

# Bees (Hymenoptera: Apoidea) as key-stone species: specifics of resource and requisite utilisation in different habitat types

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## Abstract

After a short characterisation of wild bees, their role as key-stone species in communities and a discussion of the ecological consequences of the “pollination crises” for natural and man-made habitats, the analysis is focused on the wild bees of Germany as a model for Central European wild bee communities. Three quarters of all German bee species are pollen collectors (N = 413) and the rest are so called “cuckoo-bees”. One third of the pollen collecting bees are oligolectic and two thirds are polylectic. World wide, oligolectic species dominate habitats with semiarid and mediterranean-like climates whereas polylectic bees are characteristic for temperate (boreal) regions. With 140 oligolectic species (35 %) the German bee fauna occupies an intermediate position along this climatic gradient. An analysis of the  $\alpha$ -oligolectic bee species of Germany shows that their host plants belong to 23 plant families. 43 % of all oligolectic bee species are specialised on pollen from the Asteraceae and the Fabaceae. The Asteraceae are mostly visited by species of the genera *Osmia*, *Andrena* and *Colletes* and the Fabaceae by species of the genera *Andrena*, *Osmia* and *Eucera*. *Andrena*, the genus with most oligolectic species of all genera, also prefers Salicaceae and Brassicaceae. Species of the genus *Osmia* are the second largest group of oligolectic species.

Habitat-specific bees are typically associated with plant communities of Festuco-Brometea, Artemisietea, extensively managed Molinio-Arrhenatheretea and Koelerio-Corynephoretea.

The median body size of German wild bees is 10 mm (N = 547). On average oligolectic species are significantly smaller than the polylectic bees. Body size was found to be a good determinant for host plant specialisation. Lamiaceae, Campanulaceae and Brassicaceae are visited by the smallest bees in contrast to Fabaceae, Salicaceae and Boraginaceae which are only visited by large individuals. The relation between body size and the flight radius around nesting sites may explain why small bees are habitat-specific for Koelerio-Corynephoretea, while larger bees are able to forage in *Salix*-dominated habitats where larger flight distances between nesting sites and host plant are required.

The highest percentage of habitat specific bee species in Germany might occur in habitats which correspond the most with the conditions prevailing in those assumed to be the centres of bee radiation: the semiarid regions and the mediterranean-like regions of the world. The knowledge of oligolecty, habitat and space requirements in correlation with body size are required for understanding the behaviour of wild bees and for taking the necessary conservation measures.

## 1. Introduction

Wild bees, wasps and ants (Hymenoptera) are the second largest order of insects worldwide. With almost 250,000 species (MALYSHEV 1968) they are only exceeded by the beetles

(Coleoptera). Many Hymenoptera are wild bees (Apoidea). Until today 16,000 species have been described worldwide (MALYSHEV 1968, MICHENER 2000), 700 of them in Central Europe and 547 in Germany alone.

In the first part of this publication a short biological, ecological and biogeographical characterisation of wild bees will be followed by a discussion about their role as key-stone species in communities and about the consequences of the immanent loss of bee diversity for natural and man-made ecosystems. The main part of this study is a detailed analysis of German wild bees and their resources and requisites. With its subatlantic, subcontinental, submediterranean and alpine faunal-geographic-elements and a wide spectrum of corresponding habitat diversity Germany serves as a suitable model area to analyse the principal ecological requirements of Central European bees. The analysis of bee genera occurring in Germany will focus on aspects of resource specialisation (oligolecty/polylecty) and more specifically I will ask:

- How oligolectic and polylectic species are distributed biogeographically and in what ratio they occur in Germany?
- Which bee genera are characterised by a high percentage of oligolecty?
- Are some plant families preferred over others by oligolectic bee species and genera?
- Which are the preferred habitats of German bee species and can they be characterised under phytosociological aspects?

Finally, the following hypotheses will be discussed:

- The proportion of oligolecty and polylecty occurring in one region can be predicted. In mediterranean and semiarid regions the percentage of oligolectic species is expected to be higher than in temperate regions with cooler, more oceanic climates (WASER et al. 1969, PEKKARINEN 1998). The ratio of oligolectic to polylectic bees in Germany, characterised by a temperate climate, might occupy an intermediate position along this gradient.
- The highest percentage of habitat specific bee species in Germany might occur in those habitat types which correspond most with conditions prevailing in habitats assumed to be the centres of bee radiation and diversity in the semiarid and mediterranean-like regions of the world. Consequently, most of the habitat-specific wild bees in Germany might occur in vegetation units of extremely dry and open habitats.
- The body size of bee species is an important determinant for their home range (WESSERLING 1996, GATHMANN & TSCHARNTKE 2002). Therefore, it should also be a key for the interpretation of the resource and habitat specialisation of bees. The following hypotheses will be discussed: a) Within the oligolectic bees body size determines the host plant families preferred. b) Habitats with nesting and foraging sites in close proximity might be characterised by bee communities consisting of species with low body size.

## 2. Biological and ecological characteristics of Hymenoptera Apoidea

### 2.1 Environmental conditions

Most of the wild bees are heliophilous and thermobiont, they only fly when the weather is warm and dry and the wind is not too strong. From an autecological point of view there are four factors which are responsible for the occurrence and distribution of wild bees:

**a) Temperature:** Air temperatures of below 13-16 °C reduce the flight activity of most bee species considerably (LINSLEY 1958); the lowest temperatures allowing flight activities lie between 11-13 °C (HAESLER 1972). Only very hairy wild bees (e. g. *Bombus*) fly at those low

temperatures. Optimum temperature ranges vary and appear to be species specific. It is this variety of different optimum air temperatures that leads, among other factors, to a staggering of the seasonal and daily periods of activity. HAESELER (1972) states 45 °C to be the maximum temperature of flight activities.

**b) Humidity:** Many bee species, especially endogeic ones (burrowing their nests in the soil), need dry nesting sites. High humidity and warm conditions in winter time would destroy imported storages of pollen and nectar and endanger the breed through an increased risk of bacterial infections and fungal attack. This is why these bee species prefer soils characterised by low water holding capacity, as e.g. sand. However, nests build in such soils need stabilisation. With the help of sternal glands bee species specialised in those environments (e.g. *Andrena vaga*) can secrete substances for sticking sand grains together to stabilise nests (ERTELD 1998).

**c) Wind:** The bee fauna in regions characterised by regularly strong winds, e.g. coastal areas, only includes a few species (SCHWABE & KRATOCHWIL 1984). Due to their well developed flight ability, their size and robustness, bumblebees (*Bombus*) as well as *Anthophora* species are able to fly and forage for pollen and nectar even in strong winds. Bumblebees stop flying when wind speeds increase above 6 on the BEAUFORD scale (11-14 m/sec) (TERÄS 1976). Some species are known to be much better adapted to windy habitats than others, for example *Bombus muscuorum* (FELTON 1974), typical for coastal areas.

**d) Light:** Another factor determining bee activity is the intensity of sunlight. However, even when there is no sunlight, light also plays an important role. Therefore, a clear correlation between temperature and light intensity on the one hand, and flying- and blossom-seeking activities on the other can be observed (LINSLEY 1958, SZABO & SMITZ 1972). Studies on *Lasioglossum lineare*, for example, showed a necessary minimum sky radiation of more than 0,6 cal/cm<sup>2</sup> min (KRATOCHWIL 1988) to start flight activity. Studies from other continents (e.g. Mexico, South America, Indomalayan region) revealed that some bee species only fly in the morning before sunrise and at dusk (*Lasioglossum*). In the tropics, for example, wild bees species of the genus *Perdita* are only active at night (LINSLEY 1958).

## 2.2 Behaviour

Most bee species are solitary bees, each female bee building its own nest and being solely responsible for its brood. Some of the species have evolved social life forms, reaching from communal nesting aggregations (*Andrena*), to sociality (*Halictus*, *Lasioglossum*) and eusociality (*Bombus*, *Apis*). A quite important number of wild bees has developed parasitic life forms (cuckoo bees). These bee species don't build their own nests, but use already existing brood cells with foraged pollen stores of other bee species guaranteeing optimal nutrient supply. Cuckoo bees, for example, are species of the genera *Nomada* and *Sphecodes*.

## 3. Distribution of wild bees and centres of origin

Apart from the Antarctic, some arctic, and alpine areas with permanent snow, almost every habitat can be colonised by wild bees and their coevolved angiosperms. Today the centres of highest bee species diversity are situated in semidesert regions, in steppe ecosystems and in areas with mediterranean-like climate, in regions situated outside Europe, e.g. in some western regions of North- and South America as well as in regions of South Africa and Southwest Australia. These areas are also thought of as the regions were bees originated from and later radiated into other habitats (MICHENER 2000). The criterion of high species diversity, normally valid for plant species, according to which higher temperatures and higher humidity cause a higher biodiversity (PIGNATTI & PIGNATTI 1999) is not valid for wild bees.

Examples of regions characterised by high species numbers are California: 1985 species (MOLDENKE & NEFF 1974), Mexico: about 1800 species (AYALA et al. 1996), Australia: 1618 species (MICHENER 1965). In contrast, the cool, temperate and sub-arctic regions are extremely poor in bee species diversity (e.g. Alaska: 30 species). The tropics are also poor in species: Costa Rica: 193 species (FRIESE, cited in MICHENER 1979), Panama: 353 species (MICHENER 1954), Philippines: 233 species (BALTAZAR 1966), Java: 193 species (LIEFTINCK, cited in MICHENER 1979).

Wild bee species occur all over Europe: from northern regions beyond the arctic cycle in Fennoscandia to the southern mediterranean regions. There is a diversity gradient from southern to northern and from eastern to western regions (Tab. 1). This gradient is caused mainly by the climatic requirements of bee species. Only few (e.g. bumblebees) are adapted to relatively cool and humid habitats of the north and the west of Europe. Their body size, hair covering, the ability to regulate their body temperature - to a certain extend -, and to rise nest temperatures above ambient temperatures (HEINRICH 1979), allow them to spread into extremely northern and mountainous regions. Social behaviour can be considered to be another important pre-adaptation, since only social life forms can “afford” to leave worker bees, which produce comfortable nest temperatures while others are foraging for nectar, pollen and water.

Table 1: Diversity of wild bees in selected European regions.

Region	Species number	Reference
Iceland	1	PETERSEN 1956
Ireland	80	STELFOX 1927
Denmark	217	JØRGENSEN 1921
Finland	230	VIKBERG 1986
Great Britain	240	RICHARDS 1937
Sweden	278	JANZON et al. 1991
Poland	454	BANASZAK 1992
Germany	547	WESTRICH & DATHE 1997
Czech Republic, Slovakia	700	BANASZAK 1992
France	864	RASMONT et al. 1995
Spain	1043	CEBELLOS 1956

#### 4. Wild bees species as key-stone species

Wild bees are pollinators and thus important “key-stone species”. Key-stone species are defined as species whose influence on ecosystem functions is essential and larger as predicted by their biomass alone (BOND 1993, KRATOCHWIL & SCHWABE 2001). The loss of a key-stone species always causes serious consequences for the whole ecosystem. The wild bees’ functions which make the important key-stone members of ecosystems are as follows:

- **Pollination of wild plants:** 90 % of the about 250,000 existing angiosperm species (HEYWOOD 1993) are supposed to be animal pollinated (BUCHMANN & NABHAN 1996). Wild bees play an important role for the pollination of angiosperms (BAKER & HURD 1968, STEPHEN et al. 1969, TEPEDINO 1979, WCISLO & CANE 1996), the association between wild bee species and their pollen plant is often highly adapted and coevolved. Other pollinating species belong to the flies (Diptera), butterflies (Lepidoptera), beetles (Coleoptera), birds (Aves), mammals (Mammalia) and other animal taxa (FAEGRI & v.D. PIJL 1979): An estimated 300,000 animal species are reported to visit and pollinate flowers all over the world (NABHAN & BUCHMANN 1997).

Gene exchange and gene flow between plant individuals are guaranteed by pollinators causing an important natural selection pressure during the evolution of angiosperm plant species (CAMPBELL et al. 1997). On the other hand, the phenotypes of the pollinators are selected by the plants. The coevolution between pollinators and plants is rarely a simple “pairwise coevolution” (PAULUS 1978, JANZEN 1980), which means that there is a more or less intensive correlation between two species, one of them selecting, in an alternating way, the adaptations of the other (“reciprocal coevolution”). “Diffuse or network coevolution” (GILBERT 1975, ZWÖLFER 1999) appears to be the rule.

Animal pollination (zoophily) guarantees fructification and prevents “genetic erosion” by reduced fructification of smaller plant population sizes (MATTHIES et al. 1995, KWAK et al. 1998). In most cases, the interactions between pollinators and angiosperms are highly complex and only a few plant-pollinator systems are obligatory bisystems (WASER et al. 1996). Normally, there are diverse “pollinating networks”, which are complex “polysystems” including numerous different plant and pollinator species (JORDANO 1987).

**- Pollination of cultivated plants:** Almost one third of all plant species used by man for economical purposes needs zoophily. Pollination by wild bees is essential for many plants e.g. *Brassica napus*, *Carum carvi*, *Cucumis*, *Helianthus*, *Malus*, *Medicago sativa*, *Pyrus*, *Solanum lycopersicum*, *Trifolium*.

Honey bees (*Apis mellifera*) are generalists and play an important role as pollinators of cultivated plant species (BUCHMANN & NABHAN 1996). However, due to special flower morphology, there are a number of angiosperm species which depend on the pollination of other bee species and cannot be pollinated by honey bees (CORBET et al. 1991, BATRA 1995). The coffee plant (*Coffea arabica*) in the tropics, for example, can only be pollinated by wild social bee species (*Apis*, *Trigona*) (KLEIN et al. 2003). Moreover, wild bee species also play an important role as substitution pollinators in times of sudden population declines of the honey bee and also in regions which are climatically not appropriate for apiculture. In the colder climates of northern Fennoscandia (e.g. Finland) the honey bees’ pollination function is taken over by wild bees, above all by bumblebees (TERÄS 1976).

Since about 1985, the populations of honey bees in Europe has been drastically declining due to parasitisation by *Varroa* mites (e.g. *Varroa jacobsoni*) (WILLIAMS et al. 1991). Therefore, individual-rich populations of wild bees are important pollinators in cultural landscapes, especially in cases where honey bees fail.

Animal pollination plays an important economical role (COSTANZA et al. 1997). The estimated annual economic value of pollinating activities of semi-domesticated honey bees as well as the numerous other natural pollinators amounts to several billion US Dollars. In the United States, this annual value is estimated to amount to 20 - 40 billion Dollars. With respect to global agriculture it even amounts to 200 billion Dollars (KEVAN 1991, RICHARDS 1993, PIMENTAL et al. 1997). Already today, a decline or even failure of “wild bees” as key-stone species has led to a “pollinating crisis” reported from all continents (BUCHMANN & NABHAM 1996, KEARNS et al. 1998). The reasons for this are the following:

**- Habitat fragmentation:** In many cases, reduced population sizes of zoophilic plant species lead to a decrease of fruit productivity (FRITZ & NILSSON 1994, AIZEN & FEINSINGER 1994) as generalist pollinators use other plant species of higher abundance or, due to pollen limitation, disappear themselves. The inability of honey bees as well as many wild bees to cover long distances not only leads to fragmentation but also to an increase of pollinator limitation (JENNERSTEN 1988, “genetic erosion in fragmented habitats”). The insects’ reaction on such resource fragmentations is still unknown.

- **Change of land-use systems:** Large - plant-diversity reducing - monotonous agricultural areas (BANASZAK 1996), overgrazing (KEARNS & INOUE 1997), treatment of pesticides and herbicides (BATRA 1981, KEVAN 1975) lead to an extreme decrease of bee diversity.

- **The import of non-native pollinators** causes an exclusion of indigenous species. The bumblebee *Bombus terrestris* was imported to Japan for pollination of tomatoes in greenhouses. *B. terrestris* has turned out to be especially aggressive towards native bumblebees in Japan, a behaviour unknown for this species in its native habitats of Europe. Native pollinators such as *Bombus diversus*, the main pollinator of *Primula sieboldii* (Primulaceae), are especially endangered as their queens are killed by *B. terrestris* (WASHITANI 1996, KEARNS et al. 1998). In many countries, pollination of agricultural and wild plants by imported honey bees is often less effective than pollination by native wild-bee species (KWAK 1987, PARKER et al. 1987, RICHARDS 1993, BATRA 1995).

## 5. Resources and requisites of wild bees

### 5.1 Definition of resource/requisite

Resources are those elements which are required by organisms such as water, nutrients minerals or which are essential external factors such as light, heat, space, and time. Requisites are those elements which are part of the habitat's structure. Breeding sites, sleeping sites and save sites are typical examples. Besides energy, requisites are important for the distribution of organisms and species. Thus, resources include characteristics of energy and substances, whereas requisites are structural elements of a habitat (KRATOCHWIL & SCHWABE (2001).

### 5.2 Resources of wild bees

The radiation of bees correlates with the evolution of angiosperms. This is evident from highly developed fossil taxa encapsulated in 40 – 50 million years old baltic amber (MICHE-NER 1974, 1979, LOMHOLDT 1982). Compared to fossil (sphecoid) wasps the ancestors of today's bees were more advanced characterised by breed feeding with pollen. With regard to the pollen collecting behaviour there are two functionally different types of bees: polylectic and oligolectic species.

### 5.3 Requisites of wild bees

Appropriate breeding sites are, besides sufficient food resources, indispensable prerequisites for the existence of different species. Normally, there are endogeic and hypergeic species, as well as bees that build their nests on steep-rock faces. There are also numerous species that use already existing but abandoned nests of other animals (nests of mice, Hymenoptera or Coleoptera species). Many species need different materials for covering the cells of their nests: e. g. leaf segments (*Megachile*), plant mortar (*Megachile*, *Osmia*), sand, loam, little stones (*Megachile*, *Osmia*) and resin (*Anthidium*). There are some *Osmia*-species which obligatory build their nests in lost snail shells. Some species even build open land nests, mixing sand, loam, little stones and saliva to a kind of fat mortar (WESTRICH 1989).

## 6. Bee species in Germany and their resource utilisation

The bee species of Germany can be divided into 6 subfamilies and 40 genera. The genera including most species are *Andrena* (N = 111), *Lasioglossum* (N = 70), *Nomada* (N = 64), *Osmia* (N = 45), *Bombus* (N = 40) and *Hylaeus* (N = 38) (WESTRICH & DATHE 1997). Three quarters of all species (N = 413) are pollen collectors, about 1/3 of which are oligolectic (N

= 140) and 2/3 are polylectic (N = 252) (deficient data N = 20). 25 % of all species (N = 135) are cuckoo bees.

A global analysis of the percentage of oligolectic/polylectic species shows that the highest percentage of oligolecty occurs in semi-arid and mediterranean-like regions (semiarid: 60 %, mediterranean-like: 50 %) (MOLDENKE 1976). However, the percentage of polylecty has turned out to be higher in temperate (boreal) regions (Finland 80 %, PEKKARINEN 1998). Germany occupies an intermediate position (temperate) having 35 % oligolectic bee species.

There are a number of hypotheses concerning the development of oligolecty. Polylecty is believed to be promoted by social behaviour, by bi-/polyvoltinism and by long vegetation periods. However, oligolecty is selectively promoted by short vegetation periods, by a high number of flowering plant species and by improved synchronisation of the development of wild-bee species and the flowering times of their preferred plant species. There are still contradictory hypotheses about how competition is responsible for oligolecty.

Recent theory suggests that polylecty might have evolved from oligolectic behaviour (KRATOCHWIL 1984, 1991, MÜLLER 1996, WCISLO & CANE 1996) as a consequence resulting from the development of several species to social behaviour and to bi- and polyvoltinism. However some polylectic species learn to specialise an individual host plant species (flower fidelity).

A number of studies demonstrate special morphological and ethological adaptations supporting oligolectic behaviour in bees (VOGEL 1974, 1986, ROBERTS & VALLESPER 1978,

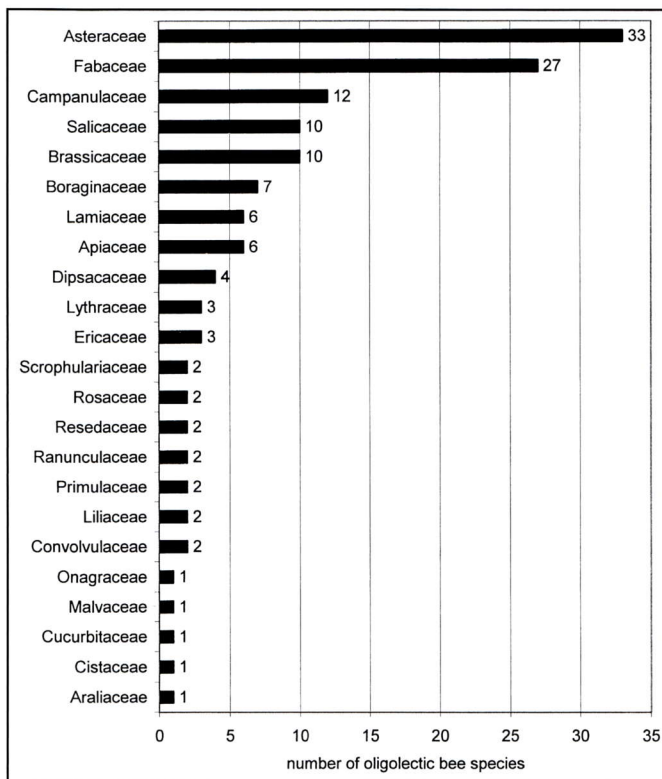


Fig. 1: Number of preferred plant families visited by oligolectic bee species in Germany (N = 140).

STRICKLER 1979, THORP 1979, EICKWORTH & GINSBERG 1989, VELTHUIS 1992, MÜLLER 1995, WESTERKAMP 1996).

Our analysis of the 140 oligolectic bees species of Germany shows, that there are 60 (43 %) bee species, which have specialised on only two plant families: on Asteraceae and Fabaceae (Fig. 1). Altogether, there are plant species of 23 families which are visited by oligolectic bee species, however only few of those bee species are specialised on species of the same plant families.

Species of the Asteraceae are mostly visited by oligolectic bee species of the genera *Osmia*, *Andrena* and *Colletes* (Fig. 2), Fabaceae by those of the bee genera *Andrena* and *Eucera* (Fig. 3). Oligolecty on Asteraceae and Fabaceae has separately evolved in different bee genera: With regard to the Asteraceae, there are 33 bee species from 13 bee genera, and 27 species from 9 genera are oligolectic specialists on Fabaceae.

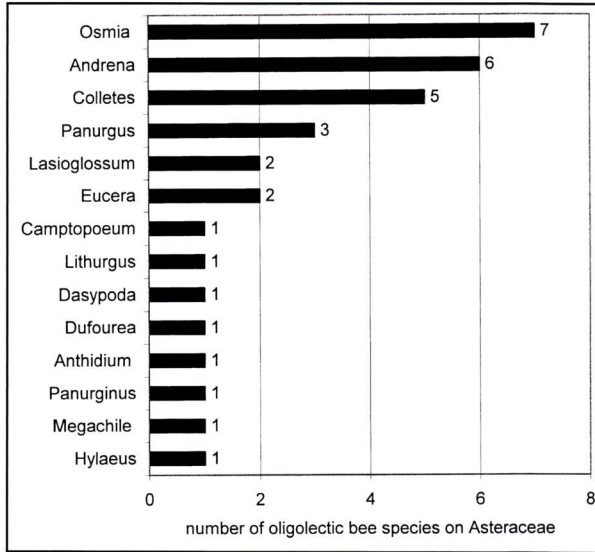


Fig. 2: Number of bee species within genera of oligolectic bee species specifically associated with Asteraceae in Germany.

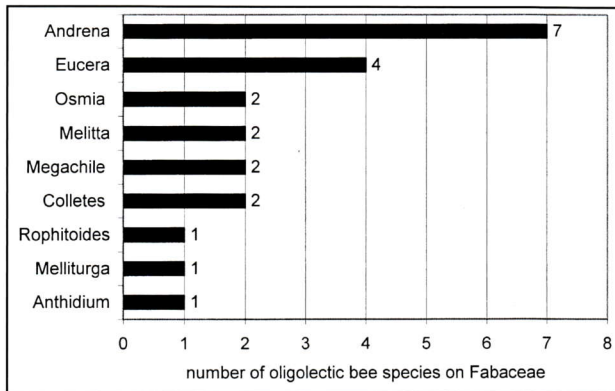


Fig. 3: Number of bee species within genera of oligolectic bee species specifically associated with Fabaceae.



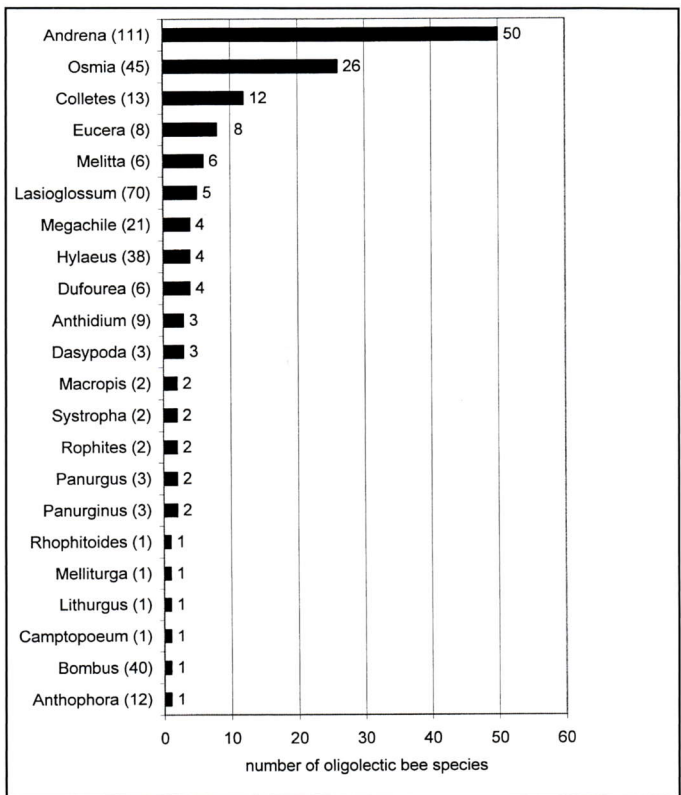


Fig. 4: Oligolectic bee species of Germany as total number of species per genus

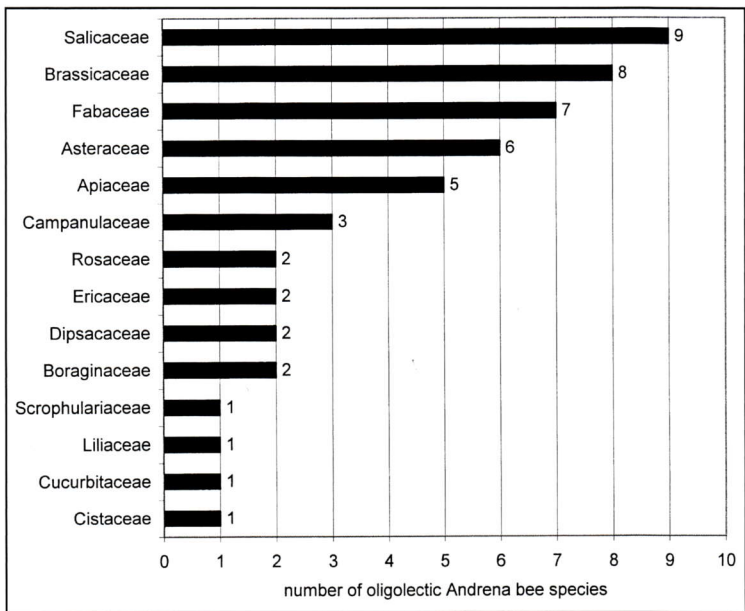


Fig. 5: Host plant family preferences of oligolectic *Andrena* species of Germany.

The analysis of bees shows that most of the oligolectic bee species are included in the genus *Andrena* followed by the genera *Osmia* and *Colletes* (Fig. 4). The different bee genera show different characteristics of resource specialisation: Thus, the oligolectic *Andrena* species obviously prefer Salicaceae and Brassicaceae followed by Fabaceae and Asteraceae. Apiaceae and Campanulaceae are of minor importance (Fig. 5). The results for the oligolectic species of the genus *Osmia* are quite different. Similar to most other oligolectic bee species, they prefer Asteraceae followed by Fabaceae, whereas Boraginaceae and Campanulaceae occupy the third and fourth place (Fig. 6). One reason for these different preferences is the genus-specific way of pollen collecting. While *Andrena*-species use their mandibles and forelegs, *Osmia*-species use their ventral hair brushes.

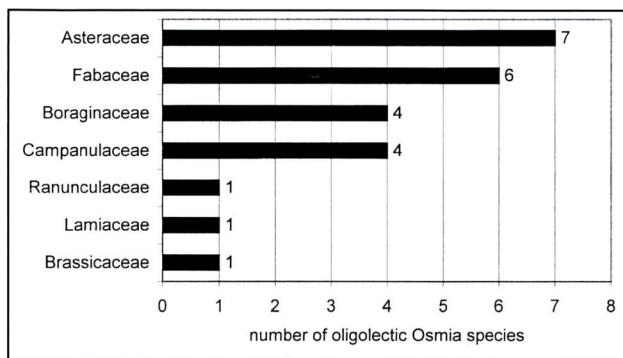


Fig. 6: Host plant family preferences of oligolectic *Osmia* species of Germany.

*Andrena* and *Osmia* have evolved their oligolectic behaviour on different plant families: *Andrena*: species on 14 plant families (Fig. 5), *Osmia*: on 7 plant families (Fig. 6). A combination of the phylogenetic tree of west-palaeartic *Andrena* species (381 species) according to WARNCKE (1968) based on morphological characters with flower-visiting preferences (KRA-TOCHWIL 1991) leads to the following theses:

- 1) Oligolecty within the genus *Andrena* represents an ancestral character.
- 2) Oligolecty concerning Brassicaceae, Apiaceae and *Potentilla/Veronica* represents an ancestral character.
- 3) Oligolecty concerning *Salix* is a highly developed feature in *Andrena*.
- 4) Polylecty, social behaviour, bivoltism and an increase in body size is a highly developed feature.

## 7. Bee species in Germany and their requisite utilisation

According to an analysis of the nesting behaviour of German bee species (e.g. WESTRICH 1989, SCHMIDD-EGGER et al. 1995), 66 % of all bee species build their nests below-ground (endogeic), 24 % above-ground (hypergeic), 2 % are endogeic or hypergeic, 3 % of the species use steep rock faces as nesting sites (5 %).

## 8. Bee species in Germany and their habitat preferences

Evaluating the existing literature reveals that 50 % of all species (N = 178) can be characterised as habitat specialists. 28 of these species were found to be associated with forests (tall

herb communities, forest clearances, waysides) and a further 28 species with sandy habitats. Only 10 species could be related to alpine and 5 to steppe habitats. The remaining 104 species could not be related to any habitat due to deficient data or missing habitat specialisation.

An analysis of those bee species with habitat preferences showed the following results (Fig. 7): Most habitat specific bee species are found in communities of Festuco-Brometea, Artemisietea, extensively managed Molinio-Arrhenatheretea and Koelerio-Corynephoretea. The total of all *Salix*-dominated vegetation units (Salicetea purpureae, Salicion cinereae and Sambuco-Salicion) is ranked fifth followed by Stellarietea. These results hold true regardless of whether or not cuckoo bees are included in the analysis. The dominance ranking of habitat preferences of bees is supported by the results of a principal component analysis (PCA) (Fig. 8).

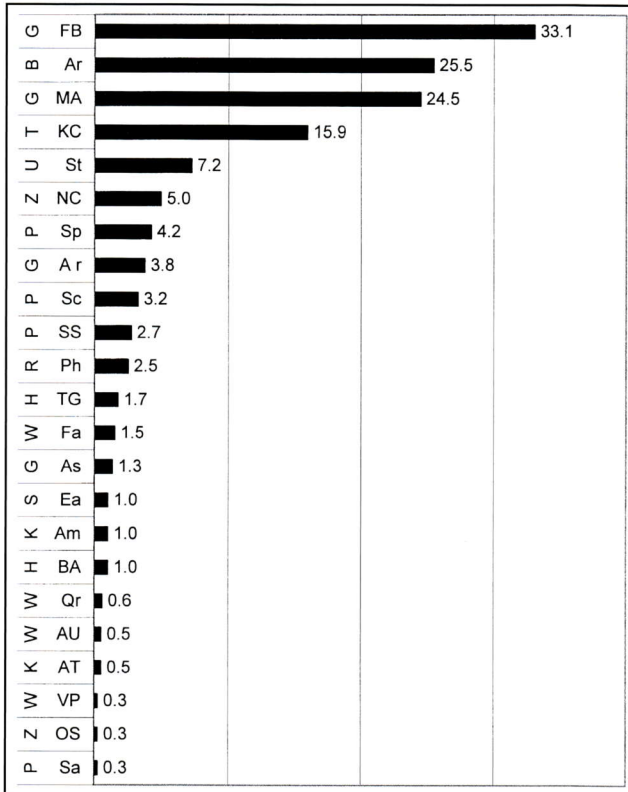


Fig. 7: Habitat-specific bee species in Germany and their preferred vegetation units on the formation and community type level (excluding cuckoo-bee species; N = 138). In the case of multiple habitat preferences the values are calculated proportionally.

Formations: B: Artemisietea stands; G: grassland; H: tall-herb communities; K: coasts; P: shrubs communities; R: reed stands; S: forest clearings; Sa: sand habitats, inland dunes; St: steppe heath; T: dry grasslands; NC: Nardo-Callunetea; U: weed communities; W: forest communities; Z: dwarf shrub communities.

Community types: Am: Ammophiletea; Ar: Agropyretea repentis; Ar: Artemisietea; As: Agrostietea stoloniferae; AT: Asteretea tripolii; AU: Alno-Ulmion; BA: Betulo-Adenostyletea; Ea: Epilobieta; FB: Festuco-Brometea; KC: Koelerio-Corynephoretea; MA: Molinio-Arrhenatheretea; Me: Mesobromion erecti; NC: Nardo-Callunetea; OS: Oxyocco-Sphagnetetea; Ph: Phragmitetea; Qr: Quercetalia roboris; RE: Rhamno-Prunetea/Epilobieta; Sa: Salicion arenariae; Sc: Salicion cinereae; Sp: Salicetea purpureae; SS: Sambuco-Salicion; St: Stellarietea; TG: Trifolio-Geranietea; VP: Vaccinio-Piceetea.

The separate localisation of the 4 vegetation types characterised by habitat specific bee species combinations is clearly visible in the ordination diagram.

The main habitat types of specialised bee species in Germany show the following characteristics:

- Extensive, phenological staggering of flowering times
- high plant species diversity, showing that for Central Europe there is a clear correlation between plant species and the diversity of bees species
- distinct “patchiness”: alternating small, open and vegetation covered habitats (close neighbourhood of resources and requisites)
- dry and warm microclimate conditions
- relatively small habitat areas and well-developed ecotone structures (e.g. Artemisietea-communities)
- highest bee species diversity in plant communities of early- and mid-successional stages
- major importance of habitat disturbances causing succession retardation (STEFFAN-DEWENTER & TSCHARNTKE 2001).

All elements characterising main habitat types of wild bees in Central Europe occurred in natural landscapes, e.g. in gravel-rich fluvial ecosystems (model Isar), at steep rocky valley slopes, at loess and sandy walls and in drift-sand areas.

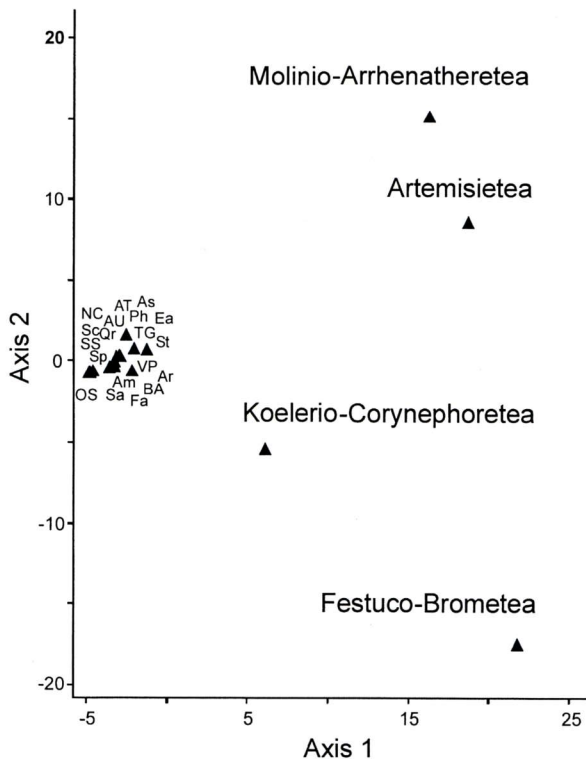


Fig. 8: PCA of the habitat preferences of the specific bee species (habitat specialists) occurring in Germany (axis 1:  $\lambda = 58.228$ , axis 2:  $\lambda = 28.224$ ).

## 9. The relation between body size and resource-/habitat utilization

In the following, we will examine the hypothesis that the body size of specific bee species plays an important role for their habitat preferences, due to a correlation between body size and flight radius (WESSERLING 1996, GATHMANN & TSCHARNTKE 2002). The body size (measured as the length from head to the end of abdomen) of the species occurring in Germany ranges from a few millimeters, e.g. in the case of some species of the genera *Hylaeus*, *LasioGLOSSUM* and *Nomioides* (3–4 mm), to up to 23 mm in the case of *Xylocopa violacea* and some bumblebee species (e.g. *Bombus hortorum*). Fig. 9 shows the body-size spectrum of the bee species occurring in Germany (N = 547). It is characterised by an irregular distribution, the median line being situated at a value of 10 mm.

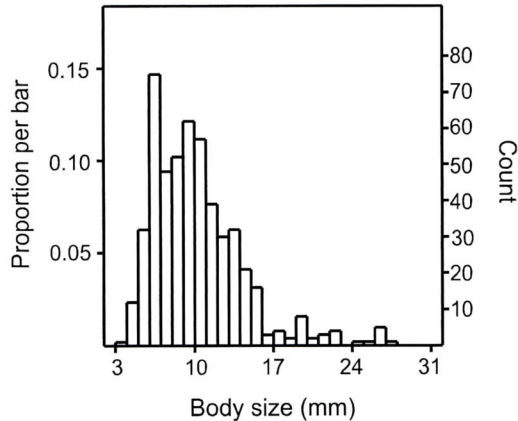


Fig. 9: Body-size spectrum of the bee species occurring in Germany, median line: 10.047mm (range 3.5–27.5mm) (N = 547).

A comparison of pollen-collecting bee species and cuckoo bees shows that they do not significantly differ in body size a fact which could be expected (ANOVA of Box-Cox transformed data [ $\lambda = -0.3$ ]:  $F_{1,509} = 1.6469$ , Pr [F] = 0.1999). Both groups are also equally variable in body size (pollen collecting bee species: coefficient of variation, CV = 0.40, cuckoo bees CV = 0.36). However, within the group of pollen collecting bees there is a significant difference between oligolectic and polylectic species. On average oligolectic species are significantly smaller (0.32 mm) than the polylectic bees (ANOVA test of Box-Cox transformed data [ $\lambda = -0.3$ ]:  $F_{1,378} = 6.7503$ , Pr [F] = 0.0097). In addition polylectic species (CV = 0.5) are 40 % more variable in body size than oligolectic species (CV = 0.3).

A comparison of the body sizes specific plant families visited also shows that plant families are only visited by bees of a certain body size (ANOVA on Box-Cox transformed data [ $\lambda = 0$ ]:  $F_{8,104} = 4.2792$ , Pr [F] = 0.0001) (Fig. 10). Lamiaceae, Campanulaceae and Brassicaceae are visited by the smallest bees in contrast to Fabaceae, Salicaceae and Boraginaceae which are only visited by large individuals.

In contrast habitat types appear to be a weak determinant of the body size of bees Fig. 11. A post hoc test indicates that the small bees associated with Koelerio-Corynephoretea are unlikely to be found in habitats dominated by *Salix* species (Tukey's LSD with  $\alpha = 10\%$ , data were Box-Cox transformed [ $\lambda = 0.3$ ]).

With the help of homefinding experiments, WESSERLING & TSCHARNTKE (1995) found out that the body size correlates with the flight radius around the nest. Due to these results, the

smaller bee species of Koelerio-Corynephoretea might dispose of a flight radius of about 50 m around their nests, whereas larger species of *Salix*-dominated habitats might cover a flight distance of about 200 m. In the case of the latter species of *Salix*-dominated habitats, longer flight distances result from the fact that the flood plain vegetation habitats lack appropriate nesting sites, whereas more distant regions, such as inland river dunes, appear to be more suitable.

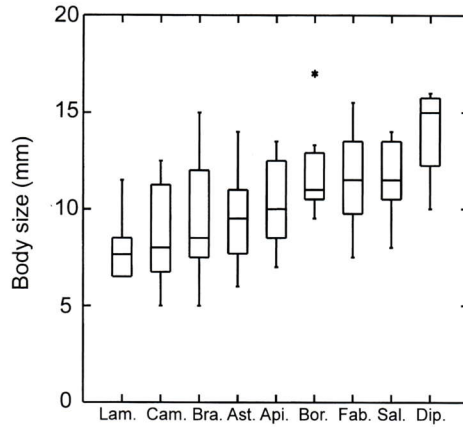


Fig. 10: Body-size spectrum (Box-Plot-diagrams) of the oligolectic bee species occurring in Germany and their preferred plant families. (Kruskal-Wallis Test high significance,  $p = 0.001$ , DF 8). Lam. = Lamiaceae (N = 6), Cam. = Campanulaceae (N = 12), Bra. = Brassicaceae (N = 10), Ast. = Asteraceae (N = 31), Api. = Apiaceae (N = 6), Bor. = Boraginaceae (N = 7), Fab. = Fabaceae (N = 27), Sal. = Salicaceae (N = 10), Dip. = Dipsacaceae (N = 4).

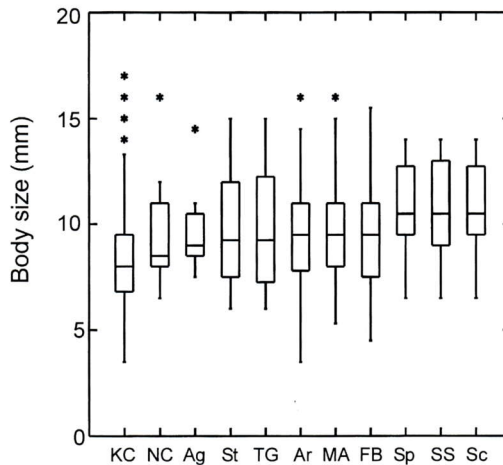


Fig. 11: Body-size spectrum (Box-Plot-diagrams) of the oligolectic bee species occurring in Germany and their preferred habitat types. Kruskal-Wallis-Test, low significance,  $p = 0.039$ , DF 10; KC = Koelerio-Corynephoretea (N = 47), NC = Nardo-Callunetea (N = 13), Ag = Agropyretea repentis (N = 9), St = Stellarietea (N = 18), TG = Trifolio-Geranietea (N = 12), Ar = Artemisietea (N = 77), MA = Molinio-Arrhenatheretea (N = 82), FB = Festuco-Brometea (N = 75), Sp = Salicetea purpureae (N = 16), SS = Sambuco-Salicion (N = 14), Sc = Salicion cinereae (N = 15).

## 10. Conclusions

The above-mentioned results lead to the following conclusions:

- The number of oligolectic bee species depend on climate conditions. With 140 oligolectic species (35 %) the German bee fauna occupies an intermediate position between semiarid/mediterranean regions (50 %) and boreal regions (20 %). The number of oligolectic species for a region characterised by climate and vegetation is predictable.
- 43 % of all oligolectic bee species are specialised on pollen from the Asteraceae and the Fabaceae, the rest spread out over 21 plant families. Many species of Asteraceae and Fabaceae are characteristic for dry, nutrient poor sites.
- The analysis of bees shows that most of the oligolectic bee species are included in the genus *Andrena* followed by the genera *Osmia* and *Colletes*. There is no correlation between the number of oligolectic bee species with total species number within a genus.
- Habitat-specific bees are typically associated with plant communities of Festuco-Brometea, Artemisietaea, extensively managed Molinio-Arrhenatheretea and Koelerio-Corynephoretea. These habitats correspond the most with the conditions prevailing in those assumed to be the centres of bee radiation: the semiarid regions and the mediterranean-like regions of the world.
- The bees' body size is a good determinant for host plant specialisation and for the home range (distances between nest and host plant). On average oligolectic species are significantly smaller than the polylectic bees. Small body size and oligolecty represents an ancestral character in bee phylogeny. Within oligolectic bee species Lamiaceae, Campanulaceae and Brassicaceae are visited by the smallest bees in contrast to Fabaceae, Salicaceae and Boraginaceae which are only visited by large individuals. This may be due to flower morphology.
- The relation between body size and the flight radius around nesting sites may explain why small bees are habitat-specific for Koelerio-Corynephoretea, while larger bees are able to forage in *Salix*-dominated habitats where larger flight distances between nesting sites and host plant are required.

There are a number of possibilities to support wild-bee species by man-made flower-rich and open grassland and ruderal communities and to protect their nesting sites. Today's risks include a deterioration of nesting and foraging sites, the lack of habitat "patterns" (resources/requisites) and of a dynamic balance (recreation of nesting habitats), the loss of pollen sources due to intensive cropping and a minimum of open field boundaries.

In summary, it has to be considered that the knowledge of oligolecty and habitat requirements (e.g. sand, steep slopes) on one hand, and of space requirements (flight radius around the nests corresponding to the indicator "body size") on the other are essential for understanding the behaviour of wild bees and for taking necessary conservation measures. In Germany the existence of Festuco-Brometea, Artemisietaea, extensively managed Molinio-Arrhenatheretea, Koelerio-Corynephoretea communities as well as *Salix*-dominated vegetation units play a special role for high wild bee diversities. Although, with the exception of Artemisietaea and Molinio-Arrhenatheretea, the most important habitat types (Koelerio-Corynephoretea pp., Festuco-Brometea pp.) are included in the European Flora-Fauna-Habitat-Directive, they are heavily endangered (SSYMANEK et al. 1998).

## 11. Zusammenfassung

Nach einer kurzen allgemeinen Charakterisierung von Wildbienen wird ihre Bedeutung als Schlüsselarten in Ökosystemen und die Konsequenzen bei ihrem Ausfallen verdeutlicht. Die Wildbienen Deutschlands als einem Modellgebiet für Zentraleuropa werden im Folgenden näher analysiert. 3/4 aller Arten (N = 413) sind Pollensammler, davon 1/3 oligolektisch (N = 140) und 2/3 polylektisch (N = 252); bei 25 % (N = 135) handelt es sich um Kuckucksbienen. Im weltweiten Vergleich dominieren oligolektische Arten in den semiariden und mediterranoide, die polylektischen in den temperaten (borealen) Gebieten. Die Verteilung für Deutschland belegt mit 35 % eine Mittelstellung. Die Analyse von 140 in Deutschland vorkommenden oligolektischen Bienenarten zeigt, dass 60 Arten (43 %) auf Pflanzenarten der Asteraceae und Fabaceae spezifisch sind. Insgesamt werden Arten von 23 Pflanzenfamilien von oligolektischen Bienenarten besucht. Innerhalb der Asteraceae überwiegen oligolektische *Osmia*-, *Andrena*- und *Colletes*-Arten, bei den Fabaceae solche der Gattungen *Andrena* und *Eucera*. In der Gattung *Andrena* kommen die meisten oligolektischen Arten vor (insbesondere an Salicaceae, Brassicaceae, Fabaceae und Asteraceae), bei *Osmia* (an 2. Stelle) solche an Asteraceae und Fabaceae. Die Habitat-spezifischen Wildbienen-Arten haben ihren Schwerpunkt in Pflanzengesellschaften der Festuco-Brometea, Artemisieta, Molinio-Arrhenatheretea (magere Ausbildungen) und Koelerio-Corynephoretea. Der Median des Körpergrößen-Spektrums der Wildbienen-Arten Deutschlands (N = 547) liegt bei 10 mm. Oligolektische Bienenarten sind signifikant kleiner als polylektische Arten. Bei den oligolektischen Arten korreliert die Körpergröße mit den Vorzugspflanzen: kleinere Arten bevorzugen Lamiaceae, Campanulaceae und Brassicaceae, größere Fabaceae, Salicaceae und Boraginaceae. Die Körpergröße korreliert ferner mit dem Flugradius um das Nest (Zunahme des Flugradius mit zunehmender Körpergröße). Aufgrund dieses Zusammenhanges kann ein geringer Flugradius der kleineren Wildbienen-Arten der *Koelerio-Corynephoretea* um ihre Nest erschlossen werden im Gegensatz zu habitatspezifischen Bienenarten von *Salix*-dominierten Lebensräumen, die größer sind und weitere Flugstrecken zurücklegen müssen. Die Lebensraumschwerpunkte der meisten habitatspezifischen und oft auch oligolektischen Bienenarten Deutschlands ähneln am ehesten denjenigen Habitattypen, die global als Radiationszentren die höchste Artendiversität zeigen (semiaride und mediterranoide Lebensräume). Kenntnisse über das oligolektische Verhalten und über Habitat- und Raumansprüche in Kombination mit der Körpergröße als einem Indikator für den Flugradius um das Nest bilden die Voraussetzung für notwendige Schutz- und Erhaltungsmaßnahmen.

### Acknowledgements

I would like to thank Till Eggers for statistical help, fruitful discussions and many useful comments on the manuscript and Birte Pahlmann for translation support.

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