

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

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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 130 m were overcome and forests covering a distance of up to 480 m were crossed by *Chelostoma florissomme*. A broad river and a motorway with intense traffic did not represent insurmountable barriers for *Hoplitis adunca*. For *C. florissomme*, total foraging distances of up to 650 m 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.

landscape barrier / fragmentation / foraging distance / *Chelostoma florissomme* / *Hoplitis adunca*

1. 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; 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 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). However, even minor vertical structures such as hedges, rows of poplar trees or plastic windbreaks can restrict movement of different groups of flying insects (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

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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, 2000; Gathmann and Tschardt, 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 florissomme* (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?

2. MATERIAL AND METHODS

2.1. Bee species

Chelostoma florissomme and *Hoplitis adunca* are strictly oligolectic collecting pollen on *Ranuncu-*

lus (Ranunculaceae) and *Echium* (Boraginaceae), respectively (Westrich, 1990; Sedivy et al., 2008). *C. florissomme* is a medium sized species with a body length of 7–11 mm and an average dry body mass of 12.5 mg, whereas *H. adunca* is a larger species with a body length of 8–12 mm and a body mass of 19.7 mg (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. florissomme* and *H. adunca* at different locations in Switzerland. These nests were transferred to artificial nesting sites in the study areas before bee emergence started.

2.2. Study areas

2.2.1. Hilly, forested site

The mark-recapture study with *Chelostoma florissomme* 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 410–600 m).

Four artificial bee nesting sites were established, two within each of two large forest clearings of 16 ha and 24 ha surface area (Fig. 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. 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 5 m and 150 m.

2.2.2. Site with open water and a motorway

The second study with *Hoplitis adunca* was conducted in an agricultural landscape intensively used

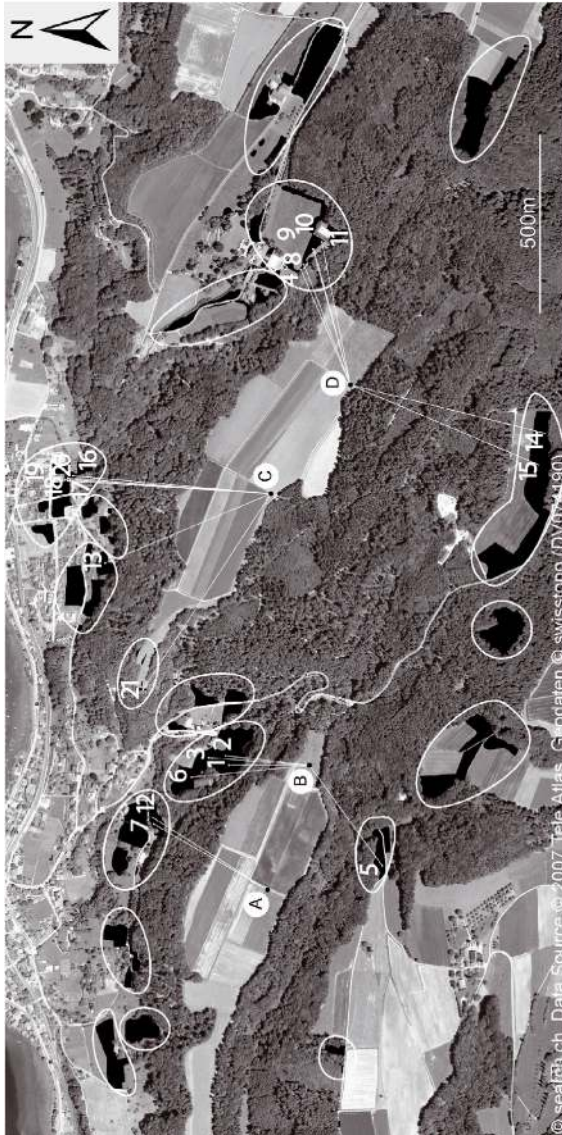


Figure 1. Hilly, forested area for the mark-recapture study with *Chelostoma florissome* in north-eastern Switzerland. The four artificial nesting sites within the two forest clearings are labelled with the letters A to D. Black areas show the mapped *Ramunculus* stands which were grouped into 19 patches (white circles). White lines indicate the foraging flights of recaptured females with the numbers referring to the individual flights listed in Table I.



Figure 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.

for field crops in western Switzerland near Selzach, Solothurn (47° 11' 63" N, 7° 27' 78" E, elevation 420 m), which is crossed by the river Aare (Fig. 2).

One artificial bee nesting site was established at a distance of 10 m 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 1200 m from the nesting site was situated at the far side of the river in a distance of 350 m from the nesting site on the roof of an underpass covering half of a motorway (Fig. 2). It was composed of 120–150 plants of *Echium vulgare* scattered in an area of about 1.2 ha.

2.3. Bee establishment and marking

Bees were established by transferring 100 occupied nests to each nesting site. Hollow bamboo sticks and wooden nesting blocks (150 × 150 × 400 mm) with pre-drilled burrows (120 mm in length, 3–5 mm in diameter for *C. florissomme* and 6–9 mm 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. florissomme*, 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 30 m 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. florissomme* were marked, ranging from 64 to 100 individuals per nesting site. A total of 20 females of *H. adunca* were marked.

2.4. Study design and data analysis

2.4.1. *Chelostoma florissomme* at a hilly, forested site

In March 2008 before flowering of *Ranunculus*, all *Ranunculus* stands around the two clearings within a radius of 700–800 m from the centre of each clearing were mapped (Fig. 1). As we had no previous information on the flight capacity of *C. florissomme*, 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 180 m for nesting site B to 460 m for nesting site D (Tab. I).

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 19.7 ha was divided into 63 sectors ranging from 0.01 ha to 1.4 ha with a median of 0.3 ha. 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. florissomme* in the study area was found to be approximately 10–15 min. 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. florissomme*. Indeed, in 90% of all sectors unmarked foraging individuals of *C. florissomme* were observed. All sectors were searched for marked females twice on different days. The total time for one complete survey was 88 h. *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 10.00 h and 17.00 h with maximum daily temperatures ranging from 20.0 °C to 25.5 °C.

To quantify the foraging distance of recaptured females of *C. florissomme*, 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 10 m.

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. 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,

Table I. 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 nos. 9 and 10, nos. 16 and 20, as well as nos. 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

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).

2.4.2. *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 12.00 h and 17.00 h 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.

3. RESULTS

3.1. *Chelostoma florissomme* 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. 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 (Tab. I) were included in the analysis below.

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

Differences in altitude overcome by foraging females ranged from 5 m to 135 m with a median of 55 m (Tab. I). 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. 3A).

The calculated direct foraging distances (d) between nesting site and place of recapture ranged from 260 m to 650 m with a median of 390 m (Tab. I). Nine bees flew more than 500 m to reach the host plant patch. Frequency of recaptures was high at host plant patches close to the nesting sites (Fig. 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 ($R_{\text{Spearman}} = -0.1785$, $P = 0.439$).

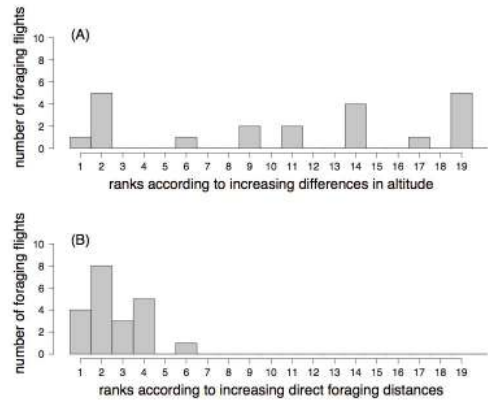


Figure 3. Total number of foraging flights of *Chelostoma florissomme* per rank with respect to (A) the difference in altitude from each nesting site and (B) the minimum direct distance to each nesting site. Rank 1 represents the *Ranunculus* patches with the least difference in altitude from each of the four nesting sites and the closest patches from each of the four nesting sites, respectively.

3.2. *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 360 m to 400 m from the artificial nesting site (Fig. 2). To reach their host plants, the bees had to fly at least 100 m over open water and 12 m 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. 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 florissomme*. 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 1200 m 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.

4.1. Differences in altitude

Pollen-collecting females of *C. florissomne* overcame differences in altitude of up to 135 m, which is close to the maximal difference in altitude of 150 m 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 10–15 min (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.

4.2. Forests

Foraging females of *C. florissomne* crossed forest areas over distances of up to 480 m 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 1.5 m 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 600 m 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 130 m (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 (Sutcliffe and Thomas, 1996; Haddad, 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. florissomme* 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.

4.3. Open water

The present study documents the phenomenon that pollen-collecting females of *Hoplitis adunca* can successfully cross a large distance (100 m) 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 *Dasygaster 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 300 m from the shore (Tautz et al., 2004; Wray et al., 2008).

4.4. 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. Distance between nest and pollen source

As a medium sized bee species, *C. florissomme* is predicted to have a maximum foraging distance of about 200–400 m (Gathmann and Tschardt, 2002). In contrast, the current study documents a flight distance of 500–650 m for several females of *C. florissomme*, 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. florissomme* 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, 2006; Williams and Kremen, 2007) and travel costs were assumed to render distant patches less profitable to foragers than closer ones (Williams and Tepedino, 2003).

4.6. 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.

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Les structures du paysage sont-elles d'insurmontables barrières pour les abeilles butineuses? Une étude par la méthode de capture-recapture sur deux espèces solitaires oligolectiques.

obstacles / paysage / fragmentation / distance d'approvisionnement / *Chelostoma florissomme* / *Hoplitis adunca*

Zusammenfassung – Sind Landschaftsstrukturen unüberwindbare Hindernisse für pollensammelnde Bienen? Eine Fang-Wiederauffang-Untersuchung mit zwei oligolectischen Wildbienenarten. In der vorliegenden Arbeit wurde mittels Fang-Wiederauffang-Methode untersucht, inwieweit Landschaftsstrukturen unüberwindbare Hindernisse für pollensammelnde Weibchen zweier oligolectischer Wildbienenarten darstellen. Zu diesem Zweck wurden besetzte Nester, die ein Jahr vor den Experimenten gesammelt wurden, so in der Landschaft platziert, dass zwischen ihnen und geeigneten Wirtspflanzenbeständen Landschaftsstrukturen wie Wälder, Hügel, Flüsse und Autobahnen lagen. Die Untersuchungen mit der auf Hahnenfuß (*Ranunculus*) spezialisierten Scherenbiene *Chelostoma florissomme* wurden in einem hügeligen und stark bewaldeten Gebiet in der Nordostschweiz durchgeführt (Abb. 1), diejenigen mit der auf Natternkopf (*Echium*) spezialisierten

Mauerbiene *Hoplitis adunca* in einem Gebiet in der Nordwestschweiz, welches von einem breiten Fluss sowie einer stark befahrenen Autobahn durchschnitten wird (Abb. 2).

Pollensammelnde Weibchen von *C. florissomme* querten zwischen Nest und Wirtspflanzen bis zu 480 m breite Waldbestände und überwandten Höhendifferenzen von über 130 m (Tab. I). Weibchen von *H. adunca* flogen über einen 100 m breiten Flussabschnitt und über eine 12 m breite Autobahn, um zu ihren Wirtspflanzen zu gelangen. Mehrere Weibchen von *C. florissomme* sammelten Pollen in einer Distanz von 500–650 m von ihrem Nest (Tab. I). Diese Beobachtung deutet darauf hin, dass die maximale Flugdistanz dieser Art, die in der Literatur auf 200–400 m geschätzt wurde, bisher unterschätzt worden ist. Trotz dieser unerwartet langen Flugdistanzen wurden die Weibchen von *C. florissomme* vorwiegend in Wirtspflanzenbeständen wiedergefunden, die in minimaler Entfernung zum Nest lagen (Abb. 3B).

Die vorliegende Untersuchung zeigt, dass Landschaftsstrukturen wie dichte Wälder, Hügel, breite Flüsse und stark befahrene Autobahnen keine unüberwindbaren Hindernisse für pollensammelnde Weibchen der beiden in Mitteleuropa häufigen und weit verbreiteten Wildbienenarten darstellen. Inwieweit sich dieselben Landschaftsstrukturen negativ auf pollensammelnde Weibchen von seltenen und gefährdeten Wildbienenarten auswirken, müssen zukünftige Untersuchungen zeigen.

Landschaftsbarriere / Fragmentierung / Sammeldistanz / *Chelostoma florissomme* / *Hoplitis adunca*

REFERENCES

- Beil M., Horn H., Schwabe A. (2008) Analysis of pollen loads in a wild bee community (Hymenoptera: Apidae) – a method for elucidating habitat use and foraging distances. *Apidologie* 39, 456–467.
- Bhattacharya M., Primack R.B., Gerwein J. (2003) Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? *Biol. Conserv.* 109, 37–45.
- Biesmeijer J.C., Roberts S.P.M., Reemer M., Ohlemüller R., Edwards M., Peeters T., Schaffers A.P., Potts S.G., Kleukers R., Thomas C.D., Settele J., Kunin W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354.
- Bischoff I. (2003) Population dynamics of the solitary digger bee *Andrena vaga* Panzer (Hymenoptera, Andrenidae) studied using mark-recapture and nest counts. *Popul. Ecol.* 45, 197–204.

- Brown M.J.F., Paxton R.J. (2009) The conservation of bees: a global perspective, *Apidologie* 40, 410–416.
- Chapman R.E., Wang J., Bourke A.F.G. (2003) Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators, *Mol. Ecol.* 12, 2801–2808.
- Chmurzynski J.A., Kieruzel M., Krzysztofiak A., Krzysztofiak L. (1998) Long-distance homing ability in *Dasypoda altercator* (Hymenoptera, Melittidae), *Ethology* 104, 421–429.
- Cozzi G., Müller C.B., Krauss J. (2008) How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands? *Landscape Ecol.* 23, 269–283.
- Dorn S., Schumacher P., Abivardi C., Meyhofer R. (1999) Global and regional pest insects and their antagonists in orchards: spatial dynamics, *Agr. Ecosyst. Environ.* 73, 111–118.
- Dover J.W., Fry G.L.A. (2001) Experimental simulation of some visual and physical components of a hedge and the effects on butterfly behaviour in an agricultural landscape, *Entomol. Exp. Appl.* 100, 221–233.
- Driscoll D.A., Weir T. (2005) Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size, *Conserv. Biol.* 19, 182–194.
- Feuerbacher E., Fewell J.H., Roberts S.P., Smith E.F., Harrison J.F. (2003) Effects of load type (pollen or nectar) and load mass on hovering metabolic rate and mechanical power output in the honey bee *Apis mellifera*, *J. Exp. Biol.* 206, 1855–1865.
- Franzen M., Larsson M., Nilsson S. (2009) Small local population sizes and high habitat patch fidelity in a specialised solitary bee, *J. Insect. Conserv.* 13, 89–95.
- Gathmann A., Tschardt T. (2002) Foraging ranges of solitary bees, *J. Anim. Ecol.* 1, 757–764.
- Greenleaf S.S., Williams N.M., Winfree R., Kremen C. (2007) Bee foraging ranges and their relationship to body size, *Oecologia* 153, 589–596.
- Gu H.N., Hughes J., Dorn S. (2006) Trade-off between mobility and fitness in *Cydia pomonella* L. (Lepidoptera: Tortricidae), *Ecol. Entomol.* 31, 68–74.
- Haddad N.M. (1999) Corridor and distance effects on interpatch movements: a landscape experiment with butterflies, *Ecol. Appl.* 9, 612–622.
- Haddad N.M., Hudgens B., Damiani C., Gross K., Kuefler D., Pollock K. (2008) Determining optimal population monitoring for rare butterflies, *Conserv. Biol.* 22, 929–940.
- Hein S., Gombert J., Hovestadt T., Poethke H.J. (2003) Movement patterns of the bush cricket *Platycleis albopunctata* in different types of habitat: matrix is not always matrix, *Ecol. Entomol.* 28, 432–438.
- Kearns C.A., Inouye D.W., Waser N.M. (1998) Endangered mutualisms: the conservation of plant-pollinator interactions, *Annu. Rev. Ecol. Syst.* 29, 83–112.
- Keil S., Gu H.N., Dorn S. (2001) Response of *Cydia pomonella* to selection on mobility: laboratory evaluation and field verification, *Ecol. Entomol.* 26, 495–501.
- Keller I., Lurgiader C.R. (2003) Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles, *Proc. R. Soc. London B-Biol. Sci.* 270, 417–423.
- Koivula M.J., Kotze D.J., Salokannel J. (2005) Beetles (Coleoptera) in central reservations of three highway roads around the city of Helsinki, Finland, *Ann. Zool. Fenn.* 42, 615–626.
- Koivula M.J., Vermeulen H.J.W. (2005) Highways and forest fragmentation – effects on carabid beetles (Coleoptera, Carabidae), *Landscape Ecol.* 20, 911–926.
- Kreyer D., Oed A., Walther-Hellwig K., Frankl R. (2004) Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae), *Biol. Conserv.* 116, 111–118.
- Kumar A., O'Donnell S. (2009) Elevation and forest clearing effects on foraging differ between surface – and subterranean – foraging army ants (Formicidae: Ecitoninae), *J. Anim. Ecol.* 78, 91–97.
- Mader H.J., Schell C., Kornacker P. (1990) Linear barriers to arthropod movements in the landscape, *Biol. Conserv.* 54, 209–222.
- Moilanen A., Hanski I. (1998) Metapopulation dynamics: effects of habitat quality and landscape structure, *Ecology* 79, 2503–2515.
- Müller A., Diener S., Schnyder S., Stutz K., Sedivy C., Dorn S. (2006) Quantitative pollen requirements of solitary bees: implications for bee conservation and the evolution of bee-flower relationships, *Biol. Conserv.* 130, 604–615.
- Murray T.E., Kuhlmann M., Potts S.G. (2009) Conservation ecology of bees: populations, species and communities, *Apidologie* 40, 211–236.
- Niemela J. (2001) Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: a review, *Eur. J. Entomol.* 98, 127–132.
- Pasquet R.S., Peltier A., Hufford M.B., Oudin E., Saulnier J., Paul L., Knudsen J.T., Herren H.R., Gepts P. (2008) Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances, *Proc. Natl Acad. Sci. (USA)* 105, 13456–13461.

- Peterson J.H., Roitberg B.D. (2006) Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, *Megachile rotundata*, Behav. Ecol. Sociobiol. 59, 589–596.
- Sarvary M.A., Bloem K.A., Bloem S., Carpenter J.E., Hight S.D., Dorn S. (2008) Diel flight pattern and flight performance of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) measured on a flight mill: Influence of age, gender, mating status, and body size, J. Econ. Entomol. 101, 314–324.
- Sciarretta A., Trematerra P. (2006) Geostatistical characterization of the spatial distribution of *Grapholita molesta* and *Anarsia lineatella* males in an agricultural landscape, J. Appl. Entomol. 130, 73–83.
- Sedivy C., Praz C.J., Müller A., Widmer A., Dorn S. (2008) Patterns of host-plant choice in bees of the genus *Chelostoma*: the constraint hypothesis of host-range evolution in bees, Evolution 62, 2487–2507.
- Steffan-Dewenter I., Munzenberg U., Burger C., Thies C., Tschardt T. (2002) Scale-dependent effects of landscape context on three pollinator guilds, Ecology 83, 1421–1432.
- Sutcliffe O.L., Thomas C.D. (1996) Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings, Conserv. Biol. 10, 1359–1365.
- Tautz J., Zhang S.W., Spaethe J., Brockmann A., Si A., Srinivasan M. (2004) Honeybee odometry: performance in varying natural terrain, Plos. Biol. 2, 915–923.
- Toepfer S., Gu H., Dorn S. (1999) Spring colonisation of orchards by *Anthonomus pomorum* from adjacent forest borders, Entomol. Exp. Appl. 93, 131–139.
- Toepfer S., Gu H., Dorn S. (2000) Selection of hibernation sites by *Anthonomus pomorum*: preferences and ecological consequences, Entomol. Exp. Appl. 95, 241–249.
- Townsend P.A., Levey D.J. (2005) An experimental test of whether habitat corridors affect pollen transfer, Ecology 86, 466–475.
- Walther-Hellwig K., Frankl R. (2000) Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape, J. Appl. Entomol. 124, 299–306.
- Westrich P. (1990) Die Wildbienen Baden-Württembergs, Ulmer, Stuttgart.
- Williams N.M., Kremen C. (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape, Ecol. Appl. 17, 910–921.
- Williams N.M., Tepedino V.J. (2003) Consistent mixing of near and distant resources in foraging bouts by the solitary mason bee *Osmia lignaria*, Behav. Ecol. 14, 141–149.
- Wolf S., Moritz R.F.A. (2008) Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae), Apidologie 39, 419–427.
- Wratten S.D., Bowie M.H., Hickman J.M., Evans A.M., Sedcole J.R., Tylianakis J.M. (2003) Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land, Oecologia 134, 605–611.
- Wray M.K., Klein B.A., Mattila H.R., Seeley T.D. (2008) Honeybees do not reject dances for 'implausible' locations: reconsidering the evidence for cognitive maps in insects, Anim. Behav. 76, 261–269.