level appear to have been underestimated so far. However, the capability to use resources on a larger spatial scale might only apply to a small proportion of individuals within a population. Consequently, for the conservation of bee populations knowledge of threshold distances at which for example 50% of females discontinue their foraging activity is supposed to be more important than the mere knowledge of species specific maximum foraging distances covered only by a small proportion of individuals. Such

threshold distances may be substantially shorter than maximum foraging distances as shown in the present study, indicating that a close neighbourhood of nesting and foraging habitats within few hundred meters is crucial to preserve populations of bees.

6 Long foraging distances impose high costs on offspring production in solitary bees³

6.1 Abstract

Solitary bees are central place foragers returning to their nests several times a day with pollen and nectar to provision their brood cells. They are especially susceptible to landscape changes that lead to an increased spatial separation of suitable nesting sites and flower rich host plant stands. While knowledge of bee foraging ranges is currently growing, quantitative data on the costs of foraging flights are very scarce, although such data are crucial to understand bee population dynamics. In the present study, the impact of increased foraging distance on the duration of foraging bouts and on the number of brood cells provisioned per time unit was experimentally quantified in the two pollen specialist solitary bee species *Hoplitis adunca* and *Chelostoma rapunculi*. Females nesting at different sites foraged under the same environmental conditions on a single large and movable flowering host plant patch in an otherwise host plant free landscape. The number of brood cells provisioned per time unit by *H. adunca* was found to decrease by 23%, 31% and 26% with an increase in the foraging distance by 150m, 200m and 300m, respectively. The number of brood cells provisioned by *C. rapunculi* decreased by 46% and 36% with an increase in the foraging distance by 500m and 600m, respectively. Contrary to expectation, a widely scattered arrangement of host plants did not result in longer mean duration of a foraging bout in *H. adunca* compared to a highly aggregated arrangement, which might be due to a reduced flight directionality combined with a high rate of revisitation of already depleted flowers in the aggregated plant arrangement or by a stronger competition and disturbance by other flower visitors. The results of the present study clearly indicate that a close

³ Based on Zurbuchen A., S. Cheesman, J. Klaiber, A. Müller, S. Hein, and S. Dorn, submitted.

neighbourhood of suitable nesting and foraging habitats is crucial for population persistence and thus conservation of endangered solitary bee species.

6.2 Introduction

Bees, which are the world's most important pollinators (Buchmann and Ascher 2005), are currently suffering a considerable decline in species diversity and population size in many regions of the world (Kremen et al. 2002, Steffan-Dewenter et al. 2005, Murray et al. 2009). As bees are typical central place foragers, which have to return to their nests several times a day with pollen and nectar, they are expected to be especially susceptible to landscape changes that lead to an increased spatial separation of suitable nesting sites and flower rich host plant stands, e.g. habitat degradation and habitat fragmentation. Sound knowledge of the individual bees' capability to cover varying distances between nest and host plants is crucial to preserve populations of endangered bee species and, indeed, bee foraging ranges have received considerable attention in the last few years (e.g. Beekman and Ratnieks 2000, Gathmann and Tscharrntke 2002, Araujo et al. 2004, Knight et al. 2005, Beil et al. 2008, Osborne et al. 2008, Pasquet et al. 2008, Zurbuchen et al. 2010a, Zurbuchen et al. 2010b).

However, the mere knowledge of maximum bee foraging distances is not enough for the preservation of populations of endangered species. To understand bee population dynamics, we need detailed and quantified information about the costs of foraging flights, but such data are very scarce. Foraging flights may impose high costs on solitary bees. A large proportion of foraging females of *Hylaeus punctulatissimus* and *Hoplitis adunca* were found to discontinue foraging already at distances considerably shorter than the species' maximum foraging distance (Zurbuchen et al. 2010a). Similarly,

females of *Chelostoma florissomne* preferred host plant patches relatively close to their nesting sites (Zurbuchen et al. 2010b), and travel costs were assumed to render distant plant patches less profitable to foraging *Osmia lignaria* than closer plant patches (Williams and Tepedino 2003). Further, the number of progeny produced within a reproductive season was negatively affected by increasing foraging distance in *Megachile rotundata* (Peterson and Roitberg 2006b), and offspring production in *Osmia lignaria* was sufficient to ensure population persistence when nesting sites were surrounded by natural habitat offering suitable floral resources, but not when nesting at sites more distant from natural habitats (Williams and Kremen 2007).

The distribution of host flowers within the flight radius of a bee is expected to influence foraging bout duration and thus reproductive output. Indeed, pollinators were shown to adjust their foraging strategy to different plant distribution patterns (Klinkhamer and Dejong 1990, Cartar and Real 1997, Cresswell 1997, Kunin 1997). However, to our knowledge the quantitative influence of host plant distribution on the reproduction of solitary bees has not yet been addressed.

For the present study, we selected the two differently sized and pollen specialist solitary bee species *Hoplitis adunca* (Panzer, 1798) (Megachilidae) and *Chelostoma rapunculi* (Lepeletier, 1841) (Megachilidae). Females of both species build several brood cells during their lifetime as adult insects, which lasts maximally four to six weeks (Westrich 1990). Each cell is provisioned with pollen and nectar before a single egg is laid. The hatched larva feeds on the pollen-nectar mixture and develops inside the cell within one year to the adult insect.

We compared the impact of (1) foraging distance and (2) spatial arrangement of host plants on bee reproduction. First, we quantified the effect of long compared to short foraging distances on the duration of foraging bouts and the number of progeny reared by a female bee, i.e. the number of brood cells provisioned per time unit. Second, we quantified the effect of aggregated compared to scattered arrangements of host plants on the duration of foraging bouts. We then set the findings from the two experiments into the context of bee ecology and bee population dynamics.

6.3 Material and Methods

6.3.1 Bee species

The two solitary bee species *H. adunca* and *C. rapunculi*, which have their reproductive period in summer (June-August), exclusively collect pollen from *Echium* (Boraginaceae) and *Campanula* (Campanulaceae), respectively (Westrich 1990, Sedivy et al. 2008). They naturally nest in beetle burrows in dead wood or hollow stems (Westrich 1990), allowing for artificial breeding in hollow bamboo sticks or pre-drilled burrows in wooden blocks, and transport pollen back to the nest in a hair brush (scopa) on the ventral side of the abdomen (Westrich 1990). *H. adunca* is a rather large species with an average dry body mass of 19.7mg and a body length of 11-13mm, *C. rapunculi* is a medium sized species with an average dry body mass of 8.6mg and a body length of 8-10mm (Müller et al. 2006). Nests of the two species were collected at different locations in Switzerland from bamboo sticks that had been offered the preceeding year as nesting sites. These nests were transferred to artificial nesting stands in the study area prior to adult emergence.

6.3.2 Plant material

To yield movable host plant patches, *Echium vulgare* (for *H. adunca*) and *Campanula rapunculus* (for *C. rapunculi*) were planted in pots (diameter: 20cm, volume: 3520cm³). To ensure a stable quantity and quality of pollen over the complete period of the experiments, flowering was phased by repeatedly trimming shoots before flowering and by cooling plants in a greenhouse chamber (15 ±2°C, 70 ±5% RH, 16L:8D light regime). The host plant stock was kept outdoors under an insect net to prevent flowers from being exploited by insects prior to the experiments.

6.3.3 Experimental agricultural landscape

The experimental area was an agricultural landscape intensively used for field crops, devoid of the specific bee host plants, in western Switzerland near Selzach, Solothurn (7° 27' 78'' E, 47° 11' 63'' N, 420m a.s.l.). Both experiments were conducted along a straight and unpaved track leading in North-South direction. Wind was generally absent or only weak during the experiments (field weather station CR10 Measurement and Control Module, Campbell Scientific Ltd., Shepshed Leicestershire, England). In case weak wind came up during the experiments, the tested females were unlikely faced by any direct headwind or downwind, as the prevailing wind direction was from the West, i.e. perpendicular to the North-South direction of the track.

6.3.4 Bee establishment and marking

Hollow bamboo sticks and wooden nesting blocks (150 x 150 x 400mm) with pre-drilled burrows (120mm in length, 4-6mm in diameter for *C. rapunculi* and 6-9mm for *H. adunca*) were prepared as artificial nests and placed in a covered shelf to protect them from rain. To support initiation of nesting activity by the newly emerged females, flowering host plants in pots (50 plants of *E. vulgare* and 100 plants of *C. rapunculus*) were placed at a distance of less than one metre from the nesting stands. These plants were removed before the onset of the experiments.

Females that started to nest were caught, immobilized by placing them for two to three minutes in a cool box at 5°C and marked individually with fast-drying enamel paint (Revell, Bünde/Germany) on the thorax (one or two positions) and the abdomen (one position), applying colour codes with eight different colours.

6.3.5 Impact of foraging distance and spatial host plant arrangement

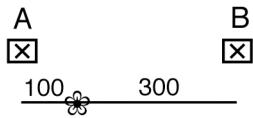
6.3.5.1 Experimental design

Females of the two tested bee species nested at different distances from a single large and movable flowering host plant patch in an otherwise host plant free environment (Fig. 6.1). Specifically, *H. adunca* was offered a single host plant patch between the two nesting stands A and B in year one (2007) and between nesting stands C and E in year two (2008). The following distance pairs were tested simultaneously each: 100 vs. 300m (year one); 225 vs. 375m and, after moving the plant patch, 450m vs. 150m (year two). To test a total of three distances at the same time, *C. rapunculi* was offered a single host plant patch North of the three nesting stands C, D and E in year two,

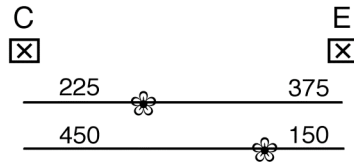
resulting in a distance triplet of 1000m vs. 500m vs. 400m. 80 and 70 nests were transferred to each of the nesting stands of *H. adunca* and *C. rapunculi*, respectively.

Hoplitis adunca

year 1



year 2



Chelostoma rapunculi

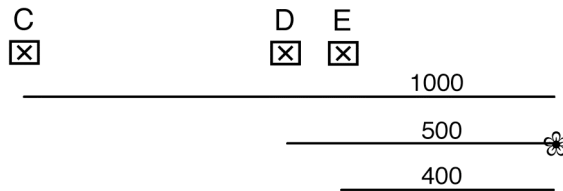
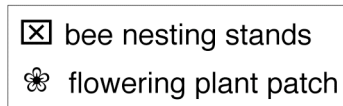


Figure 6.1 Relative position of bee nesting stands (A-E) and flowering host plant patches for the experiments with the two solitary bee species *Hoplitis adunca* and *Chelostoma rapunculi*. Resulting distance pairs and distance triplets are indicated in metres.

The number of potted plants used to form a movable host plant patch amounted to 150 for *E. vulgare*, covering an area of 4m², and 250 for *C. rapuncululus*, covering an area of 6m². Withered plants were replaced in regular intervals with fresh plants from the host plant stock. To ensure that no naturally occurring host plants were available, the area was checked prior to the start of the experiment and repeatedly during the experimental period. No flowering plants of the genus *Echium* were found within a radius of a minimum of 1200m from nesting stand A, 800m from nesting stand B, 1200m from nesting stand C and 600m from nesting stand E. During the experiments, a small patch of non-flowering *E. vulgare* was located and eliminated. No flowering plants of the

genus *Campanula* were found within a radius of a minimum of 1200m from nesting stand C, 700m from nesting stand D and 600m from nesting stand E.

Two spatial arrangements of host plant distribution were tested in *H. adunca*. In the aggregated arrangement, plants were concentrated in an area of 4m², at a density of 37.5 plants/m². In the scattered arrangement, plants were placed perpendicular to the North-South axis of the experimental track in two metre intervals and in groups of one to three plants along a line of 160m length extending both to the West and East, yielding a density of 4.7 plants/m².

To test the effect of the foraging distance and the spatial arrangement of host plants on the time needed by a bee for a single foraging bout, the duration of foraging bouts of marked females was recorded in absolute daytime to the nearest second simultaneously by one observer each per nesting stand. The duration of a foraging bout was defined as the time an individual female bee needed from leaving the nest until return to the nest with pollen and nectar. Only foraging bouts of bees returning with visible pollen in the abdominal scopa were considered. The duration of two to six foraging bouts per individual female and per observation day was recorded. For every individual bee, the mean duration of a foraging bout per distance and per spatial host plant arrangement was calculated by pooling the data from all days of observation. At each day of observation, the presence of marked females on the host plant patch was recorded during two hours by an additional observer. Foraging bouts of females that were observed at the nest but not on the host plant patch the very same day were excluded. All observations were carried out on sunny days with maximum daily temperatures ranging from 23.2°C to 30.7°C between 10am and 6pm when bee activity was high

(field weather station CR10 Measurement and Control Module, Campbell Scientific Ltd., Shepshed Leicestershire/England).

6.3.5.2 Impact of foraging distance on pollen load

The experiments conducted in the current study rely upon the crucial assumption that the number of pollen grains transported per foraging flight is independent of the foraging distance. To test this assumption, we compared the mean number of pollen grains transported back to the nest by females of *H. adunca* foraging at the experimental host plant patch at a distance of 450m and 150m from their nests, respectively (Fig. 6.1). On three days in July 2008, a total of 33 pollen-loaded females returning to their nests were caught by one observer each per nesting stand during the same observation period. Pollen contained in the abdominal scopa was washed off with 1ml ethanol (70%) to remove the adhesive pollenkitt. After ultrasonic treatment for 2min with a ultrasonic bar (Vibra Cell 72446, Bioblock, Illkirch/France) at 20kHz to loosen the pollen grains from each other, 1ml of the homogeneous ethanol-pollen mixture was centrifuged at 2500 rpm for 5min. To remove the ethanol, 0.8 ml of the supernatant was discarded and replaced by 0.8ml H₂O for a final volume of 1ml. After thoroughly stirring to evenly disperse the pollen grains within the solution, one droplet of the pollen solution was transferred to the chamber of a haemocytometer (Neubauer improved, Brand, Wertheim/Germany). The pollen grains in each of the four corner squares characterized by an exactly defined volume were counted under a microscope (Olympus BX 50, Tokyo/Japan) at a magnification of 100x. Each pollen sample was processed three times, resulting in a total of 12 squares counted per pollen load. In order to obtain an estimate of the total number of pollen grains per scopal load, the mean

number of pollen grains counted per square was extrapolated in proportion to the initial volume of the pollen solution.

6.3.5.3 Impact of foraging distance on the number of brood cells provisioned

Experiments with *H. adunca* were conducted in July 2007 and in June and July 2008. The duration of foraging bouts for the three distance pairs of 100m vs. 300m, 225m vs. 375m and 450m vs. 150m was recorded for two, seven and six days, respectively. A total of 26, 35 and 43 females were tested for the first, second and third distance pair, respectively. Experiments with *C. rapunculi* were conducted in July 2008. A total of 23 females were tested for the distance triplet of 1000m vs. 500m vs. 400m during three days.

To quantify the effect of different foraging distances on reproduction, the mean number of brood cells provisioned per time unit was estimated for each species and foraging distance tested. The quantity of pollen and nectar contained in the brood cells of solitary bees is known to vary considerably within species depending on the sex of the offspring, the size of the adult females or the quantity and availability of host plants (Bosch and Vicens 2005, 2006, Peterson and Roitberg 2006b, a, Bosch 2008). Therefore, the mean time required to provision an average sized *standard brood cell* was determined for each species and foraging distance by multiplying the mean duration of a foraging bout by the average number of flights needed to provision a single brood cell. The average number of flights (F_{BC}) needed to provision a brood cell was calculated for each species by dividing the mean number of pollen grains contained in a brood cell (P_{BC}) by the mean number of pollen grains transported per foraging flight (P_F). To estimate P_{BC} and P_F , freshly completed brood cells, in which the larvae

had not yet hatched, as well as unmarked females upon their return from a foraging bout with a filled abdominal scopa were randomly collected at the nesting stands. The procedure of pollen counting was as described above except for: (1) the pollen content of each brood cell was initially dissolved in 10ml ethanol (70%) for *H. adunca* and 5ml ethanol for *C. rapunculi*; (2) the number of pollen grains contained in a brood cell was estimated based on two samples of 1ml each, resulting in a total of 24 haemocytometer squares counted per brood cell.

The indirect method applied in the present study to quantify the number of progeny reared by a female ruled out any bias that might originate from possible unequal conditions at the nesting sites, such as abundance of natural enemies.

6.3.5.4 Impact of spatial host plant arrangement on the duration of foraging bouts

To test the effect of different spatial arrangements of host plants on the duration of foraging bouts in *H. adunca*, a single plant patch composed of 150 potted *E. vulgare* was offered to the foraging female bees either in an aggregated arrangement with a density of 37.5 plants/m² or in a scattered arrangement with a density of 4.7 plants/m² (see section 6.3.5.1) at a distance of 450m and 150m from the nesting stands C and E, respectively (Fig. 6.1). Duration of foraging bouts for both plant arrangements was recorded twice during two periods of three days each. Both periods were characterized by sunny and windless weather conditions with very similar maximum daily temperatures (July 15-17 and 24-26, 2008). During the first period, data for the aggregated plant arrangement were collected on one day, followed by data collection for the scattered plant arrangement on two days. During the second period, data for the aggregated plant arrangement were collected on two days, followed by data collection

for the scattered plant arrangement on one day. A total of 21 individual females were tested for the distance of 150m and 30 individual females for the distance of 450m. Data for the aggregated plant arrangement are part of the data set collected for the distance pair 450m vs. 150m in the experiment on foraging distances detailed above. The exact time and position of each marked female observed on the plants in the scattered plant arrangement was recorded by at least two observers to obtain information on the spatial use of the host plants.

6.4 Results

6.4.1 Impact of foraging distance on pollen load

The number of pollen grains transported per foraging flight by females of *H. adunca* was not significantly different between foraging distances of 150m and 450m (Fig. 6.2) (Two sample t-test, $p=0.511$, $n_{150}=15$, $n_{450}=18$).

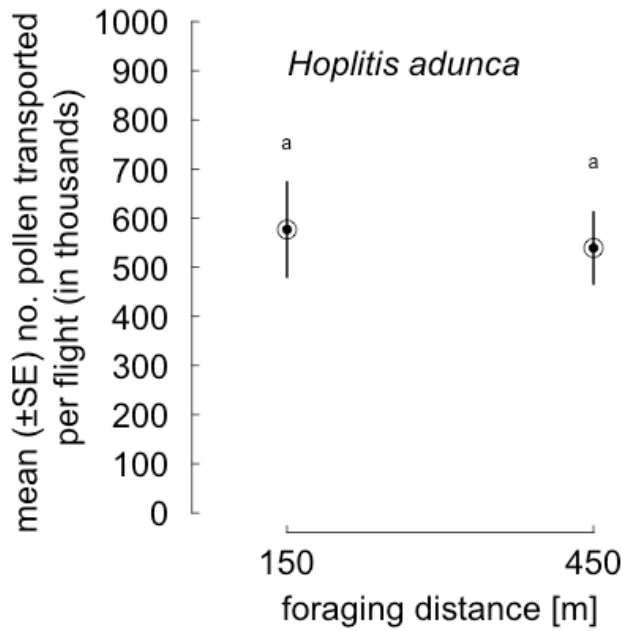


Figure 6.2 Mean number (\pm standard error) of pollen grains transported per foraging flight (in thousands) in the solitary bee species *Hoplitis adunca* for two distances. Different letters indicate a significant difference. Two sample t-test: $p=0.511$, $n_{150}=15$, $n_{450}=18$.

6.4.2 Impact of foraging distance on the number of brood cells provisioned

Foraging over longer compared to foraging over shorter distances required significantly more time for *H. adunca* females in all three distance pairs tested (Table 6.1, Fig. 6.3) (Two sample t-tests: 225m vs. 375m, $p<0.01$, $n_{225}=18$, $n_{375}=17$; 100m vs. 300m, $p<0.01$, $n_{100}=9$, $n_{300}=17$; 150m vs. 450m, $p<0.001$ (Bonferroni corrected), $n_{150}=18$, $n_{450}=25$).

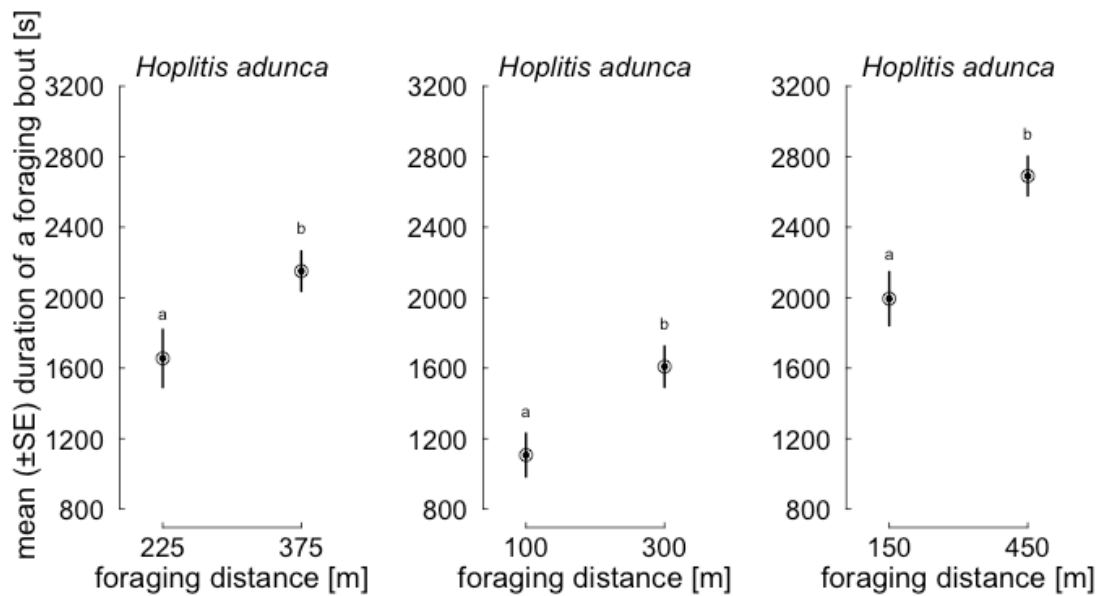


Figure 6.3 Mean duration (\pm standard error) of a foraging bout of the solitary bee species *Hoplitis adunca* for six different foraging distances tested in three pairs. Different letters indicate a significant difference. Two sample t-tests: 225m/375m, $p < 0.01$, $n_{225}=18$, $n_{375}=17$; 100m/300m, $p < 0.01$, $n_{100}=9$, $n_{300}=17$; 150m/450m, $p < 0.001$, $n_{150}=18$, $n_{450}=25$.

C. rapunculi females needed significantly more time to forage at 1000m compared to either 400m or 500m, whereas no difference in the duration of foraging bouts was found between females foraging at 400m and 500m (Table 6.1, Fig. 6.4) (ANOVA: $p < 0.05$, TukeyHSD $p_{1000-400} < 0.05$, $p_{1000-500} < 0.05$, $p_{500-400} = 0.676$, $n_{400}=11$, $n_{500}=6$, $n_{1000}=6$).

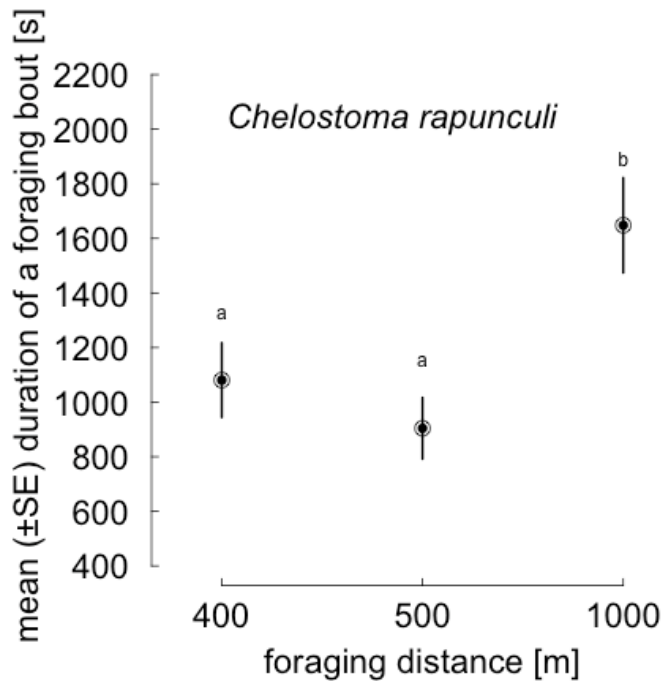


Figure 6.4 Mean duration (\pm standard error) of a foraging bout of the solitary bee species *Chelostoma rapunculi* for three different foraging distances tested simultaneously. Different letters indicate a significant difference. ANOVA: $p < 0.05$, TukeyHSD $p_{500-400} = 0.676$, $p_{1000-400} < 0.05$, $p_{1000-500} < 0.05$, $n_{400} = 11$, $n_{500} = 6$, $n_{1000} = 6$.

An average of 46 and 19 foraging flights were needed by females of *H. adunca* and *C. rapunculi*, respectively, to provision a standard brood cell based on the mean number of pollen grains transported per foraging flight and the mean number of pollen grains stored in a brood cell (Table 6.2). The time needed to provision a standard brood cell significantly increased with increasing foraging distance in both bee species (Table 6.1), except for *C. rapunculi* foraging at 400m vs. 500m. Correspondingly, the proportion of brood cells provisioned per time unit decreased in *H. adunca* by 23%, 31% and 26% with an increase in the foraging distance by 150m, 200m and 300m, respectively, and in *C. rapunculi* by 46% and 36% with an increase in the foraging distance by 500m and 600m, respectively (Table 6.1).

Table 6.1 Mean duration of a foraging bout (t_F), mean time to provision an average sized standard brood cell (t_{BC}), the proportion of a brood cell provisioned per hour (BC/hour) and calculated decrease in the number of brood cells provisioned per time unit for different distance pairs/triplets and plant distribution arrangements in the two solitary bee species *Hoplitis adunca* and *Chelostoma rapunculi*. n = number of female bees tested. Different letters indicate a significant difference in the mean duration of a foraging bout. $t_{BC}=t_F \cdot F_{BC}$, where F_{BC} is the mean number of foraging flights needed to provision a brood cell.

bee species	plant distribution pattern	n	distance pairs/triplets [m]	t_F [h:min:s]	t_{BC} [h:min]	BC/hour	decrease	statistics
<i>Hoplitis adunca</i>	aggregated	18	225	0:27:35a	21:09	0.047		t-test, p<0.01
<i>Hoplitis adunca</i>	aggregated	17	375	0:35:51b	27:29	0.036	23%	
<i>Hoplitis adunca</i>	aggregated	9	100	0:18:27a	14:09	0.071		t-test, p<0.01
<i>Hoplitis adunca</i>	aggregated	17	300	0:26:49b	20:34	0.049	31%	
<i>Hoplitis adunca</i>	aggregated	18	150	0:33:15a	25:30	0.039		t-test, p<0.001
<i>Hoplitis adunca</i>	aggregated	25	450	0:44:50b	34:22	0.029	26%	
<i>Chelostoma rapunculi</i>	aggregated	11	400	0:18:10a	5:42	0.174		ANOVA, p<0.05
<i>Chelostoma rapunculi</i>	aggregated	6	500	0:15:04a	4:46	0.210	36% (1000 vs 400)	
<i>Chelostoma rapunculi</i>	aggregated	6	1000	0:27:28b	8:41	0.114	46% (1000 vs 500)	
<i>Hoplitis adunca</i>	aggregated	17	150	0:34:44a	26:38	0.038		two-way ANOVA, distance p<0.001, distribution p= 0.721
<i>Hoplitis adunca</i>	aggregated	23	450	0:46:45b	35:51	0.028		
<i>Hoplitis adunca</i>	scattered	18	150	0:34:33a	26:29	0.038		
<i>Hoplitis adunca</i>	scattered	21	450	0:48:57b	37:32	0.027		

Table 6.2 Mean number of foraging flights needed to provision an average sized standard brood cell (F_{BC}) in the two solitary bee species *Hoplitis adunca* and *Chelostoma rapunculi*. $F_{BC}=P_{BC}/P_F$, with P_{BC} being the mean number (\pm standard error) of pollen grains per brood cell and P_F the mean number (\pm standard error) of pollen grains transported in the abdominal scopa per foraging flight. P_F and P_{BC} are rounded to the nearest 100. n_F = number of pollen loads analysed, n_{BC} = number of brood cells analysed.

bee species	n_F	P_F	n_{BC}	P_{BC}	F_{BC}
<i>Hoplitis adunca</i>	56	501 700 \pm 44 700	30	23 083 000 \pm 1 120 000	46
<i>Chelostoma rapunculi</i>	33	187 500 \pm 17 900	30	3 596 300 \pm 284 600	19

6.4.3 Impact of spatial host plant arrangement on the duration of foraging bouts

No significant difference in the duration of foraging bouts was found between the aggregated and the scattered host plant arrangement in *H. adunca* (Table 6.1, Fig. 6.5), while the duration of foraging bouts was significantly longer for the distance of 450m compared with the distance of 150m (Two-way ANOVA: distance $p<0.001$; distribution: $p=0.721$; interaction between distance and distribution: $p=0.532$ (Bonferroni corrected); $n_{aggr_150}=17$, $n_{scatt_150}=18$, $n_{aggr_450}=23$, $n_{scatt_450}=21$).

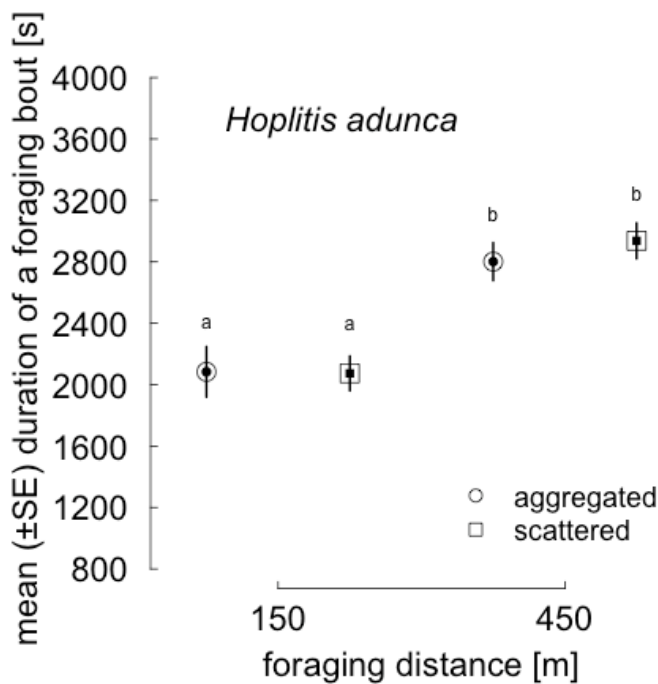


Figure 6.5 Mean duration (\pm standard error) of a foraging bout of the solitary bee species *Hoplitis adunca* measured in a two factor treatment combination: (1) foraging distance and (2) aggregated vs. scattered plant distribution pattern. Different letters indicate a significant difference. Two-way ANOVA: $p_{\text{distance}} < 0.001$, $p_{\text{distribution}} = 0.721$, $n_{\text{aggr}_{150}} = 17$, $n_{\text{scatt}_{150}} = 18$, $n_{\text{aggr}_{450}} = 23$, $n_{\text{scatt}_{450}} = 21$.

6.5 Discussion

Whenever distances between nesting stands and a single experimental host plant patch increased by more than 100m, the duration of foraging bouts consistently increased in both solitary bee species tested. This increase in the mean duration of a foraging bout can not be attributed to a larger amount of pollen collected requiring more time, as the quantity of pollen transported back to the nest by the individual female bees was found to be independent of the foraging distance. Instead, it is likely due to longer flight durations needed to cover the increased distance between nesting stand and plant patch. In fact, a direct linear relationship between duration of foraging bout and foraging distance is apparent in *C. rapunculi*. Under the assumption of a direct and

linear flight between nest and host plants with a constant flight velocity of 1.5m/s, which applies to slowly flying honeybees and orchid bees (Brodschneider et al. 2009, Combes and Dudley 2009), the extra time needed by the females of *C. rapunculi* to cover the additional distances of 2x 500m and 2x 600m, respectively, is roughly equivalent to the increase in the mean duration of a foraging bout measured in the field. In contrast, assuming again a straight flight at the same velocity, substantially more time is needed by the females of *H. adunca*. While under these assumptions flights would last only 3min20sec (for 2x 150m), 4min27sec (for 2x 200m) and 6min40sec (for 2x 300m), respectively, females spent between 4 and 6min longer for a single foraging bout. This deviation suggests that yet unknown factors might influence the duration of foraging bouts in *H. adunca*. Hardly anything is known about the directionality of a bee's flight between foraging habitat and nesting site. While the assumption of a direct and linear non-stop flight applies to certain species, such as *C. rapunculi*, it might be too simple for other species, such as *H. adunca*. Longer foraging distances could require more frequent or more extended nectar uptakes to meet the higher energy expenditure or time consuming exploratory loops for orientation. Indeed, feeding on nectar is well known to increase the flight capacity of insects, such as parasitoid wasps (Wanner et al. 2006, Rousse et al. 2009).

By applying an indirect method to quantify the time required to provision a standard brood cell based on the duration of foraging bouts and the average number of foraging flights, the number of brood cells provisioned per time unit was found to substantially decrease with increasing foraging distance in both bee species tested. The reduction in the number of brood cells in *H. adunca* amounted to 23%, 31% and 26% with an increase in the foraging distance by 150m, 200m and 300m, respectively,

and in *C. rapunculi* to 46% and 36% with an increase in the foraging distance by 500m and 600m, respectively. The non-linearity of the calculated percentage decreases with increasing foraging distance might reflect varying abiotic and biotic conditions during the experiments, including temperature and host plant quality. Temperature, humidity and light intensity strongly influence bee behaviour (Corbet et al. 1993, Stone 1994, Bosch and Kemp 2002, Klein et al. 2004) and a low pollen and nectar supply adversely affects bee reproduction (Peterson and Roitberg 2006a). The number of offspring produced by solitary bees is very low compared to many other insect taxa (Westrich 1990). Foraging for pollen and nectar accounts for an average of 72% of the total time needed to build, provision and close an entire brood cell in three different species of *Osmia* (Maddocks and Paulus 1987, Müller 1994), the sister genus of *Hoplitis*, and 51% in *Chelostoma florissomne* (Herrmann 1999), a member of the same genus as *C. rapunculi*. By applying these percentages to the two bee species investigated and considering the weather conditions at the study site in 2008, we estimate that the females of *H. adunca* and *C. rapunculi* were able to construct seven and 22 brood cells, respectively, for the longer foraging distances tested, and 15 and 32 brood cells, respectively, for the shorter distances. Given this low number of brood cells, already a moderate increase in foraging distance might lower offspring production below the threshold value needed to ensure persistence of a bee population.

The magnitude of the reduction in the number of brood cells provisioned per time unit with increasing foraging distance as found in the present study is a conservative estimate as our experimental design did not consider the impact of longer foraging distances on bee senescence and life span. Increased flight activity is expected to

further senescence and reduce life span. Indeed, life span was shown to be shortened by a high flight activity in honeybees (Neukirch 1982, Schmid-Hempel and Wolf 1988). Similarly, the wear of parts of the exoskeleton, e.g. wings or pollen collecting apparatus, as well as the physiological ageing of the flight muscles reduce flight and foraging capacity and increase mortality in adult bees (Torchio and Tepedino 1980). Longer foraging distances are not only expected to affect female reproductive capacity, they may influence offspring survival as well. With increasing costs of foraging flights, fewer resources are allocated to offspring (Kim and Thorp 2001, Bosch and Vicens 2006, Peterson and Roitberg 2006b, a), resulting in a lowered survival rate of overwintering bee larvae (Bosch and Kemp 2004, Peterson and Roitberg 2006b, Bosch 2008). In addition, parasitization of the open brood cells might increase at longer foraging distances as females spend more time away from their nest allowing for more or longer attacks by natural enemies (Goodell 2003, Peterson and Roitberg 2006b, Seidelmann 2006). In conclusion, we argue that the decrease in the number of brood cells with increasing foraging distance as found in the present study for *H. adunca* and *C. rapunculi* would have been even more pronounced when considering the effect of longer foraging distances on senescence, life span and larval survival. Indeed, in a study that included the effects of senescence and mortality, the mean number of brood cells built during one season was 74% lower in females of *Megachile rotundata* foraging in plant patches 150m away from their nests compared to females foraging in plant patches directly adjacent to the nests (Peterson and Roitberg 2006b).

Surprisingly, no effect of host plant distribution on the mean duration of foraging bouts was found in *H. adunca*. This finding is in contrast to studies on bumblebees

showing that flight durations between plants increased with decreasing plant density (Harder 1988, Ohashi and Yahara 2002). As flowers of *E. vulgare* contain only small amounts of pollen, which is successively shed by the five anthers, females of *H. adunca* have to visit a high number of flowers to fill their abdominal scopa with pollen. Thus, the considerably lowered host plant density in the scattered host plant arrangement actually forced the foraging female bees to fly substantially longer distances between individual host plants on the very same foraging bout compared to the aggregated arrangement. In fact, several marked females of *H. adunca* were observed to visit host plants spread over a distance of at least 140m during a single foraging bout. We suppose that the lack of difference in foraging bout duration between the two arrangements of plant distribution was due to the very high density of flowers in the aggregated host plant patch. Hence, less efficient pollen collection may have blurred the advantage of the short inter-plant flight distances. This hypothesis is in line with studies on bumblebees, which showed that increasing plant density resulted in a decrease of flight directionality (Cartar and Real 1997, Cresswell 1997, 2000), that the frequency of revisitation of the same flowers was almost twice as high in patchy flower arrays than in uniform arrays (Cresswell 2000), that the search for unvisited inflorescences might be easier in small than in large host plant patches (Goulson 2000), and that a higher abundance of flower visitors restricts the foraging area due to interactions with other pollinators (Comba 1999, Makino and Sakai 2005).

In conclusion, the present study clearly shows that increasing spatial separation of nest and host plants substantially reduces offspring production in two solitary bee species already at a small spatial scale. Thus, spatial separation of nesting and

foraging habitats due to past and present landscape changes might be an important reason for the current decline in local species diversity and population size in solitary bees. For the conservation of endangered solitary bee species, a close neighbourhood of suitable nesting sites and flower rich foraging habitats within a maximal distance of few hundred metres appears to be crucial, even if the species-specific maximal foraging distance is considerably longer.

7 General discussion

Availability of nesting sites and flowering plants as pollen and nectar sources within the foraging range is crucial for offspring production in bees. External factors such as landscape barriers as well as internal factors (e.g. energy, physiology, morphology) can restrict foraging ranges of bees. We found that landscape structures such as hills and forests as well as rivers and motorways are no insurmountable barriers for females of *Chelostoma florisomne* and *Hoplitis adunca*, respectively. In a structurally simple landscape, the small bee species *Hylaeus punctulatissimus*, the medium sized *Chelostoma rapunculi* and the large *H. adunca* were limited to maximum foraging distances of 1100m, 1275m and 1400m, respectively. These maximum foraging distances are substantially longer (factor 3-6) than expected from a regression model based on bee body size (Gathmann and Tschardt 2002). Thus, maximum bee foraging distances at the species level might have been underestimated so far. However, half of the individuals tested foraged at substantially shorter distances of few hundred meters only. Increasing foraging distances are expected to impose high costs causing bees to discontinue their nesting activity. In fact foraging costs in terms of duration of a foraging bout were indeed found to increase with increased distances between nesting stands and a single host plant patch in both *H. adunca* and *C. rapunculi*. The extrapolated number of brood cells provisioned per time unit by *H. adunca* was found to decrease by 23%, 31% and 26% with an increase in the foraging distance of 150m, 200m and 300m, respectively. The number of brood cells provisioned by *C. rapunculi* decreased by 46% and 36% with an increase in foraging distance of 500m and 600m, respectively. Consequently, for bee species with a short foraging radius or for which long distance flights impose high costs, changing spatial availability of resources substantially affects population dynamics.

7.1 Maximum foraging distances vs. threshold distances of bee populations

Changing spatial arrangements of nesting sites and flower resources and their effects on foraging performance is increasingly addressed in literature. Landscape studies indicate that bees do respond to their structural environment on different spatial scales (Steffan-Dewenter et al. 2002, Winfree and Kremen 2009), and much research has been done on foraging distances to elucidate the foraging capability of different bee species (section 5.5, Table 5.1). A lot of emphasis is put on investigating maximum foraging distances flown by different bee species applying different methods such as translocation experiments (Gathmann and Tschardt 2002, Pasquet et al. 2008), mark-recapture experiments (Osborne et al. 2008, Wolf and Moritz 2008, Franzen et al. 2009), trap nest colonisation experiments (Gathmann and Tschardt 2002), or the use of harmonic radar (Carreck et al. 1999, Osborne et al. 1999). Maximum foraging distances define a range within which a bee species is able to use resources for offspring production. This knowledge is of course an important information, however, it is by far not sufficient to understand the effect of spatial resource distribution on bee population dynamics. The maximum foraging distance of a bee species is very likely based on an extraordinary high foraging capacity of only few individuals of a population, while the majority of females of a population will be confined to distinctly shorter foraging ranges. In our experiments, only half of the tested individuals of *H. punctulatus* and *H. adunca* managed to forage distances of more than 100-225m and 300m, respectively, whereas maximum distances would have suggested foraging ranges up to 1100m for *H. punctulatus* and 1400m for *H. adunca*. We therefore postulate for the future to focus more on threshold distances at which a sizable proportion (e.g. 50%) of a population is able to use resources rather than on

sole maximum foraging distances, which appear to be less relevant to describe the spatial scale at which a bee species responds to resource distribution in the landscape.

7.2 Implications for bee conservation

To maintain high pollinator diversity and abundance to guarantee pollination of crop and wild plants, bee conservation has to be given high priority on local, regional, national and international scales (Byrne and Fitzpatrick 2009). As the halt in land-use change is economically and politically not very likely to occur (Brown and Paxton 2009), conservation policy will have to prioritise on minimising habitat loss and rendering agricultural habitats bee-friendly in agreement with scientifically underpinned conservation strategies (Tschardt et al. 2005, Brown and Paxton 2009, Byrne and Fitzpatrick 2009).

Structurally complex landscapes enhance local habitat diversity in agroecosystems resulting in higher species richness (Hortal et al. 2009). Bees will particularly benefit from a small scale habitat diversity as they depend simultaneously on suitable nesting sites and floral resources within their foraging range to build their brood cells. Sufficient resource abundance will have to be given high priority in conservation schemes, carefully considering spatial aspects of resource distribution. Our findings that different landscape structures were crossed by foraging bees of *C. florissomne* and *H. adunca* and that maximum foraging distances of *H. punctulatus*, *H. adunca* and *C. rapunculi* are unexpectedly long, might lead to the assumption that the foraging capacity of solitary bees is higher than previously thought. However, even though landscape structures can be overcome by certain bee species, we still do not know whether this behaviour can be found in most other species as well nor whether crossing landscape structures is associated with extra costs for foraging bees.

Similarly, the finding that threshold distances at which 50% of the females discontinued foraging were substantially shorter than the species specific maximum foraging distances indicates that not only different bee guilds respond to landscape context at different spatial scales (Steffan-Dewenter et al. 2002), but even individuals of the same species. Detailed knowledge of the spatial use of resources by bee species is particularly important if the focus of conservation managements in an area is to enhance a single endangered target species.

Furthermore, we showed that already a moderate increase in foraging distance of 150-500m resulted in a substantial reduction in the number of brood cells that can be provisioned by a female of *H. adunca* or *C. rapunculi*. Similarly, for females of *Megachile rotundata* the increase in foraging distance by 150m lowered the mean number of brood cells completed within a season by 75% (Peterson and Roitberg 2006b). Females of *Osmia lignaria* produced enough offspring to guarantee population maintenance when their nesting site was surrounded by natural habitat offering suitable flower resources, whereas the number of offspring generated by females nesting at sites more distant from natural habitats was too low for population persistence (Williams and Kremen 2007). These findings clearly show that long distance foraging involves considerable costs with direct impact on offspring production and therefore population dynamics. Such high foraging costs might also explain our observation that foraging ranges are restricted to only few hundred meters in a majority of foraging females of *H. adunca* and *H. punctulatissimus*. Therefore, spatial separation of nesting and foraging habitats of no more than few hundred meters is important for bee population persistence and even more crucial for bee population enhancement and will have to be considered in future bee conservation policy.

7.3 Importance of spatial resource availability for functional diversity and ecosystem resilience

The distribution of ecosystem services within and across scales provides ecosystems with resilience (Peterson et al. 1998, Allen et al. 2005). Ecosystem services at a specific scale is determined by interactions between species and processes operating within that scale (Peterson et al. 1998). Competitive interactions among organisms of a functional group are expected to drive the dispersion of guilds or taxa of the same functional group across scales, strengthening cross-scale resilience (Peterson et al. 1998).

Pollination is one of many important ecosystem services. The pollination service in temperate regions is dominated by bees as key pollinators. While this study elucidated the importance of spatial arrangements of nest and flower resources for population dynamics of bees, other studies showed the significance of spatial arrangements of nest and flower resources for effective crop pollination services (Kremen et al. 2004, Ricketts 2004). Due to their high resource requirements and their need to commute between nest and flower plants, bees are a pollinator taxon that is expected to be especially sensitive to landscape changes affecting foraging distances, whereas other pollinator taxa might be less affected by changing spatial resource distribution. The abundance and species richness of hoverflies (Syrphidae), which as adults feed on pollen and nectar, were shown to stay constant with increasing distance from a semi-natural main habitat tested on a spatial scale of up to 2000m, whereas both abundance and species richness of native bees significantly declined when semi-natural grassland was scarce and isolated (Jauker et al. 2009). This finding shows that not only different bee species are expected to respond to landscape context at different spatial scale (Steffan-Dewenter et al. 2002, Winfree and Kremen 2009), but that differences among pollinator taxa might be even more distinct. In contrast to bees,

which as central place foragers have to commute between nest and flower resources, hoverflies or butterflies select suitable larval microhabitats for oviposition without any need to return to these sites later on. Thus, females of hoverflies and butterflies can disperse into landscapes in a progressive manner, alternating between feeding and ovipositing. Because of different habitat requirements and movement patterns, hoverflies may play a very important role in maintaining pollination services in landscapes unsuitable for specialised or less mobile bee species (Jauker et al. 2009, Lysenkov 2009) with a positive effect on cross-scale resilience of an ecosystem.

The loss of mutualistic interactions such as pollinator-plant interactions in habitat fragments will negatively affect local population dynamics of bee species as shown in our study. In contrast, the disruption of antagonistic interactions may favour a target population and enhance their persistence (Tscharntke et al. 2002). In agriculture, antagonistic interactions of herbivore pest species of crops and predators or parasitoids as biological control agents, provide another economically very important ecosystem service. Habitat fragmentation and therefore spatial resource availability affected different parasitoids more severely than their phytophagous hosts, as parasitoids responded to landscape structures on a shorter spatial scale (Tscharntke et al. 2002, Thies et al. 2003, Thies et al. 2005, Thies et al. 2008). Habitats offering nectar as adult food resources, alternative host species, shelter from disturbances by agricultural practices or suitable overwintering sites benefited populations of parasitoids, leading to higher parasitism rates in structurally rich compared to structurally simple agricultural landscapes (Thies and Tscharntke 1999, Thies et al. 2005). Hoverfly larvae of many species are aphidophagous and therefore important agents in biological control. Structural richness most probably also enhances

ecosystem services by hoverflies as their response to landscape context was strongest at a small spatial scale within a radius of 0.5-1km (Haenke et al. 2009).

Similar effects of spatial resource availability on population dynamics can also be found in the avifauna providing manifold ecosystem services (e.g. pollination, biological control, spatial structuring by seed dispersal or landscape productivity by nutrient dispersal) (Child et al. 2009). The South African avifauna was shown to suffer from a large-scale structural homogenization in agricultural landscapes (Child et al. 2009). Insectivores and pollinators accounted for the highest levels of losses. Both bird guilds, which are highly species rich functional groups, rely on specialized niches and habitat diversity only found in heterogeneous ecosystems.

In summary, spatial aspects of resource availability that are strongly affected by fragmentation and habitat degradation, seem to affect organisms of diverse functional groups likewise. Heterogeneous and structurally rich landscapes are likely to provide resources with suitable spatio-temporal patterns to sustain high species richness and, most importantly, functional diversity and therefore ecosystem resilience (Tschardt et al. 2002, Tschardt et al. 2005, Isaacs et al. 2009) with huge benefits also for crop production in human dominated agricultural ecosystems.

8 Outlook

Our studies were done with four different oligolectic solitary bee species. Three of the four species are common whereas *H. punctulatissimus* is red listed in Central Europe. Extrapolation of our data to other bee species should be done with precaution. Endangered or polylectic bee species might show different responses on different spatial scales to changes in the spatial arrangement of their resources (Steffan-Dewenter et al. 2002, Winfree and Kremen 2009). More information is needed about other bees, especially endangered species.

Recently, many studies have investigated aspects important for bee conservation. However, the knowledge has not been transferred to policy makers. A further important step is to compile the knowledge gained from scientific studies and work out meaningful bee conservation measurements that can be communicated to stakeholders.

9 References

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11 Curriculum vitae

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