

## On flower visitors and true pollinators: The case of protandrous *Heracleum sphondylium* L. (Apiaceae)

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Received April 15, 2005; accepted July 3, 2006

Published online: December 22, 2006

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**Abstract.** Hogweed (*Heracleum sphondylium* L.), a common European umbellifer, is very variable in terms of flower and inflorescence morphology. Its flowers are visited by numerous insects, yet little is known about the importance of the particular insect taxa. I observed umbels of two colour morphs (subspecies) of *Heracleum sphondylium* growing in NE Poland, which were visited by more than 108 insect species during two study seasons. Analysis of the insects' importance suggests that the most efficient pollinators are the medium-sized flies *Eriozona syrphoides*, and *Lucilia* spp. (Diptera). Bumblebees *Bombus terrestris* (Hymenoptera), beetles of genus *Stenurella* spp. and *Dasytes* spp. (Coleoptera) and flies *Eristalis* spp., *Meliscaeva cinctella*, *Phaonia angelicae* and *Thricops nigrifrons* also contribute to pollination of the studied plants, but their efficiency shows considerable seasonal variation. Although the dense umbels of the white flowered *H. sphondylium* subsp. *sphondylium* are generally more attractive for insect visitors than the loose yellowish inflorescences of *H. sphondylium* subsp. *sibiricum*, these taxa do not seem to attract different sets of the pollinators. For both subspecies, flowers in the staminate phase were visited significantly more often than those in the pistillate phase. Some flower visitors visited the staminate phase only, which suggests they may be parasites rather than pollinators.

**Key words:** *Heracleum sphondylium*, Umbelliferae, Diptera, pollination, dichogamy, colour

morphs, pollinator importance, specialization, generalization.

Since the earliest systematic surveys of plants pollination systems, the family Apiaceae has been regarded as promiscuous (*sensu* Grant 1949) in terms of pollination biology (Bell 1971, Faegri and van der Pijl 1979, Proctor et al. 1996). However for the last several decades new research based on more detailed studies of the pollinator importance and flower biology has revealed that umbellifers are much more specialised than previously suggested, and their pollination systems may contain various sophisticated mechanisms overlooked by earlier workers (Zych 2004). Since the works of Bell and Lindsey (Bell and Lindsey 1978, Lindsey 1984, Lindsey and Bell 1985), Apiaceae are usually no longer regarded as primitive in terms of pollination biology. Although some authors (eg. Sheppard 1991, Proctor et al. 1996, Rovira et al. 2004) still consider them 'promiscuous', a series of studies focused on umbelliferean species from different geographic regions show a considerable degree of specialisation of their pollination systems (Grace and Nelson 1981; Webb 1984; Koul et al. 1986, 1989, 1993; Lamborn

and Ollerton 2000; Németh and Székely 2000; Schlessman and Graceffa 2002; Zych 2002).

In spite of numerous publications on the pollination biology of umbellifers, most of the cited studies, except the works of Lindsey (1984), Lamborn and Ollerton (2000), and Rovira and co-workers (2004), are based on one-season long observations and lack the information on long term pollinators activity which may be crucial in determining real plant-pollinator relationships (Waser et al. 1996, Johnson and Steiner 2000, Pellmyr 2002).

Some other aspects of pollination biology of the Apiaceae, e.g. insect preferences towards flower sexual phases, have also received little attention. Although the phenomenon of dichogamy in this family is well known, and has been well studied for more than a century (Foerste and Trelease 1882, Knuth 1898, Bell 1971, Webb 1981, Lovett Doust and Harper 1980, Lindsey 1982, Lovett Doust and Lovett Doust 1982, Schlessman 1982, Koul et al. 1993, Spalik and Woodell 1994, Konuma and Yahara 1997, Schlessman and Graceffa 2002), surprisingly almost none of the works have been devoted to the fact that strong dichogamy in some cases may cause discrimination of sexual phases by insects visitors (Goulson 1999). Among papers devoted to the pollination biology of the umbellifers, only Zych (2002) clearly indicated the sexual phase of the observed flowers, and some evidence of discrimination of sexual phases was given by Lindsey and Bell (1985), who observed that flowers in the male phase of plants from the American genera *Thaspium* and *Zizia* are visited more frequently by Diptera and some Hymenoptera (e.g. *Andrena ziziae*) than those in the female phase. This finding however was not thoroughly discussed by these authors and passed almost unnoticed by later workers, until Schlessman et al. (2004) experimentally showed that either female stage or smaller in size umbels of protogynous *Pseudocymopterus montanus* (North American endemic) were less attractive to its floral visitors, mostly solitary bees and flies.

Most workers focus on the pollination biology of economic Apiaceae (Braak and Kho 1958; Burgett 1980; Koul et al. 1986, 1993; Warakomska et al. 1986; Koul et al. 1989; Koul et al. 1989; Langenberger and Davis 2002a, 2002b). From among wild European taxa only three species have received the attention of researchers – *Daucus carota* (Eisikowitch 1980, Lamborn and Ollerton 2000), *Heracleum sphondylium* (Corbet 1970, Grace and Nelson 1981, Ellis and Ellis-Adam 1994, Zych 2002), and *Seseli farrenyi* (Rovira et al. 2004). The first was studied because of the Darwin (1888) controversy over the central floret and the second because of its wide distribution, importance in supporting local anthophilous fauna (Ellis and Ellis-Adam 1993), and the very variable morphology of the flowers and inflorescences (Gawłowska 1961, Sheppard 1991, Zych 2002). The third, *S. farrenyi*, is an endemic species with a very narrow distribution.

The case of *Heracleum sphondylium* especially provides not only useful insight into pollination biology but also may contribute to the studies of insect preferences and the evolution of flower morphology (Zych 2002). Two of its subspecies (*H. sphondylium* subsp. *sphondylium* and *H. sphondylium* subsp. *sibiricum*), formerly considered separate species, differ in flower and inflorescence morphology. The former has a white corolla and zygomorphic flowers with elongated petals arranged on the edge of an umbel, while the latter has greenish actinomorphic flowers and umbels with no such ‘edge effect’ (Gawłowska 1956, 1961; Sheppard 1991).

Although, in terms of the number of insect visitors, the species is regarded as very ‘popular’ among European anthophiles (Ellis and Ellis-Adam 1993, 1994), and both taxa seem to be pollinated by similar dipterans, preliminary evidence suggests that their floral characteristics serve as attractants for different groups of insects which may create a mechanism of differentiation between the two (Zych 2002). However this opinion is based only on short term observations. The present paper

addresses the following questions: (1) What is the long-term pollination biology of *H. sphondylium*? Does the species have constant (faithful) pollinators or is there considerable variation in pollinators between years? And (2) Do insect visitors show any preferences regarding floral sexual phases?

## Material and methods

***Heracleum sphondylium* L.** *Heracleum sphondylium* is a perennial (hemicryptophyte) (Rabotnov 1956, Sheppard 1991), not a biennial as often stated (e.g. Brummitt 1968), with cauline leaves arranged in a rosette producing erect flower stems up to 3 m tall. It is widespread in forests and woodland clearings, riverbanks, and tall montane-herb grasslands (Sheppard 1991). In Poland it is usually described as a common meadow species (Gawłowska 1956), growing also in thickets, on roadsides and forest fringes (Rutkowski 1998). Its geographical range includes most of the European countries, except the extreme north, parts of the Mediterranean region and some Atlantic and Mediterranean islands (Brummitt 1968, Sheppard 1991).

*Heracleum sphondylium* reproduces mainly by seeds; vegetative division of the root stock, although occasionally occurring, is not important (Sheppard 1991). The open, protandrous flowers, arranged in compound umbels, are entomophilous with insects visiting flowers for pollen and nectar exuded by exposed swollen base of the style (stylopodium). Nectar is present either in the male phase (mainly during anthesis), or in the female stage when the stigmas become receptive, in both: male and bisexual flowers, it is produced in very minute quantities and may be reabsorbed from the surface of the stylopodium, which makes it very difficult to collect and analyse in the field conditions (Zych, unpubl.). The flowers demonstrate full protandry at the level of an individual flower, the whole inflorescence and the individual plant, which means that the stigmas do not become receptive until all the pollen in the umbel has been shed (Zych, unpubl.). Most of the flowers are actinomorphic, but the outer flowers in umbellets may be zygomorphic (Gawłowska 1956, 1961; Sheppard 1991). Umbels, depending on their order, may comprise hermaphrodite or male flowers (i.e. flowers with aborted female parts). However, the

percentage of male flowers is quite variable. In some populations it does not exceed 40% in tertiary umbels (Wróblewska 1992), while in others may be close to 100% (Zych, unpubl.). In primary umbels hermaphrodite flowers usually constitute 100% (Wróblewska 1992). Flower colour varies from greenish, greenish-yellow (*H. sphondylium* subsp. *sibiricum*), to white or pinkish (*H. sphondylium* subsp. *sphondylium*).

**Study site.** The observations were conducted in 2000 and 2002 in two sites in the same forest complex in Wigry National Park (NE Poland). The distance between the two populations was  $\pm 3$  km (the same populations were also studied by Zych (2002) in 1998). The population of *H. sphondylium* subsp. *sphondylium* was situated in the forest section 119 near the village of Krzywe (N 54°05' E 23°00'), and the population of *H. sphondylium* subsp. *sibiricum* was on the border of the forest sections 133 and 134 (N 54°06' E 23°03'). Both grew in similar habitat conditions, along the forest road in mixed spruce-pine forest, and consisted of similar numbers of individuals.

**Field observations.** Field observations in both study years were conducted in July, a peak flowering month for *H. sphondylium* in NE Poland. I observed male phase umbels from 4–5 July and 18–21 July in 2000, and from 1–4 July, and 14–16 July in 2002, and female phase umbels from 22–27 July in 2000, and from 17–23 July in 2002. The method used was modified from a previous study on the pollination of *H. sphondylium* (Zych 2002). Only primary umbels in either the male or the female phase were chosen for observations, because these umbels are mainly responsible for seed production (Sheppard 1991). Observations started at 08:00 a.m. (the first recording) and ended at 07:30 p.m. (the last capturing), because earlier observations revealed that before 08:00 a.m. and after 07:00 p.m. flowers of hogweed are visited by insects only occasionally.

Every study day 12 rounds of observations were conducted, but in case of strong winds or rain the observations were halted and the remaining rounds were completed at the corresponding hour on subsequent days. Each round lasted 1 hour and consisted of three phases: random choice of an umbel, video recording, and insect capturing. Once selected, umbels were not excluded from the subsequent round, and therefore it was possible that the same umbel was observed more than once.

After an umbel had been selected it was staked to prevent wind-caused movements. Then insect activities were recorded for 10 minutes using an 8 mm video camera (Sony TR-3200). The camera was set on a tripod about 0.5–1 m from the umbel so that the recording field covered the whole umbel surface. Approx. 20 min. after recording, for 10 minutes, all the insects visiting the umbel were collected either with an entomological net (Diptera, Hymenoptera, Lepidoptera) or directly into plastic vials or an entomological exhaustor (Coleoptera, Hemiptera). Insects were killed with ethyl acetate, pinned and stored for further investigation of their pollen loads. Aphids and other small, sap sucking insects (e.g. Thysanoptera), and insects smaller than 1 mm, were excluded from the analyses. The analyses of insects activities and importance were based on 960 min of video recording and 960 min of insect capturing for each of the studied subspecies over two years.

#### **Pollen loads analyses**

Pollen grains of *H. sphondylium* resemble those of other Apiaceae, therefore during the examination of pollen loads there is a possibility of misidentification if other umbellifers grow in the same site. Indeed, close to the studied populations plants of *Chaerophyllum aromaticum* were encountered – these were also visited by some of the insects observed on *H. sphondylium*. However *Ch. aromaticum* has much smaller pollen grains ( $24.2 \pm 1.7 \times 10.9 \pm 1.4 \mu\text{m}$ ), which are relatively easy to distinguish from the large *H. sphondylium* pollen grains ( $39.3 \pm 2.7 \times 18.7 \pm 2.1 \mu\text{m}$ ; in both cases 50 pollen grains from randomly sampled five anthers were measured), so I assumed that all the pollen grains of a certain size belonged to *H. sphondylium*.

For the investigation of pollen loads carried by insects visiting flowers of *H. sphondylium* a method described by Zych (2002) was used (modified from Grace and Nelson (1981) and Lindsey (1984)). An insect was put on a microscope slide and pollen from its body was removed using a thin brush until no remaining pollen was visible. This was done under a stereoscopic microscope. The pollen was then stained with a drop of acetoorceine and covered with a microscopic cover slip. After that the brush was carefully cleaned so the pollen could not contaminate the next sample. Pollen samples

were analysed using a light microscope. If the sample contained fewer than 300 pollen grains all of them were counted. In larger pollen loads all *H. sphondylium* pollen grains were counted from nine randomly selected areas on one sample. The arithmetic mean of the counts, after extrapolation, was used to calculate the pollen load of a given individual. A paired Student *t*-test performed for 23 randomly chosen samples showed no significant difference between the two methods ( $P = 0.441$ ).

#### **Measuring pollinator activities and importance**

It is generally agreed that the number of pollinators (or rather the list of flower visitors) is a poor measure of flower specialisation and pollinators importance (Waser et al. 1996, Johnson and Steiner 2000, Pellmyr 2002). Direct methods, such as measuring pollen loads deposited on a stigma by a given pollinator species, or seed set after visits by certain pollen-carrying vectors or after exclusion of a given insect visitor, are the best descriptors of pollinator importance (Pellmyr 2002). Unfortunately, in plants such as Apiaceae, the methods cited above are usually inadequate because numerous, minute flowers packed into large inflorescences are visited daily by hundreds (if not thousands) of insects. In such situations other indirect methods must be used e.g. measuring the pollen loads carried by different vectors, and observations of their frequency, abundance and behaviour on the flowers. The sum of the above elements, even though not comprehensive, makes a reasonable description of pollination effectiveness and the importance of certain pollinators (Lindsey 1984, Lamborn and Ollerton 2000, Zych 2002). Such observations are greatly facilitated by photographic methods, especially video techniques, that have already been applied in studies of the pollination ecology of angiosperms (Kearns and Inouye 1993) and for Apiaceae especially (Zych 2002), and were also used in the present study for determining insect activities.

During the laboratory analyses I measured the frequency of visits (no. of visits per census) and within-umbel activity (no. of umbellets visited) of all insect visitors. This seems a reasonable measure because umbellets, with overlapping, elongated petals of the outer flowers, forming compound umbels, may in many Apiaceae act as reproductive units (Bell 1971, Bell and Lindsey 1978).

A separate visit was counted for each captured insect and, in video recordings, an insect was scored as a flower visitor if it touched the surface of an umbel. I did not attempt to trace the movements of flower visitors among the plants therefore if the insect flew away but remained in the field of view of the camera and then landed on (or touched) the inflorescence again this was still counted as the same visit but if it flew outside the field of view of the camera and then an individual of the same species appeared again touching the umbel it was counted as another visit.

The importance of each insect visitor species on *H. sphondylium* for every season and sex phase was individually calculated using a pollinator importance measure (I):

$$I_x = V \times U \times PL \text{ [Equation 1]}$$

Where:

$I_x$  – importance of insect species X,

V – (no. of recorded visits + no. of individuals of species X captured)/(total no. of visits recorded + total no. of individuals captured),

U – mean no. of umbellets visited by species X within an umbel / mean no. of umbellets in an average umbel in the population surveyed,

PL – average pollen load (number of pollen grains) carried by an individual of species X.

This was then summed for all insect species for each subspecies, study year and sexual phase of the flowers and the sum was treated as 100% to obtain the pollinator importance coefficient indicating pollen pick-up or deposition abilities of each insect taxon (IC). I assumed that for ‘good’ (true) pollinators ( $I_{\text{female}}/I_{\text{male}}$ ) scores should be greater than 0, but in the same time the key pollinators should also have  $IC_{\text{female}}$  at least greater than 1%.

### ***Insect identification and statistics***

Most of the insects were identified to the species level. In many cases video recordings allowed me to identify the species by comparison with a dry reference collection, when this was impossible I tried to identify insects to the lowest possible rank (usually family).

Three-way ANOVA on total insects and Diptera visit frequency was performed on pooled data from video recordings for both subspecies. The data was square root transformed for normal distribution. For further pair-wise comparisons

*post-hoc* LSD Fisher’s tests were performed for total insects and Diptera. For insects from other orders (Coleoptera and Hymenoptera) pair-wise comparisons (2000 vs. 2002, male vs. female, *sphondylium* vs. *sibiricum*) were performed using Mann-Whitney *U* test.

All statistical calculations were performed using STATISTICA 7.1 (Stat Soft Inc. 2005) run on a PC computer.

## **Results**

During two seasons of field observations more than 108 insect taxa visited umbels of the studied subspecies of *Heracleum sphondylium*. The insects represented seven taxonomic orders: Diptera, Coleoptera, Heteroptera, Hymenoptera, Lepidoptera, Mecoptera and Neuroptera (Table 1). The analyses of pollinator importance covered 3404 insects, including 1507 captured individuals for which analyses of pollen loads were performed.

### ***Insect visitors***

The most frequent insect visitors to flowers of *H. sphondylium* subsp. *sphondylium* and *H. sphondylium* subsp. *sibiricum* were dipterans (mostly Musidae and Syrphidae) and coleopterans (mostly Cerambycidae, Melyridae and Nitidulidae), and the least frequent were butterflies, neuropterans and mecopterans (only a few visits during the study period). Although this pattern was a general rule, the detailed composition of the entomofauna varied greatly between years, subspecies and sexual phases of the flowers (Fig. 1). Usually the proportion of dipteran visits much exceeded 50%, e.g. in 2000 they constituted 76% and in 2002 84% of the visits to the pistillate phase of flowers of subsp. *sphondylium*. However in 2002 almost 64% visits to staminate phase flowers of subsp. *sphondylium* were from coleopterans. The same group was also abundant (44%) during the pistillate phase of subsp. *sibiricum* in 2000. Despite of their frequency, as a taxonomic group, coleopterans were not the most efficient

**Table 1.** Insect visitors to flowers of *Heracleum sphondylium* subsp. *sphondylium* and *H. sphondylium* subsp. *sibiricum* in Wigierski National Park, NE Poland. The table contains taxa observed and captured during, and apart of, the study hours in years 2000 and 2002. Members of some families were not identified to the species level. An asterisk denotes taxa noted exclusively on the male phase umbels

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**Diptera** – **Anthomyiidae**; **Asilidae**: *Andrenosoma atra* (L.)\*; **Bombyliidae**: *Villa hottentotta* (L.)\*; **Calliphoridae**: *Calliphora vomitoria* (L.), *Lucilia caesar* (L.), *L. illustris* (Meig.); **Chloropidae**; **Conopidae**: *Conops quadrifasciatus* (Deg.)\*; **Culicidae**; **Empididae**: *Euempis tessellata* Fabr.; **Fanniidae**: *Fannia armata* (Meig.), other *Fannia* (R.-D.); **Muscidae**: *Graphomya maculata* (Scop.), *Morellia aenescens* (R.-D.), *Phaonia angelicae* (Scop.), other *Phaonia* (R.-D.), *Thricops nigrifrons* (R.-D.); **Sarcophagidae**: *Sarcophaga carnaria* (L.); **Sepsidae**; **Stratiomyidae**: *Chloromyia formosa* (Scop.)\*, *Odontomyia hydroleon* (L.)\*; **Syrphidae**: *Cheilosia honesta* (Rodani), *Ch. melanopa* (Zett.), *Ch. scutellata* (Fall.), *Ch. pilifera* Beck, other *Cheilosia* Meig., *Episyrphus balteatus* (De Geer), *E. cinctellus* (Zett.), *Eriozona syrphoides* (Fall.), *Eristalis arbustorum* (L.)\*, *E. horticola* (De Geer)\*, *E. pertinax* (Scop.), *Helophilus pendulus* (L.)\*, *Ischyrosyrphus glaucius* (L.), *Melanostoma mellinum* (L.), *Metasyrphus corollae* (Fabr.), *M. lapponicus* (Zett.), *Myatropa florea* (L.)\*, *Parasyrphus lineola* (Zett.), *P. vittiger* (Zett.)\*, *Sphaerophoria menthastri* (L.), *S. scripta* (L.), *Syritta pipiens* (L.)\*, *Syrphus ribesii* (L.), *Volucella pellucens* (L.), other *Syrphidae*; **Tabanidae**: *Tabanus bovinus* (L.)\*; **Tachinidae**: *Actia lamma* Meig.\*, *Ernestia rudis* (Fall.), *Eurithia anthophila* (R.-D.), *E. consobrina* (Meig.), *Hyalurgus lucidus* Meig.\*, *Phasia hemiptera* (Fabr.)\*; other **Diptera**.

**Coleoptera** – **Cantharidae**: *Rhagonycha fulva* (Scop.); **Cerambycidae**: *Dinoptera collaris* (L.)\*, *Leptura maculata* (Poda)\*, *Stenurella bifasciata* (O.F. Müller), *S. melanura* (Vill.); **Cleridae**: *Trichodes apiarus* (L.)\*; **Coccinellidae**: *Coccinella septempunctata* (L.)\*; **Melyridae**: *Dasytes* (Paykull); **Mordellidae**: *Mordellistena* (Costa); **Nitidulidae**: *Cychramus luteus* (Fabr.), *Meligethes* (Steph.); **Oedemeridae**: *Chrysanthia viridissima* (L.)\*; **Scarabaeidae**: *Cetonia aurata* (L.)\*.

**Hymenoptera** – **Andrenidae**: *Andrena minutula* (Kirby), *A. rosae* Panz.; **Apidae**: *B. ruderarius* (Müller)\*, *Bombus terrestris* (L.); other **Apoidea**; **Argidae**: *Arge ochropus* (Gmelin), *A. ustulata* (L.); **Cimbicidae**: *Cimbex Olivier*\*; **Colletidae**: *Hylaeus communis* (Nylander), *H. confusus* (Nylander); **Eumenidae**: *Eumenes coronatus* (Panz.), *E. pedunculatus* (Panzer), *Symmorphus mutinense* (Baldini); **Halictidae**: *Lasioglossum calceatum* (Scop.); **Ichneumonidae**; **Mellitidae**: *Macropis fulvipes* (L.)\*; other **Phytophaga**; **Sphecidae**: *Crabro cribarius* (L.), *Crossocerus assimilis* (Smith), *C. wesmaeli* (V.d.Lind.), *Ectemnius lapidarius* (Panz.); **Vespidae**: *Dolichovespula sylvestris* (Scop.), *Vespa crabro* (L.); other **Vespoidea**.

**Lepidoptera** – **Geometridae**; **Nymphalidae**: *Araschnia levana* (L.), *Argynnis paphia* (L.), *Erebia medusa* (Denis & Schiff.)\*; **Papilionidae**: *Papilio machaon* (L.)\*; **Pieridae**: *Gonepteryx rhamni* (L.)\*, *Pieris brassicae* (L.)\*; **Pterophoridae**; **Zygaenidae**: *Zygaena filipendulae* (L.)\*, *Z. trifolii* (Esper)\*.

**Heteroptera** – **Miridae**: *Calocoris affinis* (Herrich-Schaff.), *Miris striatus* (L.), *Orthops calmi* (L.); **Pentatomidae**: *Palomena viridissima* (Poda)\*, other **Pentatomidae**\*.

**Mecoptera** – **Panorpidae**: *Panorpa communis* (L.)\*.

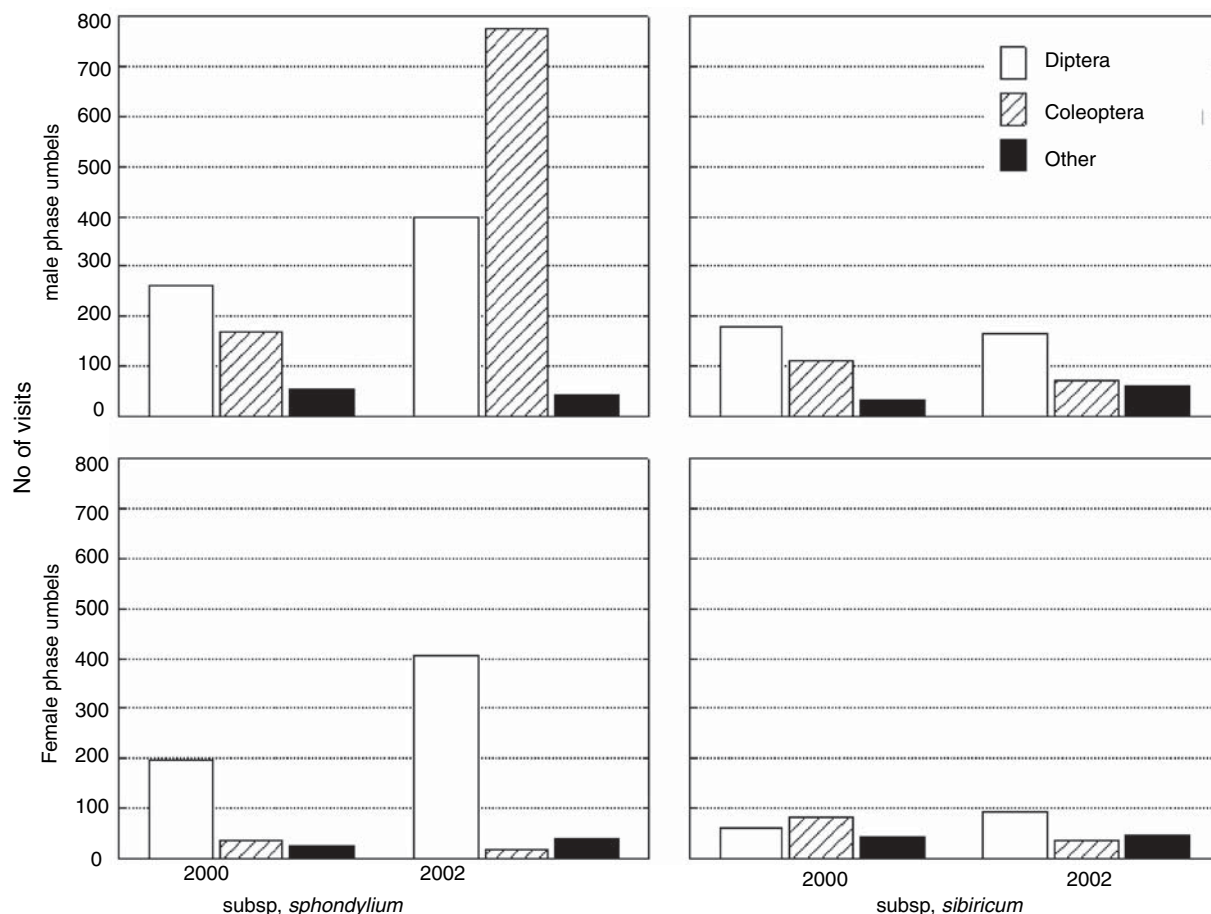
**Neuroptera** – **Chrysopidae**: *Chrysopa pallens* (Rambur)\*.

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pollinators because most of the visits were performed by individuals of the genera *Meligethes* (Nitidulidae, as much as 55% of all visits to the staminate phase of subsp. *sphondylium* in 2002) and *Dasytes* (Melyridae), which carried no pollen at all or just few pollen grains of *H. sphondylium* (Table 2). Generally 40–50% insect taxa observed on

both subspecies of *H. sphondylium* visited their flowers only occasionally (fewer than five visits, summed video and capture data). In 2000 the number of rare visitors reached 70% for pistillate phase flowers of subsp. *sibiricum*.

As well as *Meligethes* and *Dasytes*, in both seasons flies *Thricops nigrifrons* (Muscidae)



**Fig. 1.** Number of visits by insects from different orders during two days of observations of flowers of two subspecies of *Heracleum sphondylium* (subsp. *sphondylium* and subsp. *sibiricum*) in the years 2000 and 2002 (summed data for video recordings and capturing; for visit count see Material and methods). ‘Other’ denote summed data for Hymenoptera, Lepidoptera, Heteroptera and Neuroptera

were abundant (usually approx. 15% of all visits). In the case of *H. sphondylium* subsp. *sphondylium* a considerable number of visits (9–17%) were performed by small dipterans of the family Sepsidae, mostly of the genus *Sepsis* (Table 2). These insects carried no *H. sphondylium* pollen but exhibited very striking behaviour – they usually chased much larger insects (e.g. individuals of *T. nigrifrons*, *Lucilia* spp. or even *Sarcophaga carnaria*) off the umbels (details of insect behaviour on umbels of *H. sphondylium* will be the subject of a separate publication).

Some insect taxa (e.g. *Helophilus pendulus* and *Leptura maculata*) were observed only on

male stage umbels (Table 1), they constituted over 32% of total entomofauna.

#### **Frequency of visits and insect preferences**

Insects visited umbels of *H. sphondylium* with the overall mean frequency of approx.  $10 \pm 10.6$  visits per census (10 min.; mean  $\pm$  SD). The detailed analyses showed considerable differences among the two subspecies, study years and umbel sexual phases. The lowest frequency, approx.  $4 \pm 3.3$  visits/ census (mean  $\pm$  SD), was observed in 2002 for female phase umbels of *H. sphondylium* subsp. *sibiricum* and the highest, over  $23 \pm$

**Table 2.** Number of insect visits on flowers of two subspecies of *Heracleum sphondylium* during study periods in 2000 and 2002 (*V* – video recordings and captured insects, summed data), and the average pollen load (*PL*) carried by an individual showed in a relative scale<sup>a</sup> \*\*\* > \*\* > \* > t (trace) > - no pollen, x no data, *M* – male (staminate) phase umbels, *F* – female (pistillate) phase umbels. The table shows only frequently encountered insect taxa (at least 10% of the total number of visits) or large pollen loads carriers (on average more than 1000 pollen grains) in any of the studied years, *H. sphondylium* subspecies or umbel sexual phases

	2000								2002							
	subsp. <i>sphondylium</i>				subsp. <i>sibiricum</i>				subsp. <i>sphondylium</i>				subsp. <i>sibiricum</i>			
	M		F		M		F		M		F		M		F	
	V	PL	V	PL	V	PL	V	PL	V	PL	V	PL	V	PL	V	PL
<b>Diptera</b>																
<i>Eriozona syrphoides</i> (Fall.)	6	**	14	**	19	***	5	***	15	**	42	***	16	**	10	**
<i>Lucilia</i> (R.-D.) <sup>b</sup>	7	*	17	**	5	*	13	**	11	*	55	**	12	**	23	*
Sepsidae	70	-	57	-					33	t	124	t				
<i>Thricops nigrifrons</i> (R.-D.)	94	*	46	**	127	*	11	t	148	*	57	**	70	*	15	*
<b>Coleoptera</b>																
<i>Dasytes</i> (Paykull)	51	*	18	t	80	t	66	t	79	t	3	x	42	t	17	t
<i>Meligethes</i> (Steph.)	100	t	15	-	29	-	17	*	664	t	12	-	26	t	18	-
<i>Stenurella</i> (Vill.) <sup>c</sup>	15	***	2	***					23	*	3	x				
<b>Hymenoptera</b>																
Apoidea <sup>d</sup>	14	***	1	-			3	t	9	x					4	*
<i>Arge</i> (Schrank) <sup>e</sup>	3	**									2	***			2	t
<i>Bombus terrestris</i> (L.)	8	**	4	***	3	***	3	**					1	**		
<b>Heteroptera</b>																
Miridae <sup>f</sup>	13	t	10	t	19	t	23	t	18	t	18	*	44	t	27	*
<b>Other</b>	103		75		41		46		217		147		87		58	
<b>Total</b>	484		259		323		187		1217		463		298		174	

<sup>a</sup>t (trace) – 1-10 pollen grains, \* 11-100, \*\* 101-1000, \*\*\* > 1000.

<sup>b</sup>including *L. caesar* (L.), *L. illustris* (Meig.).

<sup>c</sup>including *S. bifasciata* (O.F. Müller) and *S. melanura*. (viu.)

<sup>d</sup>including *Lasioglossum calceatum* (Scop.), *Hylaeus communis* (Nylander), *H. confusus* (Nylander), *Andrena minutula* (Kirby).

<sup>e</sup>including *A. ochropus* (Gmelin), *A. ustulata* (L.).

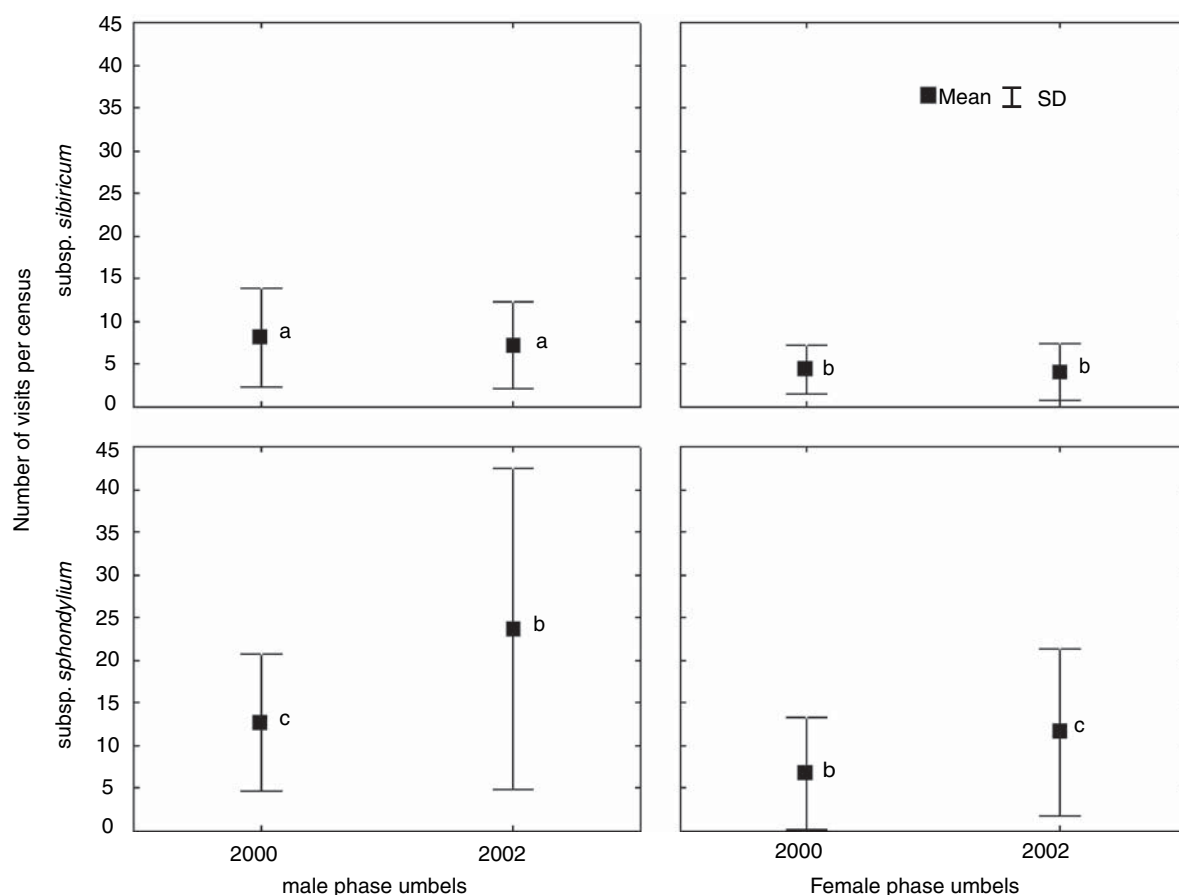
<sup>f</sup>including *Calocoris affinis* (Herrich-Schaff.), *Miris striatus* (L.), *Orthops kalmi* (L.).

18.8 visits/ census (mean  $\pm$  SD), in the same year for male phase umbels of *H. sphondylium* subsp. *sphondylium* (Fig. 2). Three-way ANOVA performed on pooled data showed that study year ( $P < 0.02$ ), sexual phase of the umbels ( $P \ll 0.001$ ) and population (subspecies) ( $P \ll 0.001$ ) each had significant direct

effects on the frequency of visit of total insects. The analysis showed also a study year  $\times$  subspecies effect (Table 3).

In both study years and sexual phases (except female phase umbels in 2000) umbels of *H. sphondylium* subsp. *sphondylium* were visited more frequently than inflorescences of





**Fig. 2.** Mean frequency (and SD) of total insects visits to two umbel sexual phases of *H. sphondylium* subsp. *sphondylium* and *H. sphondylium* subsp. *sibiricum* over two year study. Means with different letter are different at  $p < 0.05$  (LSD Fisher's *post-hoc* test, only means of the same umbel sexual phase of particular subspecies were compared across study years)

subsp. *sibiricum*. In case of both subspecies over two years, insects preferred male phase umbels over female phase umbels which were visited significantly less frequently (LSD Fisher *post-hoc* tests for total insects: in both years  $P < 0.05$  for subsp. *sibiricum* and  $P < 0.005$  for subsp. *sphondylium*). For *H. sphondylium* subsp. *sphondylium* the frequency of visits to either male or female phase umbels was higher in 2002 when compared with year 2000 (LSD Fisher *post-hoc* tests for total insects:  $P < 0.001$  for male phase umbels and  $P < 0.02$  for female phase umbels) (Fig. 2).

The same factors, except study year  $\times$  subspecies interaction, influenced the visitation frequency of Diptera (three-way ANO-

VA on pooled data: year  $P < 0.03$ , umbel sexual phase  $P < 0.003$ , subspecies  $P \ll 0.001$ , Table 3). Similarly to the results for total insects, female phase umbels of subsp. *sphondylium* were visited more frequently by dipterans than those of subsp. *sibiricum* (for 2000  $P < 0.05$  and for 2002  $P < 0.001$ ; *post-hoc* LSD Fisher's tests), in case of male phase umbels I recorded significant differences only in 2002 ( $P < 0.001$ , *post-hoc* LSD Fisher's tests). Consider preferences toward sexual phases of the umbels, significantly higher frequency of visits of Diptera to male phase umbels was observed only for subsp. *sibiricum* in 2000 (*post-hoc* LSD Fisher's test,  $P < 0.05$ ). In 2002 female phase umbels of subsp.

**Table 3.** Results of three-way ANOVA on square root frequency of visits of total insects and Diptera to umbels of *H. sphondylium*. ‘Year’ denote the effect of study year (2000–2002), ‘Sex’ the effect of the umbel sexual phase and ‘Subsp’ the effect of two studied subspecies, *H. s.* subsp. *sphondylium* and *H. s.* subsp. *sibiricum*

Source	SS	df	MS	F	p
<b>Total insects</b>					
Year	8,5238	1	8,52379	6,39152	0,012308*
Sex	47,0652	1	47,06516	35,29159	0,000000***
Subsp	55,1996	1	55,19963	41,39119	0,000000***
Year*Sex	0,5359	1	0,53594	0,40187	0,526911
Year*Subsp	16,1825	1	16,18255	12,13441	0,000619***
Sex*Subsp	4,3312	1	4,33121	3,24774	0,073159
Year*Sex*Subsp	0,5566	1	0,55663	0,41739	0,519049
Error	245,3839	184	1,33361		
<b>Diptera</b>					
Year	8,6618	1	8,66185	5,34998	0,021829*
Sex	14,8013	1	14,80130	9,14201	0,002855**
Subsp	60,1893	1	60,18926	37,17583	0,000000***
Year*Sex	2,2647	1	2,26474	1,39881	0,238448
Year*Subsp	6,1309	1	6,13087	3,78672	0,053184
Sex*Subsp	1,5244	1	1,52438	0,94153	0,333158
Year*Sex*Subsp	0,0000	1	0,00000	0,00000	1,000000
Error	297,9039	184	1,61904		

*sphondylium* were visited by these insects more frequently than in 2000 ( $P < 0.01$ , *post-hoc* LSD Fisher’s test).

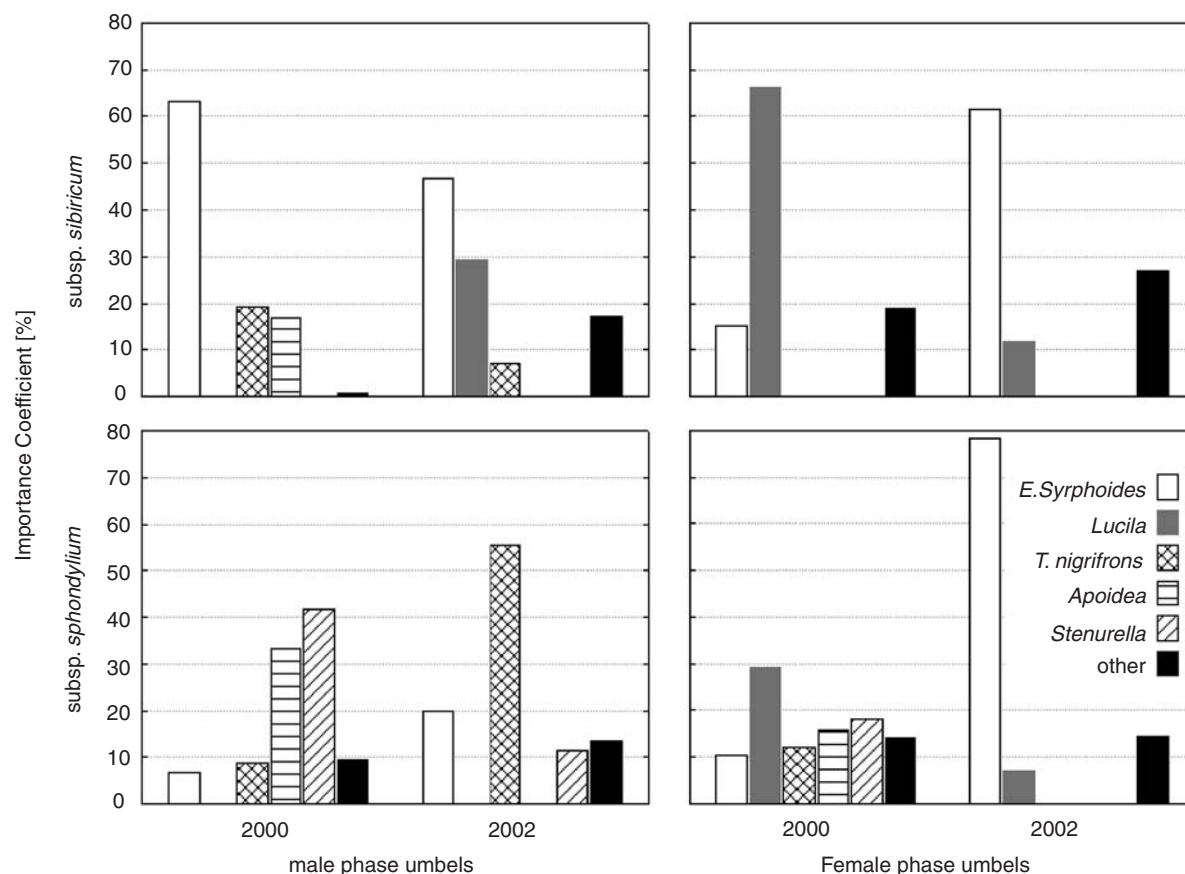
Due to the small number of recorded visits it was impossible to perform similar analyses for other insect orders. However pair comparisons showed that in case of subsp. *sphondylium* over both study years male phase umbels were visited more frequently also by Coleoptera (Mann-Whitney *U*-tests: in both years  $P \ll 0.001$ ). In 2002 these insects were especially abundant on male phase umbels of subsp. *sphondylium* (visit frequency significantly higher than in 2000 on the same subspecies, Mann-Whitney *U*-tests:  $P < 0.01$ ). In 2002 they also preferred male phase umbels of subsp. *sphondylium* over male phase umbels of subsp. *sibiricum* (Mann-Whitney *U*-tests:  $P \ll 0.001$ ). No such relationship was found for Hymenoptera (see Appendix 1 for statistical results of pair comparisons for Coleoptera and Hymenoptera).

### **Pollen loads**

Analysis of the pollen loads showed that for both *H. sphondylium* subspecies approximately half the taxa carried no *H. sphondylium* pollen grains or just trace quantities of pollen (fewer than 10 pollen grains). In 2000 for the male phase flowers of subsp. *sibiricum*, this proportion reached 75%. The largest pollen loads (on average more than 1000 pollen grains) were carried by individuals of *Bombus terrestris* (Apidae), *Stenurella* spp. (Cerambycidae), *Eriozona syrphoides* (Syrphidae), and *Arge* spp. (Argidae) (Table 2). Detailed data on the insects visits, within-umbel activity, and pollen loads are available from the author upon individual request.

### **Pollinator importance**

The Pollinator Importance Coefficients (ICs) calculated for pollen carriers exhibited considerable differences between seasons, sexual



**Fig. 3.** Values of pollinator IC (Importance Coefficient, for formula see: Material and methods) for important flower visitors of two subspecies of *Heracleum sphondylium* (only taxa with IC < 20% in at least one season were shown)

phases of umbels, and subspecies of *H. sphondylium* (Fig. 3).

In all cases the most important flower pollinators from among over a hundred taxa of flower visitors were the dipterans *Eriozona syrphoides*, *Lucilia* spp., *Phaonia angelicae*, *Thricops nigrifrons*, beetles of the genus *Stenurella*, and, less frequently, bumblebees (*B. terrestris*) or other hymenopterans. The insects encountered on umbels of *H. sphondylium* most often – coleopterans of the genera *Meligethes* and *Dasytes*, on both subspecies, and sepsid flies on subsp. *sphondylium* – did not play a significant role in pollination in either pollen collection in the male phase or pollen deposition on the stigmas of flowers in the pistillate phase. The activity of certain

groups, e.g. many syrphid flies *Helophilus pendulus*, *Syrphus ribesii*, *Ischyrosyrphus glaucius*, or bees (Apoidea) other than *B. terrestris* was largely restricted to the male phase. They were not present during the female phase of the umbels or appeared only sporadically.

On the basis of the IC for male and female phases, a hoverfly *Eriozona syrphoides* is the most constant pollinator of both studied subspecies of *H. sphondylium*. Individuals of this species were present in both study years and visited flowers in both staminate and pistillate phases. However its importance, either as pollen collector or depositor, varies considerably – on the male phase from 7% on subsp. *sphondylium* in 2000 to over 63% in the same year on subsp. *sibiricum*, and on the female

phase from approx. 10% on subsp. *sphondylium* in 2000 to almost 80% in 2002 on the same taxon. Calliphorid flies of the genus *Lucilia* were the second most important pollinators. Although together with *E. syrphoides* they perform approx. 2–21% of all insect visits (depending on subspecies, study year and umbel sexual phase; Table 2), both taxa were usually responsible for over 70% of pollination of both studied subspecies of *H. sphondylium*.

Although subsp. *sphondylium* and subsp. *sibiricum* are pollinated by similar groups of insects, the pollinator spectrum of the former is more diversified, while the latter is pollinated almost solely by dipterans. In 2000, apart from *E. syrphoides* and *Lucilia* spp., important pollinators of subsp. *sphondylium* were beetles of the genus *Stenurella* (IC=18%) and bumblebees (IC=16%). The former did not visit umbels of subsp. *sibiricum* in the study years at all (Table 2). On the other hand the syrphid fly *Volucella pellucens*, which is quite a constant pollinator of subsp. *sibiricum* (IC approx. 20% in

successive years) is scarcely present on flowers of the nominative taxon.

Among the insect taxa for which I coefficient could be calculated only 10 can be rated as the ‘key pollinators’ ( $I_{\text{female}}/I_{\text{male}} > 0$  and  $IC_{\text{female}} > 1\%$ ), however only two of them, *E. syrphoides* and *Lucilia* spp., were active and important pollinators in either year and subspecies (Table 4).

## Discussion

Flowers of *Heracleum sphondylium*, visited by over 100 insect species, are effectively pollinated by only a few taxa of mainly medium-sized flies. However the efficiency of key pollinators may be subject to considerable variations from year to year. In both subspecies of *H. sphondylium*, the most important pollinators were the medium-sized dipterans *E. syrphoides* (Syrphidae) and *Lucilia* spp. (Calliphoridae), which performed 2–21% of visits and were usually responsible for more than 70% pollinations (Fig. 3, Table 2). These

**Table 4.** List of the key pollinators of the two subspecies of *Heracleum sphondylium*. Included are only insects with  $I_{\text{female}}/I_{\text{male}} > 0$  and  $IC_{\text{female}} > 1\%$  in either of the studied subspecies or study years, x – no data. For details on I and IC calculation see Material and methods

	<i>H. sphondylium</i> subsp. <i>sibiricum</i>				<i>H. sphondylium</i> subsp. <i>sphondylium</i>			
	2000		2002		2000		2002	
	$I_{\text{female}}/I_{\text{male}}$	$IC_{\text{female}}$	$I_{\text{female}}/I_{\text{male}}$	$IC_{\text{female}}$	$I_{\text{female}}/I_{\text{male}}$	$IC_{\text{female}}$	$I_{\text{female}}/I_{\text{male}}$	$IC_{\text{female}}$
<b>Diptera</b>								
<i>Eriozona syrphoides</i>	0.21	15.1%	1.09	61.4%	1.94	10.5%	167.07	78.4%
<i>Eristalis</i> spp.	x	0.1%	x	x	x	2.3%	2594.01	3.5%
<i>Lucilia</i> spp.	150.6	66.1%	0.34	11.8%	38.81	29.3%	802.77	7.1%
<i>Meliscaeva cinctella</i>	x	x	118.60	1.2%	x	x	97.51	0.1%
<i>Phaonia angelicae</i>	x	0.1%	x	x	0.53	1.4%	86.82	6.2%
<i>Thricops nigrifrons</i>	0.01	0.2%	0.49	4.1%	1.76	12.0%	2.17	2.9%
<i>Volucella pellucens</i>	x	13.1%	73.79	19.2%	x	x	x	x
<b>Coleoptera</b>								
<i>Dasytes</i> spp.	8.76	1.4%	0.70	0.2%	0.16	0.1%	x	x
<i>Stenurella</i> spp.	x	x	x	x	0.55	18.3%	x	x
<b>Hymenoptera</b>								
<i>Bombus terrestris</i>	0.16	2.9%	x	x	8.61	15.7%	x	x

two may undoubtedly be rated as the 'key' pollinators. Muscid flies *T. nigrifrons* and *P. angelicae*, syrphid fly *V. pellucens*, beetles of the genera *Stenurella* and *Dasytes*, and bumblebees *B. terrestris* also contributed to the pollination of the studied plants, however their activity was less constant and were usually restricted to either one of the subspecies or one of the two seasons (Tables 2 and 4).

All of these insect taxa have already been observed on the flowers of *H. sphondylium* (Knuth 1898, Corbet 1970, Grace and Nelson 1981, Zych 2002) and, except for *E. syrphoides*, appear to be pollinators of its flowers throughout the species geographic range. The case of *E. syrphoides* is more complex. The first record of this species on flowers of *H. sphondylium* was that of Zych (2002) and was restricted to the same study site. The possible explanation is that the present study site was a wooded region while the earlier workers conducted observations in open habitats. *Eriozona syrphoides* is usually regarded as a woodland species and is generally described as rather rare (Bańkowska 1963). This suggests that although locally *H. sphondylium* may be characterised by a rather constant set of pollinators, the group of pollinators may change in different geographic/habitat conditions, a situation observed also for other Apiaceae, e.g. *D. carota* (Lamborn and Ollerton 2000, and lit. cit.), and plants from other families, e.g. *Lavandula latifolia* (Lamiaceae), where pollination system was highly generalised at the regional level, but differed considerably on the level of populations or even separate plants (Herrera 2005).

In such situations a problem with nomenclature arises because for many decades, plant pollination systems were seen as belonging to two separate groups: specialised or generalised, while in fact they span the whole continuum of possibilities (Waser et al. 1996, Ollerton 1996, Johnson and Steiner 2000). If we assume that a plant specialises if it is successfully pollinated by only a subset of potential visitors (Fenster et al. 2004), then specialisation is quite common even in plant groups which, like *H. sphondylium*, do

not exhibit very specialised flower architecture. However, in such situations, we have to be able to distinguish between ecological and evolutionary specialisation, for which a reference point, a (phylogenetically) sister group or population, is necessary (Fenster et al. 2004). In such situation in case of *H. sphondylium* we can probably trace both forms of specialisation: the plant specialises on a functional group of pollinators (medium-sized flies) and taxa that seem to be derived ('yellow-green-flowered' subspecies of *H. sphondylium*, e.g. *H. sphondylium* subsp. *sibiricum*; Zych unpubl.) seem to have narrower spectrum of the key pollinators, which suggests also evolutionary specialisation. This is in contrast with the traditional view of umbellifers which, from the beginning of the modern studies of pollination systems, have been rather regarded as promiscuous (*sensu* Grant 1949) in terms of pollination biology (Bell 1971; Faegri and van der Pijl 1979; Ellis and Ellis-Adam 1993, 1994; Proctor et al. 1996; Corbet 2006). This was due to the open flowers with exposed nectar-secreting stylopodium and floral sexual parts and the large diversity of flowers visitors observed on the flowers of various umbelliferean taxa.

The first papers with arguments in favour of specialised pollination biology of Apiaceae appeared about three decades ago (Bell 1971, Bell and Lindsey 1978). Since then only a few authors have conducted detailed studies of pollination systems of various umbelliferean species (Grace and Nelson 1981; Lindsey 1984; Lindsey and Bell 1985; Koul et al. 1986, 1989; Lamborn and Ollerton 2000; Zych 2002; Rovira et al. 2004). The most complete data refer to the American protogynous genera *Thaspium* and *Zizia* (Lindsey 1984, Lindsey and Bell 1985) and to the protandrous cosmopolitan *Daucus carota* (Lamborn and Ollerton 2000). The remaining studies are either restricted to short term observations (Corbet 1970, Grace and Nelson 1981, Zych 2002) and/or their statistical analysis is somewhat unclear (Koul et al. 1986, 1989). Although quite diversified, most of the above works present one general conclusion: only small portion of

the large number of the Apiaceae flower visitors are effective pollinators. This finding is also confirmed by the present study.

It is interesting why such plants do not exhibit any specialised floral morphology to better fit the pollinators involved. Perhaps in case of *H. sphondylium* the lack of more specialised floral characters may be the result of the various evolutionary constraints which do not allow new and more ‘elaborated’ floral forms to evolve (Ollerton 1996, Johnson and Steiner 2000). This explanation has already been presented for Apiaceae (Bell 1971). The other reason for the stability of this kind of pollination system may be the long term advantages of a more generalist strategy. Even though as suggested by theoretical models (Waser et al. 1996), plant specialisation towards the most frequent flower visitors is advantageous in terms of reproductive success, it is less likely to occur if the given pollinator populations are subject to considerable fluctuations in abundance among successive seasons, as shown for *D. carota*, where in some populations in successive years the group of the key pollinators changed from beetles (*Rhagozycha fulva*) to sawflies (*Tenthredo* sp.) and syrphid flies (Lamborn and Ollerton 2000). The specialisation is even less likely to occur because of the wide distribution of the plant species which, due to the gene exchange among populations, may balance various selective forces operating on local or even individual-plant level (as shown for *L. latifolia*, Herrera 2005). This kind of more generalist strategy could therefore be stable in terms of the reproductive success of local populations where there are pollinator population fluctuations, but it also allows colonisation of new regions, where plants with more specialised pollination systems may suffer pollination decline. Subspecies of *H. sphondylium* described in the present study are probably good examples of such a system and earlier suggestions of their ‘local’ (ecological) specialisation (Zych 2002), although based on observation of the male phase of the umbels, were correct. This kind of “facultative” generalist pollina-

tion system is probably the most common reproductive strategy among angiosperms (Waser et al. 1996, Pellmyr 2002), especially among short-lived species, which in terms of reproduction rely solely on production of seeds (Bond 1994, Lamborn and Ollerton 2000), and among plant species with wide geographic distributions from, for example, European and North American floras, which in their history colonised post-glacial landscapes and now spread in modern agricultural-urban mosaics (Johnson and Steiner 2000). So far such opportunistic pollination systems have been described for example for some species of the genus *Asclepias* (Woodson 1954, Ivey et al. 2003), and for the moth-pollinated *Silene vulgaris* (Pettersson 1991).

The case of the two, morphologically different, subspecies of *H. sphondylium* also shows that the flower characteristics may not necessarily reflect actual relationships between the plant and its pollinators. As in the case of the darker central floret in *D. carota* umbels (Darwin 1888, Lamborn and Ollerton 2000), the flower colours of *H. sphondylium* subspecies are no longer functional in attracting different pollinators. Although subsp. *sphondylium* is more attractive for insects and is pollinated by a slightly larger assemblage of insect taxa, the very key pollinators remain almost constant. This confirms the opinion of many authors (Fishbein and Venable 1996, Herrera 1996, Waser et al. 1996, Ollerton 1998, Johnson and Steiner 2000, Lamborn and Ollerton 2000, Pellmyr 2002, Zych 2002, Ivey et al. 2003) on the concept of pollination syndromes (Faegri and van der Pijl 1979), application of which in some cases may obscure the view rather than give useful explanations. A little explanation on the phenomenon of the occurrence of two colour forms may perhaps be given by tracing the phylogeny of these taxa and studying their life strategies. Most of the ‘white-flowered’ taxa are mountain forms, and ‘greenish-yellow’ are distributed at lower elevations towards the eastern part of the species range (Brummitt 1968; Gawłowska 1956, 1961;

Zych 2003). Perhaps due to stronger competition for scarce pollinators in high elevations (Arroyo et al. 1982, Bingham and Orthner 1998) such showy floral displays as that of subsp. *sphondylium* were advantageous in terms of attracting pollinators – mostly bumblebees and flies, while in lowlands (covered by more dense vegetation) the dull umbels were attractive for beetles. This hypothesis is supported by phylogeny which suggests mountain origin of the genus and ‘greenish-yellow’ displays as derived floral character (Zych 2003, Zych unpubl.).

The present work reports another interesting observation. From my analysis it is evident that in general floral visitors preferred the staminate phase of umbels of both studied subspecies of *H. sphondylium*, and almost one-third of insect taxa encountered on *H. sphondylium* umbels visited exclusively male phase inflorescences. This preference is especially noteworthy for Diptera (mainly some syrphid flies), as in most studies of pollination biology of umbellifers show their importance as pollinators (Corbet 1970; Grace and Nelson 1981; Koul et al. 1986, 1992, 1989; Ellis and Ellis-Adam 1993; d’Albore cited in Bouwmeester and Smid 1995; Lamborn and Ollerton 2000; Schlessman and Graceffa 2002; Zych 2002; Rovira et al. 2004). Similar preferences of some dipterans (e.g. *Helophilus pendulus*) for pollen-presenting inflorescences were also reported by Larsson (2005) for unspecialised *Knautia arvensis* (Dipsacaceae), which is visited by specialist bee *Andrena hattorfiana*, but pollinated mainly by generalist flower visitors. Larsson (2005) analysed pollinator activities and effectiveness of flower visitors and showed that although specialist *A. hattorfiana* removes and deposits more pollen per visit than any other insect, the females of *A. hattorfiana* have very strong preferences towards pollen-presenting inflorescences that they contribute very little to overall pollen transfer in *K. arvensis*. In fact most of insects observed by Larsson (2005) showed similar inclination, those which did not prefer male phase plants included some

bee species (‘other bees’ as termed by the author) and some dipterans (‘furry dipterans’).

Although discrimination of the sexual phases has already been observed in other angiosperm species and usually referred to the male (staminate) phase (Goulson 1999, and lit. cited), this phenomenon seems largely underestimated and therefore usually unstudied element of the pollination systems. For Apiaceae for instance some indirect evidence of this phenomenon was presented by Lindsey and Bell (1985), and Langenberger and Davis (2002b), and the only thorough experimental evidence for this phenomenon in the Apiaceae, known to the author of the present paper, was presented by Schlessman et al. (2004), who showed that female stage umbels of North American protogynous *Pseudocymopterus montanus* are significantly less attractive for insect visitors.

Most of the available literature on Apiaceae, either that containing solely lists of potential pollinators (Knuth 1898; Drabble and Drabble 1917, 1927; Corbet 1970; Warakomska et al. 1986; Sheppard 1991; Proctor et al. 1996; Schlessman and Graceffa 2002) or more detailed analyses of insect importance (Grace and Nelson 1981; Lindsey 1984; Koul et al. 1986, 1993, 1989; Bouwmeester and Smid 1995; Lamborn and Ollerton 2000; Rovira et al. 2004), except the study by Zych (2002), who observed the staminate phase umbels of *H. sphondylium*, lack even information on the sexual phases of the studied plants. Webb’s (1984) research on pollinators of South American *Myrrhidendron donnellsmithii* (bumblebees, Coletidae bees and three syrphid flies) for example contains the information that “all of these visitors were observed to touch stigmas and dehiscid anthers while foraging for nectar and pollen.” This observation however is not supported by more detailed analyses of the insects importance, similarly to the study of Schlessman et al. (2004), who noted only insect visits and did not focus on whether these were certain taxa that avoided female phase or the insect visitors were taxonomically the same but

less abundant. Of course this may be relatively unimportant in taxa with overlapping sexual phases, but seems of great importance regarding plants characterised by the “temporal dioecism” (Cruden and Hermann-Parker 1977), called by Schlessman et al. (1990) “multicycle protandry”, where there are at least two reasons why it should be studied more carefully. The first is evolutionary and concerns the reproductive success of the given sexual phase (Goulson 1999). This is especially interesting in the case of umbellifers in the light of many studies describing “overproduction” of male flowers (Bell 1971; Lovett Doust 1980a, 1980b; Lovett Doust and Harper 1980; Webb 1984; Warakomska et al. 1982, 1983, 1986; Lindsey and Bell 1985, Wróblewska 1992, Koul et al. 1993, Spalik and Woodell 1994, Schlessman and Graceffa 2002, Zych 2003) and information that the seed production is not pollinator-limited (Bell and Lindsey 1978). Both elements are usually connected with the sexual selection mechanisms (Stephenson and Bertin 1983, Andersson and Iwasa 1996). The second reason is more practical and refers to the problem of pollination of certain economic or rare plants. If we consider that some pollinator species, such as many flies, bees and beetles in the present study, visit only the staminate phase of dichogamous flowers, it is likely that they do not contribute to seed set at all (or contribute very little) and have to be regarded poor (“ugly” *sensu* Thomson and Thomson 1992) pollinators (if not parasites) in spite of their abundance and large pollen loads. The question however arises: what kind of insect performance should be treated as ‘good’ pollination service? Perhaps, when pollinator importance coefficients are calculated for separated sexual phases, only insects that perform balanced services (e.g.  $I_{\text{female}}/I_{\text{male}} > 0$  or even equal 1) should be termed ‘pollinators’, while the key pollinators in the same time should also have  $IC_{\text{female}}$  at least greater than 1%. This is however very difficult to measure, especially for plants with the very wide array of potential pollinators, as *H. sphondylium* or other Apiaceae.

Among the works devoted to umbellifers conclusions on insect preferences for staminate or pistillate phase are to be found only in studies of Lindsey and Bell (1985) and Schlessman et al. (2004). In the first case of the protogynous *Thaspium barbinode* and *Zizia trifoliata* their main insect pollinator, *Andrena ziziae*, clearly preferred the staminate phase umbels of both species. Similar preferences were shown by syrphid flies, while other bees and wasps (Colletidae, Eumenidae and Sphecidae) were encountered more frequently on the pistillate phase of the umbels (Lindsey and Bell 1985). These observations however were conducted for a 36 hour period only.

A very carefully designed experimental study of Schlessman et al. (2004) showed that in the case of mountain parsley, *P. montanus*, there is a clear correlation between the sexual phase of the umbels and the number of visits – insects visited male stage umbels three times more frequently. The authors conclude that it may be explained by the lack of floral reward during the female phase (pistillate flowers of this plant do not produce pollen nor nectar), and the whole phenomenon involves some degree of flower deception. In protandrous Apiaceae however the nectar production pattern may be different. In *C. carvi* (Langenberger and Davis 2002), *C. sativum*, *D. carota* (P. Koul et al. 1989, 1993), Australian *Trachymene incisa* subsp. *incisa* (Davila and Wardle 2002) or *H. sphondylium* (Zych unpubl.) nectar is produced in either sexual phase, and it may be even more abundant in female stage flowers. Female stage flowers of *C. carvi*, for instance, produced approx. 70% of the total flower nectar volume (Langenberger and Davis 2002). It is explained as a compensation effect for the lack of pollen in the female phase flowers (Koul et al. 1993). However, as in *H. sphondylium*, it is probably still not enough for attracting some predominantly pollinivorous syrphid flies or pollen collecting bees, which visit only male stage umbels, and should not be counted as pollinators.



Probably similar results could be obtained for other umbellifers if more precise observations were conducted. This is especially the case with economic plants, where *a priori* the honey bee (*Apis mellifera*) is invoked as the principal pollinator (Buchmann and Nabhan 1996). To confirm this statement analyses of the insects' corbicula pollen are usually quoted, which in the opinion of many authors is not available for pollination (Parker 1981, Buchmann and Nabhan 1996). Studies of other non-umbelliferean plants suggest that the behaviour of honey bees is often influenced by the insects' preferences for a given sexual phase of the flowers (Goulson 1999, and literature cited). In the present study however I did not observe *A. mellifera* and it was not observed in earlier studies at the same study site (Zych 2002), but I could observe preferences in the other Apoidea and most of them (except e.g. *Bombus terrestris*) were, at least in case of *H. sphondylium* subsp. *sphondylium*, active mostly in the staminate phase (Fig. 3, Table 2). Studies of the economically important *Carum carvi* state that "honey bees collecting pollen represented 85–90% of all honey bees visiting caraway florets" (Langenberger and Davis 2002b), which suggests that only 10–15% of these insects are available for pollination service (however see Davila and Wardle (2002), who observed honey bees on either sexual phase of the umbels and concluded that they were the principal pollinators of *Trachymene incisa* subsp. *incisa*).

This means that studies of the pollination systems of many dichogamous plants, not only umbellifers, have to be carefully designed and in spite of decades of research there are factors influencing the pollination biology of angiosperms that we still know very little about. This is especially important for such 'cornucopia' species as *H. sphondylium* (Ellis and Ellis-Adam 1993, 1994) as they contribute enormously to the maintenance of the local insect biodiversity and

may be of a great conservation value (Corbet 2006).

All the above arguments confirm also that the pollination biology of Apiaceae is a more complex phenomenon than previously suggested. Undoubtedly these plants should not be regarded as 'promiscuous'. Considering their opportunistic strategies it is difficult however to support the opinion of some researchers (Bell 1971; Koul et al. 1989, 1993; Koul et al. 1986, 1989) of their high specialisation. The problem with more general opinion on this family, and others of similar biology, is the lack of appropriate terminology on the one hand which would embrace the whole continuum of possibilities, and on the rarity of long term studies, which should also embrace the spatial diversity of the species both geographically and in terms of habitat.

I would like to thank Wojciech Celary, Agnieszka Draber-Mońko, Anna Krzysztofiak, Ewa Skibińska, Piotr Tykarski and Waldemar Żyła for help in insect identification, and Wigry National Park for the possibility of conducting field research. Krzysztof Spalik made valuable comments during the lab work and on earlier drafts of the paper. I am also grateful to Mark Schlessman and Piotr Dawidowicz, and three anonymous reviewers for invaluable comments on the manuscript. Last but not least I thank my wife Iza for her understanding, help and company during field trips, and Hanna Werblan-Jakubiec for constant support.

**Appendix 1.** Results of statistical comparisons of the mean frequency of visits of Coleoptera and Hymenoptera to two umbel sexual phases of two *H. sphondylium* subspecies over two years (2000 and 2002). A Mann-Whitney *U*-test was performed for each pair ( $N=24$ ); 'sibiricum' and 'sphondylium' denote *H. sphondylium* subsp. *sibiricum* and *H. sphondylium* subsp. *sphondylium* respectively, *M* – male phase umbels, *F* – female phase umbels; *ns* – not significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.005$

## Appendix 1.

	Coleoptera		Hymenoptera	
	U	P	U	P
sibiricum F 2000 v. sibiricum F 2002	203.0	ns	265.0	ns
sibiricum F 2000 v. sphondylium F 2000	221.0	ns	259.0	ns
sibiricum M 2000 v. sibiricum F 2000	245.0	ns	270.5	ns
sibiricum M 2000 v. sibiricum M 2002	266.0	ns	256.5	ns
sibiricum M 2000 v. sphondylium M 2000	224.0	ns	210.0	ns
sibiricum M 2002 v. sibiricum F 2002	201.5	ns	278.5	ns
sphondylium F 2000 v. sphondylium F 2002	233.5	ns	271.0	ns
sphondylium F 2002 v. sibiricum F 2002	271.0	ns	253.0	ns
sphondylium M 2000 v. sphondylium F 2000	113.0	***	219.0	ns
sphondylium M 2000 v. sphondylium M 2002	155.5	**	226.5	ns
sphondylium M 2002 v. sphondylium F 2002	55.5	***	269.0	ns
sphondylium M 2002 v. sibiricum M 2002	97.5	***	244.5	ns

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