CHAPTER

1

Habitat requirements of central European bees and the problems of partial habitats

PAUL WESTRICH

CONTENTS

Abstract

The various types of habitat colonized by bees can differ greatly in their microclimate, their physical structure and their vegetation and thus in their suitability for particular species. A nest-building bee can only reproduce if its habitat fulfils the following conditions: the habitat must contain (a) a specific nest site, (b) in the case of certain species, specific nest-building materials and (c) a sufficient amount of food plants as a source for nectar and pollen. Nest sites, building materials and food plants are not only essential needs in the environment of every nest-building bee; these resources must also be available in combination within the home range of a female. Most bees are highly specialized in their resource selection. Some types of habitat, such as moors, heaths, inland dunes or unimproved meadows, actually contain all the resources a female needs for reproduction and her home range does not exceed the habitat boundaries. Therefore conservation and

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management of these habitat types are effective means of species protection. But the entire habitat complex of a bee species very often consists of several partial habitats, especially when each partial habitat contains only one of the required resources. The nest site can lie several hundred metres away from the foraging site and a completely different type of habitat not used by the bee can divide them. Typical partial habitats are vertical faces, sparsely vegetated slopes or rocks (nesting sites) and meadows, ruderal places or fens (pollen collecting sites). An intensive use of land very often leads to the destruction of one of the two needed partial habitats and thus to the loss of either the nesting or the foraging site. Consequently the bee population depending on this partial habitat, or rather on the resource in this habitat, becomes extinct. Therefore the protection of bees must always give special attention to the entire home range and all the resources a given species needs.

> The major threat to biological diversity is loss of habitat, and the most important means of protecting biological diversity is habitat preservation.
>
> (Primack, 1993, p. 115)

INTRODUCTION

In central Europe bees can be encountered from early spring to late autumn in nearly any type of terrestrial habitat, from the coast up to the alpine regions: in cool moors as well as on warm inland dunes, in woodlands as well as in meadows, even in gardens. But the fauna that can be observed change from habitat to habitat and from season to season. This is due to the fact that the habitats of bees differ greatly in respect to their size, their microclimate, their physical structure and their vegetation. Furthermore, many bees are highly seasonal, having only one generation a year, and time their emergence to coincide with the peak of flowering of their particular food plants in their specific habitats.

Regarding their reproduction strategy, bees can be divided into two major groups: (a) bees that build nests as a protected environment for their young and (b) parasitic bees that use the nests and provisions of other bees. Whereas nest-building bees gather pollen as food for the young and therefore have evolved different body structures for transporting the pollen, parasitic bees (cuckoo bees) depend completely on the brood care of their hosts for their own offspring. They lay their eggs in the nests of other bees and therefore never collect pollen themselves. Nevertheless, conserving parasitic bees requires the protection of their hosts.

HABITAT REQUIREMENTS OF NEST-BUILDING BEES

A nest-building bee can only produce offspring if its habitat fulfils the following basic conditions:

1. It must contain a specific nest site.
2. In the case of certain species, the habitat must also contain specific materials to construct the nest.
3. The habitat must contain a sufficient amount of food plants that serve as a nectar source to fuel all the activities of the bees and as a source for gathering pollen as the essential component of the larval food.

Bees are remarkably specialized in their requirements for nesting and foraging, and they are able to locate potential sites and to discriminate among them. A general view is given in Westrich (1990). Nevertheless, a few examples might aid understanding of the particular habitats and the conservational needs of bees.

Nesting sites

Most bees are miners and burrow in the ground. Roughly 75% of the approx. 560 central European nest-building species are ground-nesting, often favouring south-facing banks and cliffs, unstable slopes and field-paths, particularly when bare or sparsely vegetated. Some prefer sand, others clay soil. Suitable nest sites are often likely to be scattered and transient in places. Typical ground-nesting bees are species of *Andrena*, *Panurgus*, *Panurginus*, *Melitturga*, *Halictus*, *Lasioglossum*, *Rophites*, *Rhophitoides*, *Dufourea*, *Halictus*, *Lasioglossum*, *Melitta*, *Macropis* and *Dasypoda*. Other bees nest in regular or irregular cavities such as insect borings in dead wood or small holes and fissures in rocks. Usually they are opportunists and nest in a wide variety of places like a number of mason bees, such as *Osmia rufa*, *O. cornuta* and *O. caerulescens*, and leaf-cutter bees like *Megachile willughbiella*, *M. centuncularis* and *M. versicolor*. Several of these opportunists can easily be attracted and promoted by artificial nesting aids in gardens.

Others use only empty snail shells for nesting, such as *Osmia aurulenta*, *Osmia bicolor*, *Osmia rufohirta*, *Osmia spinulosa* and *Osmia versicolor*. Vacated galls of the chloropid fly, *Lipara lucens*, induced in the flower heads of the reed *Phragmites australis* are the exclusive nesting site chosen by the masked bee *Hylaeus pectoralis*. A number of bees dig their burrows in the soft pith of stems of bramble (*Rubus*) or mullein (*Verbascum*) such as *Osmia leucomelana*, *O. claviventris* and *O. tridentata* and all species of *Ceratina*. Exposed stem nest sites are highly ephemeral and can therefore only be used once. Carpenter bees like *Xylocopa violacea* and *Xylocopa valga* excavate their tunnels in dead wood.

Building materials

There is also a great variety in the specific materials used by bees for constructing the nest or lining the brood cells. The majority of mining bees line their cells with a secretion of an abdominal gland, the so-called Dufour's gland. Species of the genus *Colletes*, such as *C. cunicularius* and *C. succinctus*, form a transparent, cellophane-like membrane which is waterproof and resistant to fungal attack (Albans *et al.*, 1980; O'Toole & Raw, 1991). Many bees only use materials found in the vicinity of their nest and are highly specialized in what they select. Some mason bees, such as *Osmia ravouxi* and the alpine *Osmia loti*, embed pebbles in a mortar of calcareous clay mixed with saliva and build the nest on the surface of stones or rocks. Leaf-cutters, such as *Megachile willughbiella*, *M. nigriventris* or *M. lapponica*, use pieces of leaf to line their cells. *Osmia inermis* constructs the cells of masticated leaf pulp in small rock cavities or on the underside of flat stones. Carder bees, such as *Anthidium manicatum* and *A. oblongatum*, line and partition their cells with cottony down gathered from the leaves of lamb's ear (*Stachys byzantina*), mullein (*Verbascum* spp.) and other hairy plants. The closely related *Anthidium strigatum* uses only resin and constructs strangely formed brood cells on the surface of stones, on stems or on the bark of trees. Some bees line their burrows and cells exclusively with petals. *Osmia papaveris* favours the flowers of *Papaver* (poppy), *O. tergestensis* and *O. villosa* prefer *Geranium* (cranesbill), *Campanula* (bellflower) or *Helianthemum* (rockrose). Having detached a piece of petal and compressed it to a little parcel, the female flies off to her nest, carrying the parcel in her jaws (Westrich, 1991).

Food plants

Nectar
Bees are generally not confined to specific nectar sources. Even oligolectic bees (see 'Pollen' below) often feed on flowers from which they never gather pollen. However, sufficient sources of nectar as an energy-rich food are necessary to fuel all the activities of bees, to gather a specific component of the larval food and in the case of bumble bees to fill the 'honey pots' in the comb.

Floral oil
The flowers of some plants provide oils rather than nectar as a reward. *Macropis labiata* and *M. fulvipes* collect floral oil from species of *Lysimachia* (loosestrife), with which they presumably line their cells to make them waterproof (Vogel, 1986).

Pollen
The females of a great number of so-called polylectic bee species forage from a very wide spectrum of unrelated plants for pollen. The mason bee *Osmia rufa*, for instance, collects pollen from flowers belonging to 19 plant families. The best known polylectic bee is the honey bee (*Apis mellifera*). Eusocial bees like most bumble bees (*Bombus*) and several species of *Lasioglossum* as well as many solitary bees also show this type of pollen-collecting behaviour. In Central Europe polylectic bees are known in the genera *Hylaeus*, *Andrena*, *Halictus*, *Lasioglossum*, *Anthidium*, *Osmia*, *Megachile*, *Anthophora* and *Bombus*. The less specialized a bee is, the better it can survive in today's landscapes.

The so-called oligolectic bees are highly specialized, visiting only a single species or a group of closely related plant species for pollen throughout their whole range of distribution. This behaviour presumably has a genetic basis. Oligolectic bees therefore can only provision brood cells if they find sufficient sources of pollen in the vicinity of the nest. A major shift in the flora can be fatal. Because of this dependence it is not surprising that the percentage of oligolectic bee species is relatively high in Red Data Lists owing to the still-continuing decline of their particular food plants. There are more oligolectic species in central Europe than polylectic ones. In Germany about 30% of the nest-building species have been proved to be oligolectic.

In central Europe the pollen sources of oligolectic bees are to be found in 24 plant families. Table 1 gives examples for each plant family or genus and its oligolectic bees.

HOME RANGE AND SIZE OF HABITAT

Nesting sites, building materials and food plants are resources (in the sense of Begon *et al.*, 1990, p. 79) that are not only essential needs in the environment of every nest-building bee species, but must also be available in combination within the home range of a nesting female. The total size of a bee habitat therefore depends on the distance of the required resources from each other. The distance a female is able to cover during a foraging trip is

Table 1 Examples for oligolectic bees and their pollen sources (data from Westrich & Schmidt, 1987; Westrich, 1990; Schmidt & Westrich, 1993)

Plant family or genus	Species of bee
Apiaceae	*Andrena proxima*
Asteraceae	*Andrena denticulata*
Boraginaceae	
Anchusa	*Colletes nasutus*
Cerinthe	*Osmia cerinthidis*
Echium	*Osmia adunca*
Symphytum	*Andrena symphyti*
Brassicaceae	*Andrena agilissima*
	Osmia brevicornis
Campanulaceae	
Campanula	*Andrena curvungula*
	Melitta haemorrhoidalis
Jasione	*Dufourea halictula*
Cistaceae	*Andrena granulosa*
Convolvulaceae	
Convolvulus	*Systropha planidens*
Cucurbitaceae	
Bryonia	*Andrena florea*
Dipsaceae	*Andrena hattorfiana*
	Dasypoda argentata
Ericaceae	*Andrena lapponica*
Fabaceae	*Trachusa byssina*
Vicia, Lathyrus	*Andrena lathyri*
Chamaecytisus	*Andrena ratisbonensis*
Hederaceae	
Hedera	*Colletes hederae*
Lamiaceae	*Osmia andrenoides*
Liliaceae	
Allium	*Hylaeus punctulatissimus*
Linaceae	*Osmia mocsaryi*
Lythraceae	*Melitta nigricans*
Malvaceae	*Tetralonia macroglossa*
Onagraceae	
Epilobium	*Megachile lapponica*
Primulaceae	
Lysimachia	*Macropis fulvipes*
Ranunculaceae	
Ranunculus	*Chelostoma florisomne*
Resedaceae	*Hylaeus signatus*
Rosaceae	
Potentilla	*Andrena potentillae*
Salicaceae	
Salix	*Andrena vaga*
	Colletes cunicularius
Scrophulariaceae	
Veronica	*Andrena viridescens*
Odontites	*Melitta tricincta*

not known yet in many species. It is probably strongly influenced by the species' size, its specialization and the conditions of the respective habitats. A longer distance is presumably accepted, especially for pollen collecting, provided that nectar sources fuel the flight on the way.

A few examples: females of *Macropis fulvipes* have been found nesting in a meadow only 70 cm away from a stand of *Lysimachia punctata*, their specific pollen source (Vogel, 1986). In a sand pit the distance between flowering *Centaurea stoebe* (knapweed), the pollen source of the oligolectic long-horned bee *Tetralonia dentata*, and several hundred nests was between 1 and 50 m (unpublished). Once I found *Systropha planidens* gathering pollen of *Convolvulus arvensis* in a vineyard 20–50 m away from the nests in a field path (unpublished). Münster-Swendsen (1968) found *Panurgus banksianus* collecting pollen 250 m away from the nests. In *Osmia spinulosa* the distance between the nest in a snail shell and the plant for obtaining masticated leaf pulp as building material was only 0.5–4 m (Müller, 1994). *Anthidium manicatum* gathered down more than 50 m away from its nest (unpublished).

NATURAL HABITATS

Man has destroyed most of the natural habitats in central Europe by his intervention in the landscape for the sake of agriculture, forestry, industry, recreation and urban development. But some are still left, especially in the higher regions of the Alps. Such a natural habitat is, for instance, the alpine rock-steppe of the Rhone basin in southern Switzerland and in other parts of the south-western European Alps, a habitat type I have been studying over the last ten years (Fig. 1). Until now it has been useless to man in terms of agricultural or forest cultivation. This situation is mainly due to the rocky surface which keeps this habitat always open. It is only partly covered with shrubs of *Juniperus sabina*.

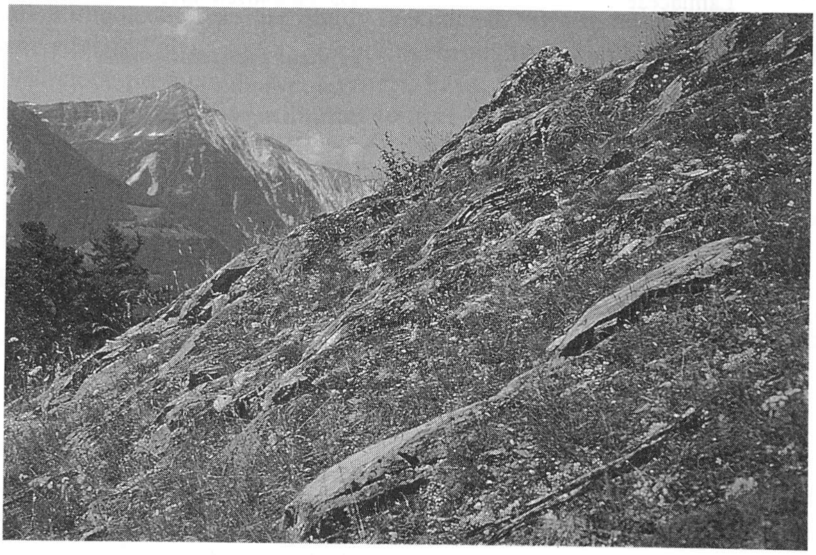

Figure 1 A rock-steppe in southern Switzerland (canton Valais) at a height of 1400 m above sea level in July. This natural habitat is colonized by several highly adapted bee species like the mason bee *Osmia dalmatica*.

Here, from the middle of June until the end of July, we find very small populations of the solitary bee *Osmia dalmatica* which is highly adapted to this type of habitat and has only been recorded from three sites in the Swiss cantons of Valais and Tessin (Figs 1 and 2). No more than 6–10 females per year and site could be observed. *Osmia dalmatica* nests exclusively in crevices of lime rocks, constructs the walls of the brood cells exclusively of leaf bits of *Helianthemum nummularium* (rockrose), lines and seals the cells exclusively with petals of *Linum tenuifolium* (a species of flax) or *Geranium sanguineum* (red cranesbill) and collects pollen only from species of *Knautia* and *Scabiosa* (scabious) (Westrich, 1994). All the required resources, the nesting site as well as the forage plants used for nest building and pollen gathering, are typical elements of the rock-steppe. Usually they are to be found very close to each other. The female's radius of activity with the nest in the centre mostly does not exceed 50 m.

Protecting this highly adapted, very rare and doubtless threatened bee species makes it imperative to conserve the habitat as a whole. Only then will the protection be effective and there will be no need of managing this very stable habitat. But until now not a single rock-steppe in the Swiss Rhone basin is protected as a nature reserve despite both its national and international importance and despite the fact that primary habitats like rock-steppes are by no means replaceable by man-made ones. The question might arise as to why it is necessary to protect such a habitat at all, if it is useless to man. Unfortunately on some swiss rock-steppes wooden holiday houses are being built, leading not only to a destruction of the natural vegetation but also to a severe threat to bees that are confined to this habitat.

Another type of natural habitat is the limestone scree slopes in various parts of southern Germany (Swabian and Franconian Alb, Tauber valley, Wutach gorge). This type of habitat is also naturally unwooded, very stony, south-facing and therefore very dry and warm especially during the summer: in July I measured a ground temperature of 62°C during midday hours. A typical bee occurring here is *Osmia andrenoides*. It nests exclusively in empty shells of small snails such as *Helicella itala* and presumably *Zebrina detrita*. The shells have most likely to be situated underneath flat stones (Ferton, 1894). Masticated leaf pulp of *Helianthemum* (rockrose) is used to seal the cells. The species is confined to certain Labiatae as pollen sources, especially *Teucrium montanum*, *Teucrium*

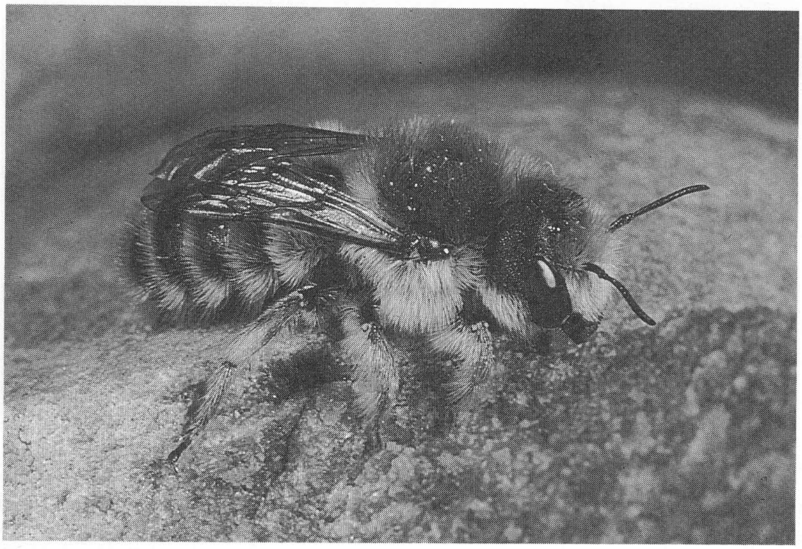

Figure 2 A freshly emerged female of the mason bee *Osmia dalmatica*.

chamaedrys, *Ajuga genevensis*, *Acinos arvensis* and *Stachys recta* (Westrich, 1990). As in the case of *O. dalmatica* the necessary resources of the highly adapted *O. andrenoides* are to be found within the boundaries of the stony habitat. Furthermore, the species has obviously no tendency to disperse. Its populations are very small, like those of *O. dalmatica*, and can only be protected by a strict preservation of their habitat, which at several locations has already been destroyed by quarrying. In the German state of Baden-Württemberg six of eight populations known at present are already being protected in nature reserves.

MAN-MADE HABITATS

Since the New Stone Age (Neolithic) man has changed most of the landscapes in Europe by cultivation. Though primary habitats have been irretrievably destroyed to a great extent, use of land was not always disadvantageous to bees. An extensive use has led to various types of semi-natural habitats, often very attractive to bees.

In central Europe unimproved meadows over calcareous soils, formerly cut only once a year to make hay, belong to the most important bee habitats and are colonized by a great number of bees especially those favouring warm and dry areas. In the German state of Baden-Württemberg many of these areas are now nature reserves and protected by law. Two of the most famous ones are the 'Badberg' and the adjacent 'Haselschacher Buck' in the Kaiserstuhl near Freiburg im Breisgau, a group of hills of volcanic origin mainly covered with a deep layer of loess and characterized by an exceptionally warm climate (Fig. 3). These reserves are of national importance representing a type of habitat now rarely to be found in Germany and central Europe. They cover an area of 136 hectares of

Figure 3 The semi-natural nature reserves 'Haselschacher Buck' and 'Badberg' in the Kaiserstuhl in Southern Germany. They mainly consist of large unimproved meadows, steep rocky slopes with a steppe-like vegetation and bushy areas and are surrounded by vineyards. They serve both as an entire as well as a partial habitat and offer many threatened bee species suitable nesting sites and/or foraging sites.

mainly unimproved meadows, steep rocky slopes with a steppe-like vegetation and bushy patches. Both reserves contain numerous bare spots (caused by frost erosion), several vertical faces and rocky sites offering many bee species appropriate opportunities for nesting. Moreover, the very diverse flora provides specific pollen sources for many oligolectic bees. In a recent (unpublished) survey 132 species of bee have been recorded, 59 of which are included in the Red Data List of Baden-Württemberg (Westrich, 1990).

The following species find all the necessary resources within the boundaries of the two nature reserves and thus might be maintained with success, provided the areas are managed properly (future monitoring will have to show if this assumption is correct): *Andrena curvungula*, *Andrena fulvago*, *Andrena gelriae*, *Andrena hattorfiana*, *Andrena pallitarsis*, *Andrena pandellei*, *Andrena potentillae*, *Andrena rosae*, *Andrena wilkella*, *Anthophora aestivalis* (cuckoo bee: *Melecta luctuosa*), *Dufourea dentiventris*, *Dufourea inermis*, *Eucera interrupta*, *Halictus smaragdulus*, *Hylaeus punctulatissimus*, *Lasioglossum albocinctum*, *Lasioglossum costulatum*, *Lasioglossum griseolum*, *Megachile pilidens* (cuckoo bee: *Coelioxys afra*), *Melitta haemorrhoidalis*, *Melitta leporina*, *Osmia andrenoides*, *Osmia anthocopoides* (cuckoo bee: *Dioxys tridentata*), *Osmia aurulenta*, *Osmia bicolor*, *Osmia gallarum*, *Osmia mitis*, *Osmia ravouxi*, *Osmia rufohirta*, *Osmia spinulosa*, *Rhophitoides canus*, *Rophites algirus* (cuckoo bee: *Biastes emarginatus*).

Several species use the nature reserves either for nesting or for foraging only. The mining bee *Halictus quadricipctus*, for instance, nests in an aggregation containing more than a hundred nests in a marginal vertical face, but forages in extensively used vineyards or on ruderal sites outside the nature reserves. The carpenter bee *Xylocopa violacea* regularly flies into the nature reserves for pollen collecting, but nests in the timber of old houses or senescent trees in surrounding areas.

Unimproved meadows have greatly decreased mainly owing to the cessation of traditional use. A 'leave-it-alone' policy with regard to these areas would not be the appropriate strategy of preserving the bee community because succession would lead to a change of flora and microstructures and also to a change of the bee fauna. Most of our grassland would revert to woodland if left unmanaged. To prevent this, the reserves are regularly managed more or less in imitation of the traditional use. To increase the diversity of structures and plants the sites are cut on a rotational mosaic basis, incorporating deliberate ground disturbance. A previous survey of the insect fauna and its requirements was to guarantee that the management plan not only covers the vegetation but also the needs of insects present. The current preference for late cuts (late summer or early autumn) as carried out in many other reserves is not universally appropriate. The rotational pattern should therefore include selected sites that are already cut during early summer.

PARTIAL HABITATS IN A FRAGMENTED LANDSCAPE

In a fragmented landscape, the entire home range of a species often covers a habitat complex consisting of several partial habitats. Each partial habitat contains just one of the needed resources and functions either as a nesting area or as a foraging area. Due to landscape fragmentation and to meliorations (re-allocation and consolidation of farm land) in the recent past, partial habitats are often divided by a habitat of a completely different kind not suitable to the bee (roads, railways, canals, sprayed arable fields etc.) and are much more widely scattered. In any case, the partial habitats have to be situated at a distance from each other the female can overcome. The loss of one of the partial habitats can lead to the extinction of local bee populations.

These facts can be well illustrated by the example of a levee in the Rhine valley. Several hundred kilometres of levees serve a purely technical purpose, namely to prevent settlements from flood damage. However, these man-made habitats are important secondary refugia for many bee species which primarily colonized flood plains in times before the river correction (Westrich, 1985).

There are three alternative functions a levee may have for a given bee species. They depend on its vegetation, on its physical structure (sand, clay soils), on its exposition and on its surrounding habitats.

1. The nesting site lies on (or in) the levee, whereas the particular food plants occur outside of it.
2. The required forage plants grow on the levee, whereas the nesting site lies outside of it.
3. The levee provides both nesting site and foraging site.

The following examples may explain the various possible combinations. The masked bee *Hylaeus pectoralis* nests in vacated reed galls in a relatively dry reed-bed close by the levee, but visits various flowers on the levee (Fig. 4A). The oligolectic mining bees *Andrena vaga* and *Colletes cunicularius* collect pollen from *Salix cinerea* and *Salix purpurea* (grey and purple willow) found in bushes, but nest in large aggregations in the levee (Fig. 4B). The polylectic mining bees *Halictus subauratus* and *Andrena flavipes* find suitable food plants as well as nesting sites on the levee (Fig. 4C). At some localities also the oligolectic *Andrena viridescens*, confined to *Veronica*, and *Dasypoda hirtipes*, confined to Asteraceae, forage on the levee and nest within it (Fig. 4C). The oligolectic mason bee *Chelostoma florisomne* collects pollen only from *Ranunculus* (buttercup), flowering in the meadow-like vegetation of the levee, but nests in insect borings in the dead wood of senescent trees (Fig. 4D). The oligolectic long-horned bee *Tetralonia salicariae* digs its nests on sparsely vegetated spots in the levee, but collects pollen exclusively from *Lythrum salicaria* (purple loosestrife) on river banks or damp ditch sides (Fig. 4E). There are quite a number

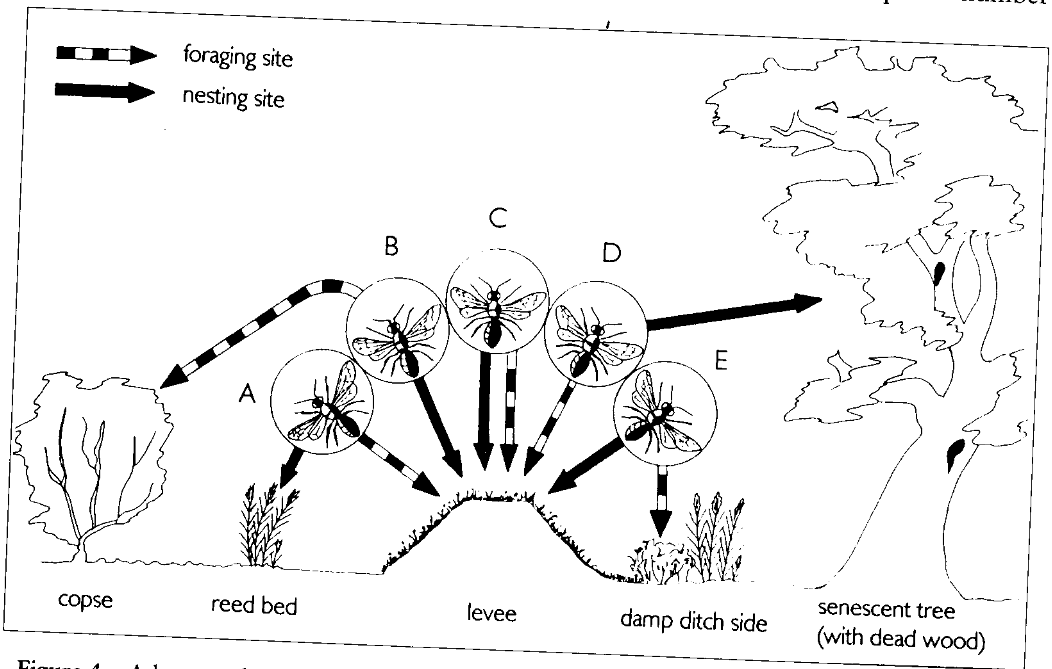

Figure 4 A levee and its function as an entire or partial habitat (adapted from Brechtel, 1987).

of other relationships between the levee as one of the partial habitats and specific resources found in other partial habitats in the vicinity. For example: the masked bees *Hylaeus annularis* and *H. communis* visit *Daucus carota* (wild carrot) and other flowers on the levee, but nest in dry stems of *Rubus* (bramble) close by. The oligolectic mason bee *Osmia anthocopoides* forages from *Echium vulgare* (blue viper's gloss) on the levee, but builds the nest on the surface of field-stones. The mason bees *Osmia aurulenta* and *O. bicolor* favour *Lotus corniculatus* (bird's foot trefoil) on the levee, but nest in empty snail shells, lying scattered around in a hedgerow.

By focusing on two more species, *Andrena agilissima* and *Colletes hederae*, both scarce and threatened, the problems of partial habitats will be illustrated in greater detail.

Andrena agilissima

In landscapes covered with loess like the Kraichgau region in southern Germany, hollow ways belong to the most typical habitats. Loess is a sediment very susceptible to water erosion. Man, cattle and the wheels of vehicles, passing along a field path, destroy the sediment structure on the surface. Then rain washes the loose soil particles away resulting in a deep hollow way in the course of time (Hassler & Hassler, 1993). Vertical faces characterize this habitat and serve as nesting sites for many bees favouring vertical structures, if fully exposed to the sun.

Several hollow ways in the region have been protected as nature reserves in order to conserve threatenend bees and wasps. But it must never be forgotten that a hollow way for many bees is only a partial habitat and mainly serves as a nest site. Without appropriate foraging sites in the vicinity the preservation of hollow ways is not wholly effective, at least if the protection of particular bee species is aimed at. This is especially problematical in cases where hollow ways are only surrounded by monotonous, intensively used arable fields.

The mining bee *Andrena agilissima* is a typical hollow way bee and easily recognized by its bluish colour. This species is specialized in two ways: it requires a vertical face for nesting and certain Cruciferes as food plants. In southern Germany it collects pollen mainly from *Sinapis arvensis* (wild mustard) (Westrich, 1990). But this annual does not occur in hollow ways or on vertical faces; rather it grows on unsprayed summer grain fields or on ruderal places in the earliest successional phase. Therefore, the bee can only survive and reproduce in areas where these transient forage sites lie close to a potential nesting site, a situation that has become very rare in the intensively used agricultural landscape. It is therefore not surprising that *A. agilissima* has greatly declined. Larger nest aggregations of this beautiful bee are hardly to be found anymore. Therefore, the typical cuckoo bee *Nomada melathoracica* has also become very scarce. So what has to be done to maintain the remnant populations?

A recent study has shown that *S. arvensis* is of great importance for many bees, not only for *A. agilissima* (Westrich, 1996). Therefore it is vital to promote this wild plant in our agricultural landscapes. First of all it is necessary to persuade farmers of the Kraichgau region to create unsprayed border strips, especially on summer grain fields, to provide for the specific germinating requirements of *S. arvensis* (field margin programme). This will also help a number of other bees nesting in vertical faces, like *Halictus quadricinctus* and *Lasioglossum limbellum*. Another way of promoting *S. arvensis* is to let fields lie fallow under the set-aside programme of the European Union to allow annuals to regenerate naturally. These fields should either be rotated or ploughed again after one or two years, preferably in early spring to promote wild mustard or in late autumn to allow overwintering annuals to germinate. On fields very intensively used in the recent past, *S. arvensis* might not grow anymore, even under the conditions described. In this case I recommend sowing wild mustard in early spring, adding other annuals (and biannuals) favoured by wild bees and changing the sites every one or two years. The Tübingen seed mix ('Tübinger Mischung') (Bauer & Engels, 1992) advocated for sowing in set-aside land in south-west Germany doubtless helps honeybees but does not reflect the needs of oligolectic or especially threatened bees, thus being of little benefit to species like *A. agilissima* (Paxton, 1993).

Most likely *A. agilissima* and *N. melathoracica* as well as many other bee species exist as metapopulations not only in the Kraichgau region. A metapopulation is a collection of local populations, connected by occasional dispersal, in which there are local extinctions and colonizations (Gilpin & Hanski, 1991). In a local population most invidivuals will remain within one habitat patch (complex) throughout their adult life, but some will disperse (cf. Thomas, 1995). A proportion of these will either reach other local populations or colonize fresh habitats. So far there have been no detailed empirical studies on bee metapopulations in central Europe. In 1994, for instance, I observed two females of *A. agilissima* colonizing a recently restored vertical face. A female of *N. melathoracica* has also been recorded. At another locality I observed a female of *N. melathoracica* searching for host nests in a vertical face where the host was not (yet?) nesting at all. They all might have dispersed from the largest population known in the region, consisting of over a hundred females of *A. agilissima* and at least 50 females of *N. melathoracica* and only 5 km away from the newly colonized localities. This central or core population, according to metapopulation models (Murphy *et al.*, 1990), has to be maintained by all means because the elimination of such a core population could lead to the regional extinction of a species over a much wider area.

Colletes hederae

In 1993 a new species of bee was described and named *Colletes hederae* after *Hedera helix* (ivy), the bee's specific pollen source (Schmidt & Westrich, 1993). Because of this peculiar

Figure 5 This vertical face in southern Germany serves as nesting site for a small population of the mining bee *Colletes hederae*.

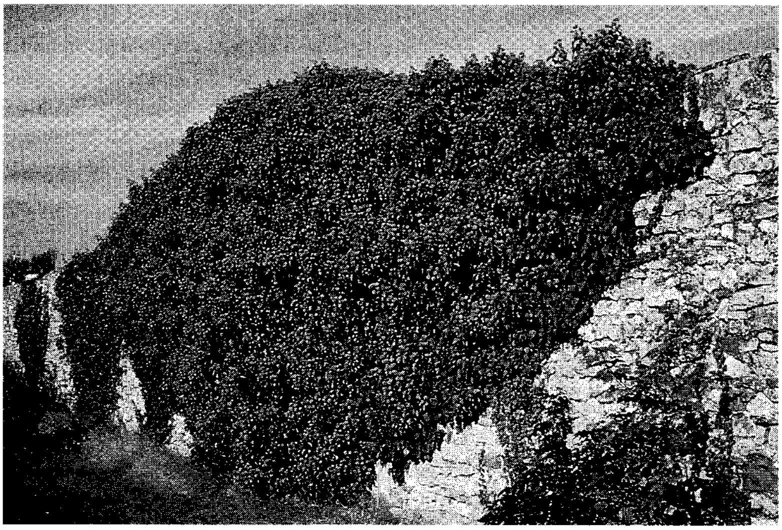

Figure 6 A village wall covered with flowering ivy (*Hedera helix*), the exclusive pollen source of *Colletes hederae*.

oligolectic behaviour the bee emerges very late in the season and its flight period in some years lasts until early November. In October 1994 I was able to study a population of this species near Grünstadt in southern Germany (Figs 5 and 6). The species nested in a south-facing sparsely vegetated loess slope surrounded by intensively used vineyards. Close by there was a large village. More than a hundred nests could be found, most of them in vertical parts of the slope. All the females alighting at their nest entrances were loaded with yellow pollen (Fig. 7). Pollen analyses showed that they had exclusively visited *Hedera*, as was the case at several other localities in Great Britain (Channel Islands), France, Italy, Croatia and Slovenia. In the direct vicinity of the slope I did not find a single ivy. So I had

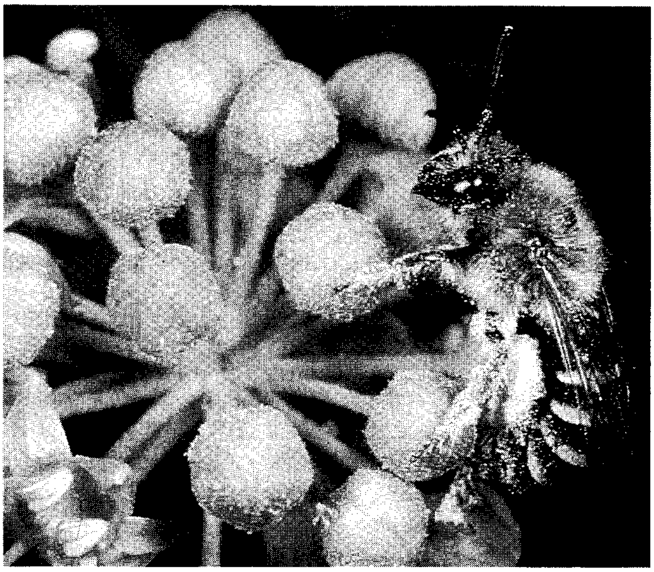

Figure 7 A pollen collecting female of *Colletes hederae*.

to concentrate my search on the village. And indeed, in the middle of the village, more than one kilometre away from the nesting site, a number of large walls were profusely covered with ivy fully in flower. Therefore the bees always had to fly from the slope into the village and back. Only when the sun was shining onto the ivy were the bees collecting. As soon as the ivy was thrown into shadow the bees stopped visiting. In order to protect this large population of *C. hederae* as a core population of a probable regional metapopulation both partial habitats, the slope and the walls covered with ivy, have to be maintained. Therefore, the local authorities and owners were asked to comply with our recommendation for long-term maintenance which they agreed to do.

CONCLUSIONS

There is a general consensus that the decline of bees in central Europe has been largely caused by the loss of areas with suitable resources or by changes in the character of such areas. Species have disappeared at localities where the opportunities for nesting are still good; a closer look showed that the appropriate food plants were lacking. Very often the case is the other way round. Thus, the reason for the decline of bees, both in quality and quantity, is the loss of one or of all of the needed resources, often distributed over several partial habitats.

Except for species inhabiting constant natural or semi-natural habitats, most bees in the agricultural landscape are, like many of their food plants, pioneers and adapted to the dynamics of their habitat, to the mosaic of habitat change in time and space and to periodically recurrent events. They most likely had their primary habitats in the vast flood plains of wild river systems with their great variety of dynamic habitats providing suitable nesting and foraging resources for very many species (Klemm, 1996). The continuing spread of agriculture since the Neolithic Age resulted in a large extension of newly created habitats gradually colonized by bees dispersing from the riverine habitats. It was the agricultural landscape of former centuries that probably had the greatest variety of structures, utilizations and bee species. River corrections carried out since the second half of the last century have stopped morpho-dynamic processes resulting in a great loss of primary habitats. The agricultural landscape, developed over centuries, has also lost its high dynamics taking place on a minimum of space and its structural richness, all owing to modern land use. Meliorations of farm land in the last few decades and the intensification of farming resulted in a cessation of traditional land use, a much greater monotony of agricultural landscapes and an increasing fragmentation. Since a restoration of the original flood plain dynamic is only possible, if at all, to a very small extent, man has a great responsibility to maintain the traditional diversity and connectivity of man-made habitats in landscapes where they still exist or to restore new habitat stepping stones by management in landscapes where they have already been destroyed.

An effective way of protecting habitats for bees is the establishment of nature reserves. In the German state of Baden-Württemberg, for instance, several hundred nature reserves are already established representing a great variety of habitats, such as bogs, wetlands, heaths, inland dunes, scree slopes, unimproved meadows, extensively grazed limestone pastures and old vineyards left fallow. The majority of these sites have been selected because they represent good examples of natural or semi-natural habitats, but a few have actually achieved nature reserve status, mainly due to the presence of significant populations of scarce and threatened bee species. Reserves first of all aim at the protection of local populations but they can also act 'as refugia from whence parts of the surrounding countryside may be recolonized, should more land be managed in ways compatible with sustaining wildlife in future' (McLean *et al.*, 1995). The role of nature reserves in conserving the bees of Baden-Württemberg and the representation of bees on nature reserves are at present being studied in a special programme ('Auswertung und Umsetzung des Grundlagenwerks Die Wildbienen Baden-Württembergs') of the Landesanstalt für Umweltschutz Karlsruhe in cooperation with the author. These studies not only give detailed information on the present status of bees in Baden-Württemberg but also help to develop measures for long-term conservation of local populations (and metapopulations if possible) within nature reserves and outside them (Westrich *et al.*, 1994).

But mere preservation of an area is not sufficient. The availability of the required resources, the size and the distance to equivalent habitats is vital for long-term conservation of bees in nature reserves. Moreover, semi-natural habitats have to be managed and management plans have to meet the ecology of the community to be protected. But not all threatened bees can be conserved within nature reserves and not all of a given countryside can be established as a reserve. Therefore we should implement programmes which encompass reserves as well as non-reserved habitats. Outside of reserves woodland clearings and edges, hedgerows, unimproved meadows, old orchards, levees, old sand and gravel pits, disused quarries, vertical faces, field margins, waysides, ruderal sites, damp ditch sides and wildlife gardens are important habitat patches.

Creation of new habitats is not a substitute for protecting the original habitat and should always be seen as lower priority than managing any valuable habitat that already exists. But especially in the case of monotonous agricultural landscapes we should not hesitate to create new nesting sites and foraging sites, serving as new stepping stones in the countryside and helping to reduce the chance of a regional extinction (Samways, 1994). This would, at least, help pioneer species being capable of colonizing fresh habitats.

Finally, the importance of bees as pollinators of crops and wild flowers makes it imperative that conservation measures are incorporated into land use as widely as possible (O'Toole, 1993).

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