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**Ecological and evolution strategies of necrophagous beetles
(Coleoptera)**

Doctoral thesis

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Declaration

I hereby declare that this submitted thesis, "Ecological and evolution strategies of necrophagous beetles (Coleoptera)", is my own work, all co-authors of the manuscripts are properly listed, and only sources listed in the References were used.

Pavel Jakubec

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Abstract

Necrophagous beetles (Coleoptera) are very interesting and diverse ecological group of species with an immense impact on a natural nutrient cycle. Their main food source and breeding ground are carions of vertebrates, human remains included. This relationship is often used in various ways by forensic entomology, but its potential was not yet fully reached, because our knowledge of biology of these beetles is very much incomplete.

In this thesis I would like to explore geographic distribution, ecological requirements and developmental biology of several Central European necrophagous beetles as an outcome of their ecological and evolutional strategies. For that I raised three broad research questions. Which factors are determining the local abundance of carrion beetles (Coleoptera: Silphidae)? How the current geographical distribution of open-landscape carrion beetles looks like in the Czech Republic? How is the temperature affecting the development of *Sciodrepoides watsoni* (Spence, 1813)?

We found that soil type can have significant effect on abundance of carrion beetles and they showed preference for chernozem – *Nicrophorus antennatus* (Reitter), *N. germanicus* (Linnaeus), *N. interruptus* (Stephens), *N. sepultor* (Charpentier), *Silpha obscura obscura* (Herbst), *T. sinuatus* (Fabricius) or for fluvisol as did *N. humator* (Gleditsch). These findings support our hypothesis that soil type could be an important factor determining the occurrence of necrophagous European carrion beetles.

To collect novel data of the current geographical distribution of carrion beetles we used 420 baited pitfall traps and, at 84 localities, and we collected 71 234 specimens of 15 silphid species. Among them, three endangered carrion beetle species listed on the Czech Red List of Invertebrates, were found. Two are vulnerable thermophilic species of open landscapes, *Nicrophorus antennatus* (Reitter, 1884) (collected around Louny and Židlochovice) and *Nicrophorus germanicus* (Linnaeus, 1758) (Louny, Zábřeh and Židlochovice). The third is the

near threatened species, *Nicrophorus sepultor* Charpentier, 1825 (collected around Louny, Kutná Hora, Zábřeh and Židlochovice), which also prefers open landscapes.

We studied development of common Holarctic beetle *Sciodrepoides watsoni* under five constant temperature regimes in laboratory (15, 18, 21, 25 and 28°C). Parameters of thermal summation models and their standard errors were calculated for each developmental stage (egg, three larval instars and pupae). We also find a new character for larval instar determination (head width) and proposed novel approach for future studies of size-based characters in instar determination.

Keywords: Coleoptera, Silphidae, Cholevinae, geographical distribution, developmental biology, larval instar determination, forensic entomology, nature protection

Abstrakt

Nekrofágní brouci (Coleoptera) jsou zajímavou a velmi diversifikovanou ekologickou skupinou, s velkým dopadem na přirozený cyklus živin. Jejich hlavní složkou potravy, a zároveň místem rozmnožování, jsou mršiny obratlovců, člověka nevyjímaje. Tento vztah je často různě využíván ve forenzní entomologii, ale jeho potenciál není zdaleka využit, protože znalost biologie těchto brouků je velmi kusá.

V této disertační práci chci prozkoumat geografické rozšíření, ekologické nároky a vývojovou biologii několika středoevropských druhů nekrofágích brouků, tedy výsledek jejich ekologických a evolučních strategií. Za tímto účelem jsem si položil tři velmi široce formulované otázky. Které faktory jsou určující pro lokální abundanci mrchožroutovitých brouků (Coleoptera: Silphidae)? Jaké je současné geografické rozšíření mrchožroutů otevřené krajiny v České republice? Jak ovlivňuje teplota vývoj druhu *Sciodrepoides watsoni* (Spence, 1813)?

Zjistili jsme, že půdní typ má statisticky významný vliv na početnost mrchožroutů. Šest druhů preferovalo černozemě – *Nicrophorus antennatus* (Reitter), *N. germanicus* (Linnaeus), *N. interruptus* (Stephens), *N. sepultor* (Charpentier), *Silpha obscura obscura* (Herbst), *T. sinuatus* (Fabricius), a jeden fluvizemě – *N. humator* (Gleditsch). Tyto závěry podporují naši hypotézu, že půdní typ by mohl být jedním z určujících faktorů pro výskyt nekrofágích evropských mrchožroutů.

Za účelem zjištění geografického rozšíření mrchožroutů jsme položili 420 vnazených padacích pastí na 84 lokalitách a takto jsme získali 71 234 kusů 15 druhů těchto brouků. Mezi nimi byly i tři druhy hrobaříků, kteří jsou na Červeném seznamu bezobratlých. Dva z nich jsou zranitelné, teplomilné druhy otevřené krajiny *Nicrophorus antennatus* (Reitter, 1884) (nalezen okolo Loun a Židlochovic) a *Nicrophorus germanicus* (Linnaeus, 1758) (Louny, Zábřeh a Židlochovice). Třetí je téměř ohrožený druh *Nicrophorus sepultor* Charpentier,

1825 (nalezen okolo Loun, Kutné Hory, Zábřeha a Židlochovic), který taktéž preferuje otevřenou krajinu.

Studium vývoje běžného holarktického druhu *Sciodrepoides watsoni* probíhalo v laboratoři za několika konstantních teplot (15, 18, 21, 25 a 28°C). Na základě pozorování délky vývoje jsme vypočítaly parametry termálně sumačního modelu s jejich standardní chybou pro každé stádium vývoje (vajíčko, tři larvální instary a kukla). Zároveň jsme zjistili, že šířka hlavové kapsule je u tohoto druhu dobrým nástrojem pro určení stupně larválního instaru. Popisná statistika tohoto znaku a nová metodika jak studovat velikostně definované znaky je přiložena k práci.

Klíčová slova: Coleoptera, Silphidae, Cholevinae, geografické rozšíření, vývojová biologie, determinace larválního instaru, forenzní entomologie, ochrana přírody

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1. General introduction

How beetles cope with the environment and competition provoked scientists for generations. Ultimately, studies on ecological and evolutional strategies become a very broad topic with various impacts on our lives and it is important to see that general understanding of direct and indirect interactions in nature is highly important for applied and theoretical fields of science (Begon *et al.*, 2006; Galante & Angeles, 2008).

Beetles are very diverse order with some 300,000 – 400,000 described species (Stork, 2009), so in this thesis I narrowed my focus down only to some selected species of necrophagous beetles of Central Europe. I would like to provide a new insight at how the ecological and evolutional strategies could be used for answering pressing issues in forensic entomology and nature protection.

My selected species came from two particular groups of beetles, family Silphidae (carrion beetles) and subfamily Cholevinae of the family Leiodidae (small carrion beetles). More specifically, I targeted necrophagous, Central European species of family Silphidae and one particular species of subfamily Cholevinae (Leiodidae), *Sciodrepoides watsoni* (Spence, 1813). All those taxa are connected by the fact that they develop and feed on carriions, which is also very interesting ecological and evolutional strategy itself (Szymczakowski, 1961; Šustek, 1981).

Only one species in the group I selected, *Necrodes littoralis* (Linnaeus, 1758), was earlier recognized as potential bio-indicator species for forensic entomology (Matuszewski, 2011; Fratczak & Matuszewski, 2014). This disinterest of forensic entomology in beetles is global phenomenon (Midgley *et al.*, 2010). Beetles were for a long time perceived as not as good as flies (Diptera), because they usually arrived latter at the scene, but this image is crumbling.

The first crack in this picture was made when it was proven that African carrion beetle, *Thanatophilus micans* (Fabricius, 1794), is able to locate and start to breed on corpse in the first 24 hours (Midgley & Villet, 2009a). However, beetles in the Middle Europe are not that fast, probably due to lower ambient temperatures (H. Šuláková 2014, pers. comm.), but there are other benefits for forensic entomology they could offer.

General introduction

First of all, beetles tend to have longer development than flies (Midgley & Villet, 2009a; Richards *et al.*, 2009; Velásquez & Viloria, 2009; Ridgeway *et al.*, 2014); therefore they stay on the body for longer period and we can use them as evidence not only in early stages of decomposition. Second of all, they also do not need to form a maggot ball and individual rearing is less difficult (Midgley *et al.*, 2010), so they are easier to handle in laboratory conditions. But we think that the biggest advantage is possibility to cross validate the estimates between species and groups like flies and mites. This is important mainly in times when one of these groups or species could have been affected by external factors (restricted access to body, too high or low temperature, etc.) and give biased estimation (H. Šuláková, 2014 pers. comm).

Only few beetle species were studied specifically for further use in forensic entomology, so in this thesis I would like to look closely on developmental biology of *Sciodrepoides watsoni* and find the thermal summation model for this species, which will enable to estimate the post mortem interval. Further, I would like to find a new character for instar determination and propose a new methodology for estimation of size-based larval characters (section B).

Some species of burying beetles that we studied could not only be useful bio-indicators. They are also listed in the Red List of endangered species (Růžička, 2005), but their protection is lacking behind of other groups and nothing happened except the statement that they are indeed endangered.

In comparison, American burying beetle (*Nicrophorus americanus* (Oliver, 1790)) (Silphidae) was recognized as federally endangered in U. S. A. in 1989. In 1991, two years after, the recovery plan was prepared and this plan is still running (Jurzenksi *et al.*, 2014). What is maybe even more important than the recovery plan is a fact, that this unfortunate fate put this beetle in a spot light of a scientific world. On the Web of Science you can find 38 articles for a topic query: "Nicrophorus americanus", but nothing on "Nicrophorus antennatus" or "Nicrophorus vestigator" (accessed 27.8.2015).

Because we are currently few decades behind on this task, it is necessary to address very basic questions, which will allow us to proceed further. One of those, which I will cover in this thesis,

General introduction

is current geographical distribution of necrophagous carrion beetles (section **C**) and what are the ecological requirements of the European carrion beetle (section **A**).

2. Literature review

Necrophagy

In every natural or semi-natural habitat we can found three types of organism – producers, consumers and decompositors. Function of the whole ecosystem is affected by their direct and indirect interactions and it is balancing itself. Producers are organisms that transform an inorganic compounds and energy to organic compounds; consumers are heterotrophic organisms directly feeding on producers or other organisms (Galante & Angeles, 2008), and they can be labeled as predators, parasites or herbivores. These organisms are influencing the rate in which their resources are created. Therefore they harm the production of their food source. Decompositors are very different in that aspect and the production of their food is beyond their control and they depend on misfortune of others (illness, age or injury) (Begon *et al.*, 2006).

Decomposition process is one of the most important processes for ecosystem functions. Decomposition can be defined as a process of transformation of dead organic matter to molecules or basic elements. In general it is a process of releasing energy contained in the matter and mineralization of nutrients from organic back to inorganic (Galante & Angeles, 2008).

Decomposition can be divided into two inseparable parts, destruction and degradation of organic matter. Destruction is the first phase of the process. It is done by mechanical means and outcome are smaller particles of organic matter (Galante & Angeles, 2008). Degradation is mostly done by bacteria and fungi (Begon *et al.*, 2006), therefore it will not be cover in here. But destruction is often done by saprophagous species of insect, which are the ones I was dealing with.

Saprophagy is general term for group of animals feeding on dead matter of plants and animals (Begon *et al.*, 2006). This term can be narrowed down to more specific types as is necrophagy. Necrophagous species feeds on dead bodies of other animals. Main advantage of this strategy is that animal tissues are nutrient, especially with nitrogen, and they have very low level of

indigestible parts, compared to plant tissues. These qualities make a perfect food source in, but carriions are very rare on spatial and temporal scale (Zimmer, 2008).

Necrophagous species of invertebrates are very common among Diptera and Coleoptera species (Zimmer, 2008). In Europe, we can find an obligate necrophage, thus species feeding predominantly on carriions, in several beetle families: Silphidae, Trogidae, Dermestidae, Nitidulidae, Leiodidae (Cholevinae more specifically) and Staphylinidae (Szymczakowski, 1961; Kočárek, 2003; Archer *et al.*, 2006; Dekeirsschieter *et al.*, 2013).

Species composition of necrophagous community on carrion is largely affected by its stage of decomposition (Zanetti *et al.*, 2015). These stages are a bit arbitrary and differ between authors and studies. First time they were defined by Mégnin (1894) and then re-described by many others (e.g., Fuller, 1934; Reed Jr., 1958; Payne, 1965; Abell *et al.*, 1982) so to avoid confusion I chose to follow the stages described by Goff (2009):

1. Fresh – phase between time of dead and the first signs of bloating. In this phase is carrion usually discovered by flies from family Calliphoridae and Sarcophagidae and they will lay eggs on it (these species prefer to lay their eggs around the openings (natural or inflicted)) (Goff, 2009).
2. Bloated – carrion is starting to decay and gases are causing the bloating. Bacteria and fly larvae activities are rising inner temperature and fluids are leaking from the body and they change pH of surrounding soil to more alkaline. Calliphoridae are strongly attracted to the body in this stage (Goff, 2009).
3. Decay – this stage begins by rupture of the bloated body due to accumulated gases. Fly larvae are predominant group and they occur in big feeding groups that clean soft tissues of the bones. Carrion attracts many necrophages and predators like beetles, ants and wasps (Goff, 2009).
4. Postdecay – only skin, cartilages and bones are remaining. Diptera are no longer predominant. Diversity and predominant taxa are predetermined by humidity of the habitat. In xerophytic and mesophytic habitats Coleoptera starts to dominate, which is associated with increased number of their predators and parasites. However, in wet habitats like swamps or rain forests do Diptera and their predators and parasites predominate over Coleoptera (Goff, 2009).

In the Czech Republic this phase is often linked with presence of family Dermestidae, Trogidae, Cleridae and some Staphylinidae (Kočárek, 2003).

5. Skeletal – this stage can be recognize when only fur and bones remains. This stage does not have any clear ending because even composition of the soil fauna, which was changed during the second stage, remains noticeable after months and years. This phase is not linked with occurrence of any specific taxa (Goff, 2009).

Carrion is rather ephemeral and unpredictable food source therefore species have to be able to locate it quickly and at the right moment (Dekeirsschieter *et al.*, 2011). This is crucial especially in severe competition of other necrophagous species. To accurately locate their food source, without wasting time on random search, burying beetles use chemosensory organs on their antennae, which are sensitive to multiple volatile organic compounds (VOC) emitted by decomposing carrion, like methanethiol, methyl thiolacetate, dimethyl sulphid, dimethyl disulphide and dimethyl trisulphid (Kalinová *et al.*, 2009; Podskalská *et al.*, 2009). There is even some evidence that insect can detect chemical changes of VOC and thus their appearance in particular time is not coincidence (Archer & Elgar, 2003b; von Hoermann *et al.*, 2011).

Another prerequisite for success among completion is ability to fly, because it allows to cover more ground while searching (Ikeda *et al.*, 2007, 2013). Chemical analysis of food composition in guts of some carrion beetles shown that only true necrophages posses functional wings while closely related wingless species, which were previously considered as necrophagous, are in fact predators (Ikeda *et al.*, 2007).

Thermal summation models and all that

Body temperature of insect is dependent on the ambient temperature and they have very limited options how to control it (muscle contractions, behavioral responses) (Denlinger & Lee, 2010; Chapman, 2012). Also their development rate is dependent on the temperature, and because of that even their seasonal pattern and phenology is governed by temperature (Schwartz, 1998). The effect of temperature on developmental rate can be model as curve

where the rate increase with increasing temperature until optimum is reached (T_{max}) and then it decreases rapidly (Lardeux *et al.*, 2008; Voss *et al.*, 2010a). Around the extreme values, the mortality increases and could prevent development altogether (Régnière *et al.*, 2012).

Developmental rate characteristics were historically considered as species specific trait, but this is not supported by current research. Geographically distant populations of the same species differ as they probably adapt to their environment (Kipyatkov & Lopatina, 2002, 2010). Interestingly, those characteristics could differ even between methodologies. When one group was reared in constant temperature and the other one in fluctuating, the group in fluctuating will develop faster. This is called Kaufmann effect (Ikemoto & Egami, 2013).

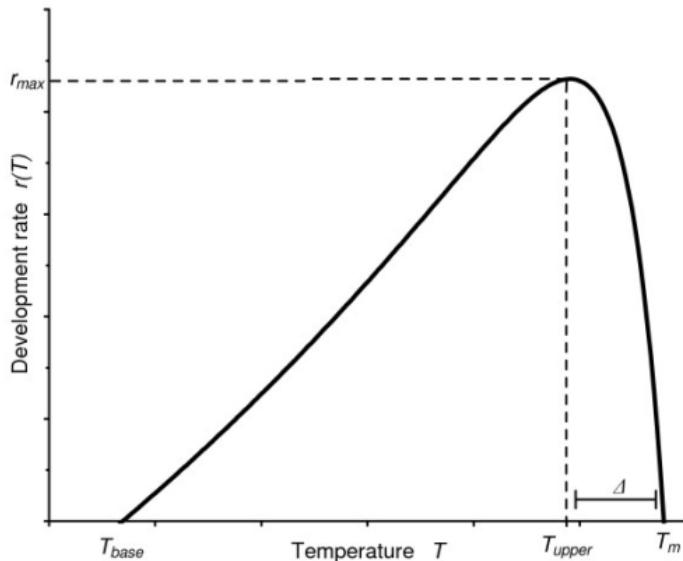


Fig. 1: Relationship between developmental rate and temperature (Lardeux *et al.*, 2008).

There are three approaches to modeling development of poikilotherms. The first is based on assumption that development of immature stages is linear (Higley *et al.*, 1986). This model is very simple and easy to establish, because only few measurements over optimal range of temperatures are needed (Kipyatkov & Lopatina, 2010). Its mathematical formulation is following $1/D = - (t/k) + (1/k)T$ where D is duration of development, t is lower developmental threshold, k is sum of effective temperatures and T is ambient temperature and is called linear

degree-day model or thermal summation model (Briere *et al.*, 1999; Richards & Villet, 2008). This model had some flaws and especially it was disproportionate for upper and lower parts, which distorted and exaggerated lower temperature range and also resulted in lower slope of regression. In reaction to these issues, new formula was offered by Ikemoto & Takai (2000): $(DT) = k + tD$. This formula corrected some problems of the first one and also gives estimation of the variance directly in contrast to the first method where it needed to be recalculated separately. This method is widely accepted and was used in number of studies across different fields of research (Brewer & Hoff, 2002; Chong & Oetting, 2006; Villet *et al.*, 2006; Richards & Villet, 2008; Midgley & Villet, 2009a; Velásquez & Viloria, 2009; Kay, 2010; Ridgeway *et al.*, 2014).

The second and third approach is nonlinear. They both try to model the entire range of temperatures including the extremes based fitting data, but third also tries to incorporate biophysical and biochemical constants to explain processes behind the development (Sharpe & DeMichele, 1977; Jarošík *et al.*, 2002). These models allow estimating the optimal temperature and go beyond linear parts of development (Briere *et al.*, 1999). Problem with many of them is that their parameters have no biological meaning and the fitting process reflects not only true trend, but also biases of data (Jarošík *et al.*, 2002).

Estimation of the post mortem interval (PMI)

Estimation of post mortem interval (PMI) is one of the most common usages of insect in forensic entomology. There are several ways how the PMI can be estimated. The most basic way how to estimate PMI is succession pattern. This method is based on knowledge of chronological changes in species composition on carrion (Matuszewski *et al.*, 2010, 2011). Other method is isomegalen diagram. These diagrams are visualization of larval growth for various constant temperatures (Reiter, 1984). These estimates are quick, but they can be misleading when specimen is killed improperly or it experienced some issues during the development (Amendt *et al.*, 2007; Midgley & Villet, 2009b). Another methods is pre-appearance interval, which is estimating the time of arrival at the corpse based on ambient temperature

(Matuszewski, 2011; Matuszewski & Szafarowicz, 2013). There is very little experience with this type, but it could be nice complementary information for thermal summation models.

Thermal summation models are considered as the most sophisticated available models used for PMI estimation (Amendt *et al.*, 2011). They are estimating PMI based on calculation of time from colonization of cadaver by necrophagous species till the moment of its discovery (Amendt *et al.*, 2007). This estimate can be done only for species with known relationship between rate of development and temperature as was described above. Additional and very obvious condition is that it should be possible to correctly identify the species and distinguish between larval instars.

Identification of adult specimens is often not a problem and there are many keys for identification of adult specimens of necrophagous beetles (Szymczakowski, 1961; Šustek, 1981), but determination of eggs and larvae is much more challenging especially for beetles. Morphological descriptions of larvae are unknown for many species and especially older descriptions suffer with many issues. Only one instar was described (usually only the mature larva); description was inadequate; figures are not accurate and features are simplified or imagined; determination of larvae was based on association with adults not by confirmed parent-offspring relationship (J. Růžička, pers. comm.). This problem can be solved by modern morphological description or re-description of larvae as Kilian & Mądra (2015) did in case of *Sciodrepoides watsoni* (Spence, 1813) or applying molecular methods like DNA barcoding for species identification (Schilthuizen *et al.*, 2011).

Another challenge is correct larval instar determination and this problem is closely connected to the previous one, but goes beyond that. Often species does not possess any morphological features that could be used for instar determination (see Velásquez & Viloria, 2010; Fratczak & Matuszewski, 2014). In these papers authors tried to estimate the stage of development based on the size of selected characters without prior knowledge of the true stage of the specimen. This approach is from our point of view a little bit problematic, because those measured characters are correlated, therefore bigger larvae could be misidentified as higher instar than

they really are. This bias would probably not affect the obtained mean values, but it would give distorted picture about variation.

Beetles in forensic entomology

Because utility of beetles in forensic entomology was overlooked for a long time (Midgley *et al.*, 2010), there is not many species of beetles with known and statistically robust thermal summation models. Recent studies were focused on carrion beetles (Silphidae). Namely *Thanatophilus micans* (Fabricius, 1794) (Ridgeway *et al.*, 2014), *T. mutilatus* (Castelnau, 1840) (Ridgeway *et al.*, 2014) and *Oxelytrum discicolle* (Brullé, 1840) (Velásquez & Viloria, 2009). But also other PMI related features were studied in this group such as pre-appearance interval of *N. littoralis* and some other carrion beetles (Matuszewski, 2011; Matuszewski & Szafarowicz, 2013).

These carrion beetles colonize corpses in earlier stages of decomposition often along with flies. Larder beetles (Dermestidae) on the other hand arrive very late in decomposition (Goff, 2009). There are developmental data for several larder beetles (see Amos, 1968; Coombs, 1978, 1979; Jacob & Fleming, 1980; Richardson & Goff, 2001) and some notes about their rearing and breeding (see Roche & Smith, 1974; Woodcock *et al.*, 2013), but the more statistically robust models are needed (Midgley *et al.*, 2010).

As far as my target group is concerned, Silphidae: Nicrophorinae (the burying beetles) have very limited utilization in forensic entomology, because they do not breed on larger carriions and they only act as predators of flies (Sikes, 2008). Silphidae: Silphinae (the carrion beetles) and Leiodidae: Cholevinae (small carrion beetles) on the other hand can be very useful, because they are breeding on larger carcasses and even on human remains (Sikes, 2005; Schilthuizen *et al.*, 2011; Ridgeway *et al.*, 2014).

Silphidae

Taxonomy

Family Silphidae (Coleoptera: Staphylinoidea) currently contains 186 described species in two monophyletic subfamilies, Nicrophorinae and Silphinae (Sikes, 2008; Grebennikov & Newton, 2012).

Silphidae are closely related with family Staphylinidae (rove beetles) and there is an ongoing scientific discussion if they should be placed as inner lineage within Staphylinidae. Main difference between Silphidae and Staphylinidae adults is that in Silphidae are 3 or 4 visible terga on abdomen instead of 2 as in Staphylinidae. Many similarities were discovered between these two families, namely shortening of elytra (Šustek, 1981), but molecular taxonomy did not show any sign that they should be merged into Staphylinidae (Dobler & Müller, 2000; Grebennikov & Newton, 2012; Ikeda *et al.*, 2013). However, see rather controversial results of McKenna *et al.* (2015).

Subfamily Nicrophorinae is rather small, with 73 recognized species and according to paleontological records, it originated 135 million years ago (Sikes & Venables, 2013). It currently contains four taxa of generic rank, *Eonecrophorus* Kurosawa, 1985, *Ptomascopus* Kraatz, 1876, and genus *Nicrophorus* Fabricius, 1775, with two subgenera *Necroxenus* Semenov-Tian-Shanskij, 1933 and *Nicrophorus* Fabricius, 1775 (Sikes, 2003; Sikes & Venables, 2013). Recently, some unnamed transitional forms were discovered in Jurasic and Cretaceous formations from China and Myanmar (Cai *et al.*, 2014).

Subfamily Silphinae is composed of 14 genera (*Ablattaria* Reitter, 1884, *Aclypea* Reitter, 1885, *Dendroxena* Motschulsky, 1858, *Diamesus* Hope, 1840, *Heterosilpha* Portevin, 1926, *Heterotemna* Wollaston, 1864, *Necrodes* Leach, 1815, *Necrophila* Kirby & Spence, 1828, *Oiceoptoma* Leach, 1815, *Oxelytrum* Gistel, 1848, *Phosphuga* Leach, 1817, *Ptomaphila* Kirby & Spence, 1828, *Silpha* Linnaeus, 1758 and *Thanatophilus* Leach, 1815,) and originated some 165 million years ago (Sikes, 2005, 2008; Sikes & Venables, 2013; Qubaiová *et al.*, 2015).

Many new species of carrion beetles were discovered and described recently, especially from Eastern Palaearctic, Oriental and Neotropical Regions as result of increased interest of

entomologist in this group, thus number of species and probably even genera can change in the near future (see Ryabuchin, 1990; Koz'minykh, 1995; Háva *et al.*, 1999; Cho & Kwon, 1999; Sikes & Peck, 2000; Růžička *et al.*, 2000; Sikes *et al.*, 2006; Khachikov, 2011; Ruzicka & Schneider, 2011; Oliva, 2012; Sikes & Mousseau, 2013; Amat-García & Valcárcel, 2014).

Geographical distribution

Distribution of all organisms is outcome of their ecological and evolutional history. The oldest records of carrion beetles were found in China and they were at least 165 million years old (Cai *et al.*, 2014), therefore the whole group probably occurred first on Laurasia continent in Jurassic period (Sikes & Venables, 2013). The appearance of these fossil specimens is very similar to present-day burying beetles (Nicrophorinae) and they possessed some highly specialized features of their modern cousins as three-segmented antennal club covered with sensilla (Sikes, 2008; McHugh & Liebherr, 2009; Cai *et al.*, 2014).

Current distribution of Nicrophorinae is almost exclusively limited to Holarctic region, but some species inhabit mountain regions of Indo-Malaysia islands and South America (Sikes, 2008; Sikes & Mousseau, 2013). This pattern could be explained by competition exclusion of Nicrophorinae in warmer regions by ants and other, more aggressive carrion feeders (Sikes, 2008).

The current distribution of Silphinae compared to Nicrophorinae is covering much broader area. They inhabit Afrotropical and Australian Regions that Nicrophorinae never reached (Peck, 2001; Sikes, 2008). This geographical disparity could be linked with higher taxonomic diversity and longer evolution history of the Silphinae. Other advantage of Silphinae is that they use bigger carcasses for breeding, where the size of carcass allows coexistence of multiple necrophagous species. Almost all Nicrophorinae use small carcasses, but they have to usurp the whole body to themselves for successful breeding, which is much harder to accomplish in competition of flies, ants and other large necrophagous beetles (Sikes, 2008).

From the Czech Republic, 24 species of Silphidae were reported. Nine belongs to subfamily Nicrophorinae and the rest to Silphinae (Růžička, 1993; Háva & Růžička, 1997). Also, nine of these species are on the Czech Red List of endangered species of invertebrates. One species is

regionally extinct (*Thanatophilus dispar* (Herbst, 1793)), one species is endangered (*Aclypea souverbii* (Fairmaire, 1848)), five species are vulnerable (*Ablattaria laevigata* (Fabricius, 1775), *Aclypea undata* (O.F. Müller, 1776), *Nicrophorus antennatus* (Reitter, 1884), *Nicrophorus germanicus* (Linnaeus, 1758) and *Nicrophorus vestigator* Herschel, 1807) and two species are near threatened (*Nicrophorus sepultur* Charpentier, 1825 and *Silpha tyrolensis* Laicharting, 1781) (Růžička, 2005).

Ecology

Differences between Silphinae and Nicrophorinae are not just in their appearance, but also in their ecology and behavior. Especially striking feature is bi-parental care of Nicrophorinae. This phenomenon attracted a lot of attention of scientific community and is well documented (see Pukowski, 1933; Špicarová, 1982; Müller *et al.*, 1990; Eggert & Müller, 1992, 2011; Trumbo & Fiore, 1994; Trumbo & Fernandez, 1995; Steiger *et al.*, 2012; Engel *et al.*, 2014). Adults usually search for fresh carrion in particular part of day, which is often species specific (Kočárek, 2002). If the male finds a carrion without any female on it, they can attract the female with pheromones (Eggert, 1992). The mating pairs are formed on the carrion and encounter of multiple individuals of the same sex lead to fights. These fights, tends to have some rules and males and females are fighting only individuals of the same sex as they are. The dominant couple will chase away weaker beetles and usurp and bury the carrion. This is sometimes accompanied by nest parasitism when loser females lay their own eggs around the carcass in hope that their larvae might sneak into the winner's nest and develop alongside of their brood (Sikes, 2008).

Majority of Silphidae has functional wings. Ability to fly seems to be crucial for necrophagous beetles, because as I already mentioned, carriions is very ephemeral food source and they have to locate it as soon as possible. This is reflecting reactive nature of necrophagy compared to proactive approach of predators in obtaining the food and according to some authors it can cause a loss of the flight ability of the former group as evolutionary unnecessary trait (see Ikeda *et al.*, 2007, 2013).

Flight ability differs between species. Especially larger species appears to be able to flight over longer distances than the small ones. This was confirmed for *Nicrophorus germanicus*, which is the largest species of Silphidae in the Czech Republic. In experiment this species was recorded to fly over the distance of more than four kilometers during 24 hours (Petruška, 1964). Even more robust burying beetle (*Nicrophorus americanus* (Olivier, 1790)) was recorded as far as 7.41 kilometers from the place of origin after one night, but this record was an outlier and 90% of observed beetles did not move further than 1.6 kilometers over the same period of time (Jurzenksi *et al.*, 2011). Smaller necrophagous species are less mobile and *Thanatophilus sinuatus* Fabricius, 1775 and *T. rugosus* Linnaeus, 1758 distance recorded as they dispersion over period of 24 hours was 395 and 375 m, respectively (Petruška, 1964).

It was found that flight height is probably also positively correlated with body size, and bigger species fly higher than smaller ones (Ohkawara *et al.*, 1998).

Distribution of necrophagous species of carrion beetles over landscape is not homogenous, but as it seems, some species are preferring different types of habitat, which was reported by number of studies (Novák, 1961, 1962; Růžička, 1994; Kočárek, 2003; Looney *et al.*, 2004, 2009).

Many European species seemed to be more abundant in open landscape (e.g., *Thanatophilus sinuatus*, *T. rugosus*, *Nicrophorus germanicus*, *N. vespillo* (Linnaeus, 1758), *N. antennatus*, *N. sepultor* and *N. vestigator* (Novák, 1962; Růžička, 1994; Kočárek, 2003)). On the other side, several species (e.g., *Oiceoptoma thoracicum* (Linnaeus, 1758), *Nicrophorus vespilloides* Herbst, 1784 and *N. humator* (Gleditsch, 1767)) visit open landscape only occasionally and they prefer forested biotopes (Růžička, 1994). Similar pattern was observed between different soil types and some species were observed more often on one particular soil type (Pukowski, 1933; Paulian, 1946; Theodorides & Heerdt, 1952; Novák, 1961, 1962) All these beetles are necrophagous and they are not especially picky about the food source so researchers are very interested in revealing the reason, why they prefer to occupy particular type of habitat or soil, because it could be useful for their protection and it would improve our general understanding of interactions in the nature.

What is the cause of this pattern is still not fully understood, but it was shown for some North American burying beetles, that deeper and loess soils are hosting more abundant communities of these species, but some of them prefer the exact opposite, shallow and rocky soils (Muths, 1991; Bishop *et al.*, 2002; Looney *et al.*, 2009). The exactly same pattern was observed for some European burying beetles. For example, *N. antennatus* was observed more often on loessal soils, but *N. vestigator* seems to prefer dry and sandy soils (Novák, 1965). Looney *et al.* (2009) offered three possible explanations for this phenomenon. Beetles are either simply more abundant in areas with a particular soil type, or they preferentially colonize, or they are more competitive in such areas.

Temporal distribution

Temporal distribution of burying beetles of genus *Nicrophorus* is governed by the state in which they overwinter. Several species overwinter as larvae (*Nicrophorus sepultor*, *N. investigator* and *N. interruptus*) and most of them as adults (*N. antennatus*, *N. vespillo*, *N. vespilloides*, *N. germanicus*, *N. humator* and *N. vestigator*) (Novák, 1962; Šustek, 1981; Růžička, 1994). It is obvious that overwintering as adult give them opportunity to emerge early in the spring and species overwintering as larvae are emerging during late in spring or in summer, depending on the latitude and altitude (Růžička, 1994).

In general, there is difference in number of generations per year between bigger and smaller species. *Nicrophorus germanicus* (body length around 4 cm) has usually one generation per year in the Czech Republic. In comparison, *N. vespillo* (body length around 3 cm), which is sharing the same habitat with the previous, has two generations per year (Novák, 1961). Even smaller silphids like *T. sinuatus* and *T. rugosus* (body size about 0.5 cm) are able to have even three generations per year (Novák, 1966).

Circadian activity

Activity of probably all animals is changing on temporal scale. The mechanism behind these rhythms can be triggered by some external (reaction to change of environment) or internal impulse (controlled by circadian or another oscillation) (Sanders *et al.*, 2002). It was found that predominant type of activity (nocturnal, diurnal) differs between ecological groups. Diurnal activity is common for predators and herbivores, probably because they are using sight for food searching, but saprophagous and necrophagous beetles use chemo-receptors to do so therefore they prefer low light conditions (crepuscular and nocturnal activity) (Lewis & Taylor, 1965).

Špicarová (1974) shown in the laboratory conditions that young adults of *N. germanicus* are leaving soil predominantly right after sundown. This was in contrast to her laboratory observations of *N. vespillo* (Špicarová, 1972), which left the soil predominantly right after noon. Field observations did not support asserted theory of diurnal activity of *N. vespillo* (Kočárek, 2001), but they found that *T. sinuatus*, *T. rugosus* and *O. thoracicum* are almost exclusively diurnal. Repeated experiment confirmed that these species have diurnal activity in Central Europe (Kočárek, 2002).

Intraspecific and interspecific competition

Carrion is very good source of nutrients and the competition associated with such a source is very harsh. Nicrophorinae and Silphinae differ in their competitive strategies. Nicrophorinae prefer smaller corpses (<100 g) and Silphinae prefer larger carions (>300 g), which limits competition between these two groups (Sikes, 2008).

Nicrophorinae avoid an interspecific competition by burying carrion underground, which limits ability of other species to locate it. Springett (1968) and others (Anderson, 1982a; Ratcliffe, 1996; Sikes, 2008) offer an theory that Silphidae and especially Nicrophorinae have symbiotic relationships with mites from genus *Poecilochirus* G. Canestrini & R. Canestrini, 1882 (Mesostigmata: Parasitidae), which are often hitchhiking on carrion beetles, and they are feeding on fly eggs. Therefore they eliminate them from competition before they have a chance to escape or hide.

Beetles from subfamily Silphinae have to fight their competition directly, because they cannot hide food from other competitors, but because they use much bigger carions for breeding, they have enough time and resources to finish their development (Sikes, 2005).

Competition between species of subfamily Nicrophorinae is also very intense and each breeding pair has to occupy their own, small corpse. In these fights are bigger species of Nicrophorinae in clear advantage (Safry & Scott, 2000). Such a situation would have to result in competitive exclusion and ultimately extinction of smaller species, but we are not witnessing such situation. Most probable reason for such a peaceful coexistence of several species is their temporal and spatial separation, because fights would result in wasting resources of everybody involved (Anderson, 1982a). Intraspecific competition, as I already described, is very physical and larger individuals tend to win over small ones, but several cases of communal breeding were reported (see Trumbo & Fiore, 1994; Trumbo, 1995; Scott *et al.*, 2007).

Leiodidae: Cholevinae

Taxonomy and geographical distribution

Subfamily Cholevinae is monophyletic and currently placed inside of family Leiodidae and it is one of its largest groups with approximately 1 605 species (Newton, 1998, 2005; Perreau, 2004). The place of origin of the entire group was probably on south part of Gondwana continent (today's Antarctica) in Triassic period (250 – 200 MYA) and Cholevinae spread from there to all continents, but they went extinct on the Antarctica itself (Giachino *et al.*, 1998).

Biodiversity hot spot for Cholevinae is Mediterranean thanks to cave dwelling tribe Leptodirini, with high rate of endemism (Newton, 1998; Zolia, 1998).

In the Czech Republic 48 species in 11 genera were recorded so far (*Nemadus* C.G. Thomson, 1867, *Eocatops* Peyerimhoff, 1924, *Anemadus* Reitter, 1884, *Nargus* C.G. Thomson, 1867, *Choleva* Latreille, 1796, *Attaephilus* Motschulsky, 1869, *Dreposcia* Jeannel, 1922, *Sciodrepoides* Hatch, 1933, *Catops* Paykull, 1798 and *Cholevinus* Reitter, 1901 (Růžička & Vávra, 1993; Vávra & Růžička, 1993; Perreau, 2004).

Majority of these species are saprophagous generalist, which feeds on decaying biological material or they could be sporophagous or mycophagous (Jeannel, 1936; Peck, 1990, 1998; Růžička & Vávra, 1993; Betz *et al.*, 2003). Some species were often observed on carriions (Szymczakowski, 1961) and it was proposed that they could be used as bio-indicators in forensic entomology (Archer & Elgar, 2003a; Schilthuizen *et al.*, 2011).

The most promising species in this regard are the ones with autumn and winter activity like *Catops nigricans* (Spence, 1813), *Catops tristis* (Panzer, 1793), *Nargus wilkini* (Spence, 1813) *Choleva agilis* (Illiger 1798) and *Choleva elongata* (Paykull, 1798) (Topp, 1994, 2003). These species can occur on carriions in temperatures, which are too low for many species of flies (Diptera), which are usually used in forensic entomology.

Other promising species are the ones with very wide geographical distribution like *Sciodrepoides watsoni* (Spence, 1913), which occurs across the Holarctic region (Peck & Cook, 2002).

Ecology

Cholevinae of the Central Europe prefer to be in climatically stable environment like leaf litter, ant colonies, caves or burrows and dens of small mammals (Szymczakowski, 1961). It is very interesting that some species are developing during the cold season (sometimes they are called cold season species), which is season usually avoided by other species (Topp, 1994). These species try to avoid temperature higher than 20°C and they aestivate during summer heats (Topp, 1990). Optimal temperature for their breeding is from 5 to 10°C (Topp, 2003). Some of these species were listed by Topp (1994), but this list is far from complete.

Some cold season species were probably uncovered by Růžička (1994) when he studied seasonal dynamics of Cholevinae around Velký Blaník in the Czech Republic. He discovered four groups. First group had a one activity peak in spring (*Catops subfuscus subfuscus* Kellner, 1846, *Sciodrepoides fumatus* (Spence, 1815) and *S. alpestris* Jeannel, 1934. Second group peaked during the summer (*S. watsoni* (Spence, 1813) and *C. coracinus* Kellner, 1846). Third group peaked in autumn (*C. grandicollis* Erichson, 1837, *C. kirbyi* (Spence, 1815) and *C. morio* (Fabricius, 1792)). Fourth group had bimodal activity and peaked in spring and autumn (*C.*

picipes (Fabricius, 1792), *C. tristis* (Panzer, 1794), *C. fuliginosus* Erichson, 1837 and *Ptomaphagus sericatus* (Chaudoir, 1845)).

It is very likely that autumn group is the one, which contains also the cold season species. This theory could be proved by simple lab breeding experiment or by field observations. The reason for existence of these separate groups is unknown and Peck & Anderson (1985b) hypothesized that competition is probably not the answer, unlike for Silphidae.

As I already mentioned, Cholevinae are often associated with ant colonies or burrows of mammals. Species living with ants seems to be specialized on specific host, but this was not observed for species living with mammals (Szymczakowski, 1961; Peck & Cook, 2007).

Some species lives in caves and especially Mediterranean is filled with species truly adapted for the life in dark (Peck, 1998), but species of small carrion beetles occurring in the Czech Republic do not posses any features of true troglobionts, like prolonged legs and antennae, loss of sight or other developmental adaptation (Szymczakowski, 1961).

In the Czech Republic we can found species almost exclusively associated with open landscape (*Catops fuliginosus*, *C. grandicollis*, *C. morio* and *Ptomaphagus sericatus*) or forest species (*C. subfuscus subfuscus*, *C. tristis*, *C. coracinus*, *C. picipes*, *S. fumatus* and *S. alpestris*). Some species are not specialized and they occur almost regardless the habitat as *C. kibyi* or *Sciodrepoides watsoni* (Růžička, 1994).

3. Aim of the Thesis

Aim of the thesis is to study the ecological and evolutional strategies of necrophagous beetles from family Silphidae and subfamily Cholevinae. Thesis is dealing with their habitat preferences, geographical distribution and effect of temperature on the rate of their development. Possible applications in forensic entomology and nature protection are discussed in each article and the chapter General conclusions.

Specific goals:

- a) Is the type of soil an important factor determining the local abundance of carrion beetles (Coleoptera: Silphidae)?

The main goal of this article is to determine the habitat preferences of European open-landscape carrion beetles, especially those on the local Red list (*Nicrophorus antennatus*, *N. germanicus* and *N. sepultor*), and to discuss the effect of intra- and interspecific competition on their abundances.

- b) Thermal summation model and instar determination of all developmental stages of necrophagous beetle, *Sciodrepoides watsoni* (Spence) (Coleoptera: Leiodidae: Cholevinae)

To allow future utilization of *S. watsoni* in forensic entomology, the article will offer the parameter estimates of the thermal summation model. Also, a new size-based character for accurate larval instar determination will be provided together with new methodology of establishing such characters.

c) Distribution of open landscape carrion beetles (Coleoptera: Silphidae) in selected lowlands of the Czech Republic

This article will publish large dataset with key information about spatial and temporal distribution and abundance of open-landscape carrion beetles in the Czech Republic. Information about population trends and ecology of those beetles will be also included.

A Is the type of soil an important factor determining the local abundance of carrion beetles (Coleoptera: Silphidae)?

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Key words. Ecology, Nicrophorinae, Silphinae, burying beetles, soil type, chernozems, fluvisols, diversity

Abstract. Carrion beetles (Coleoptera: Silphidae) provide a valuable ecosystem service by promoting nutrient cycling and controlling pests like noxious flies (Diptera: Calliphoridae and Sarcophagidae). Our main goal was to examine the relationship between the occurrence of carrion beetles and soil type. We used pitfall traps to collect 43,856 specimens of 15 species of carrion beetles in the Czech Republic during 2009. We found that the abundance of seven of the carrion beetles – *Nicrophorus antennatus* (Reitter), *N. germanicus* (Linnaeus), *N. humator* (Gleditsch), *N. interruptus* (Stephens), *N. sepultor* (Charpentier), *Silpha obscura obscura* (Herbst) and *T. sinuatus* (Fabricius) – was significantly higher either in areas with chernozem or fluvisol soils. These findings support our hypothesis that soil type could be an important factor determining the occurrence of necrophagous European carrion beetles. Our findings could be helpful when selecting important nature conservation sites (particularly inasmuch as *N. antennatus*, *N. germanicus* and *N. sepultor* are listed as endangered species on the Czech Red List of Invertebrates) as in this respect localities where there are chernozem soils are potentially valuable.

A.1 Introduction

The majority of carrion beetles (Coleoptera: Silphidae) are obligate carrion feeders. They are frequently associated with the corpses of vertebrates and provide a wide range of ecosystem services, such as promoting nutrient recycling and removing potential breeding sites of noxious flies (Diptera: Calliphoridae and Sarcophagidae), by effectively removing the corpses (burying beetles – Nicrophorinae) or eating fly larvae (Nicrophorinae and some Silphinae) (Anderson & Peck, 1985; Sikes, 2008; Goff, 2009).

Despite their relatively low global species diversity (186 species), they occur widely throughout the Holarctic region (Sikes, 2008; Grebennikov & Newton, 2012). Carrion beetles can be divided into two taxonomic groups, the subfamilies Silphinae and Nicrophorinae, which are morphologically and also ecologically different (Sikes, 2005). Burying beetles of the subfamily Nicrophorinae are well known for their biparental care, while beetles of the subfamily Silphinae do not manifest such behaviour (Peck & Anderson, 1985a; Sikes & Venables, 2013).

The phenology and habitat selection of carrion beetles have been intensively studied in recent years (e.g., Peck & Anderson, 1985b; Creighton et al., 1993; Růžička, 1994; Lingafelter, 1995; Lomolino & Creighton, 1996; Kočárek, 2001; Archer, 2003; Hocking et al., 2007; Mullins et al., 2013). The relationship between soil characteristics and the occurrence of carrion beetles is often mentioned in the literature, but this has been based only on the authors' observations and without appropriate statistical testing (Pukowski, 1933; Paulian, 1946; Theodorides & Heerdt, 1952; Novák, 1961, 1962). The logical reason behind this hypothesis is that the developmental cycle of many carrion beetles is tightly connected with soil. For example Nicrophorinae bury the corpses of small vertebrates for breeding and Silphinae pupate underground. It has been proposed that a possible explanation for preferring a particular type of soil could be that some soils are better able to maintain a stable environment in terms of moisture and temperature, which is beneficial for the beetles (Novák, 1961, 1962). In a study of Nearctic insects, Looney et al. (2009) report that deep, loess soils host more abundant populations of necrophagous beetles than do shallow rocky soils. They also found that some

species actually prefer shallow rocky soils to deep, loess soils. This niche differentiation could be due to interspecific competition (Anderson, 1982a; Bishop et al., 2002).

Detailed information about the biology of the different species can be used to identify important conservation sites for endangered carrion beetles, as Jurzenksi et al. (2014) did for *Nicrophorus americanus* (Olivier).

Our field study is aimed at determining the habitat preferences of European open-landscape carrion beetles. Interspecific competition is discussed only in respect to other carrion beetles, because our trapping method was not designed for collecting other necrophagous invertebrates. We expected that most species of the subgenus *Nicrophorus* would be more abundant in areas where there are chernozem rather than fluvisol soils. Beetles of the subfamily Silphinae do not interact with the soil as closely as do Nicrophorinae, and we therefore had no reason to think that their abundance would differ in areas with chernozem or fluvisol soils.

A.2 Material and Methods

A.2.1 Site selection

This study was done during 2009 in the Czech Republic in regions with a similar medium warm (MT10) to very warm (T4) climate (Cenia, 2008) and similar occurrence of two different types of soil (chernozem and fluvisol) in open-landscape habitats. In order to select suitable locations, we uploaded data on climate, soil type and land use from a Cenia (2008) database into the geographical information system software ArcGIS 9.2 and looked for locations where these three conditions overlapped (ESRI, 2008). Accessibility was also taken into account.

We selected an equivalent number of locations on chernozem (33) and fluvisol (33) soils, which were clustered in three regions (see Fig. 1). These locations were at least 1.5 km apart, and we arranged them more or less while alternating linearly between sites on fluvisol and chernozem soils as in Fig. 2. There is a detailed description of the sites in Jakubec & Růžička (2012).

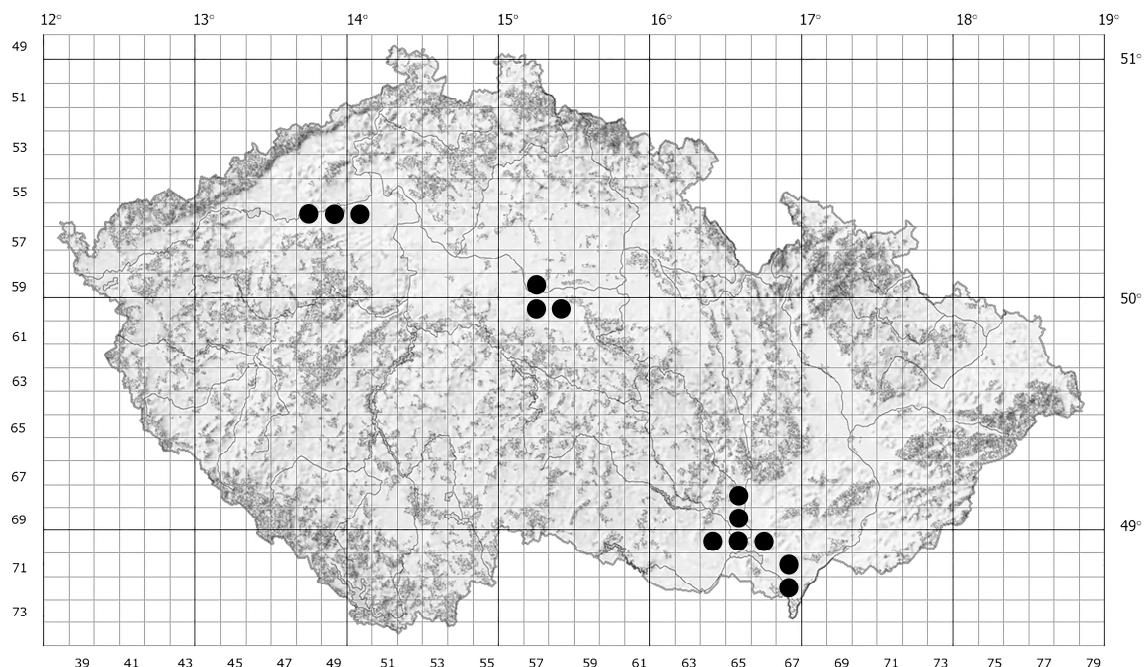


Fig. 1. Locations of the areas studied in the Czech Republic, which are indicated by black dots on a faunistic grid map (Jakubec & Růžička, 2012).

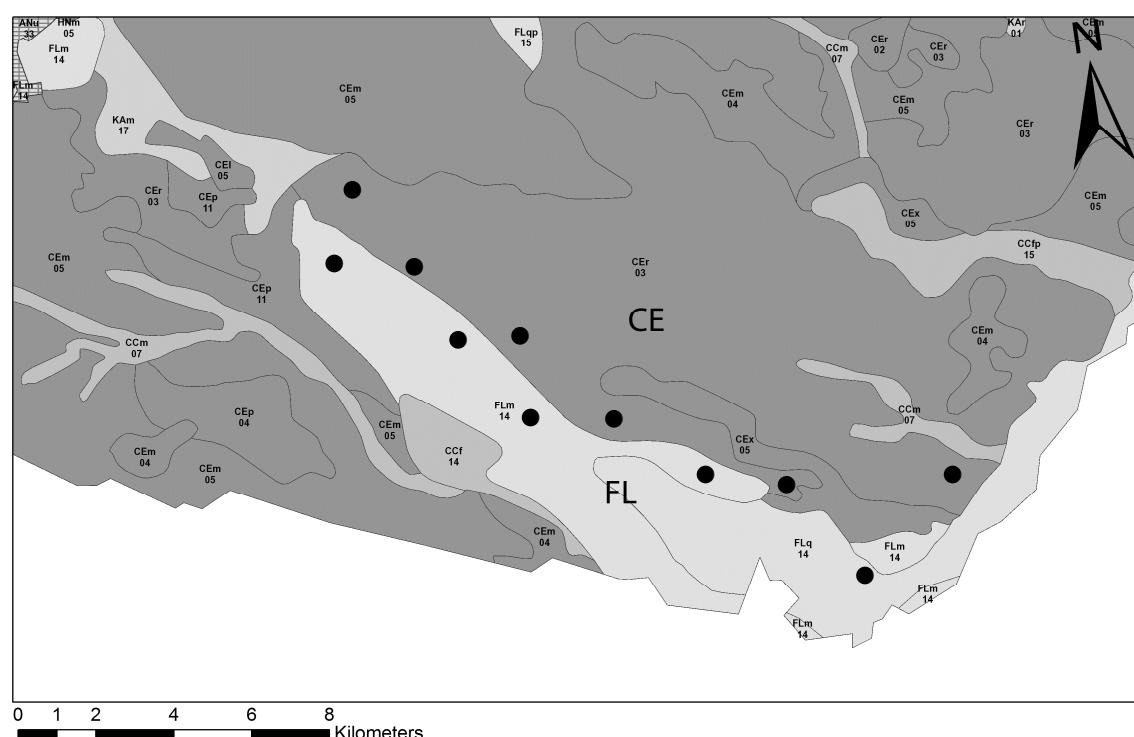


Fig. 2. Distribution of the localities (black dots) based on soil type (CE = chernozem; FL = fluvisol) in the South Moravian region (Cenia, 2015).

A.2.2 Trapping

For collecting beetles, we used baited pitfall traps designed by Růžička (2007), which were made from 1,080 ml plastic buckets (opening of 103 mm and 117 mm deep). These traps were part filled with a preservation solution of 200 ml water and 100 ml ethylene glycol. Traps were covered with a net of 2 cm mesh and an aluminum roof as protection against scavenging animals and flooding by rain. Frozen fish meat (cod) and ripening cheese (Romadur) were used as bait, placed in a small container (\leq 5 cm and 1.5 cm deep) and hung above the preservation solution.

A line of five traps was established at each location. The distance between these traps was at least 20 m. They were placed within one continuous agricultural field, and no closer than 50 m from the edge of the field. In an attempt to minimize the effect of extraneous confounding variables fields were selected as target habitats because soil properties in agricultural fields are more homogenous and the water regime more stable than anywhere else.

These traps were set for two weeks during the main peaks in carrion beetle activity (season): 17–31 May 2009 (spring), 5–19 July 2009 (summer) and 13–27 September 2009 (autumn), based on the data on activity in Růžička (1994). A complete sample consists of the contents of each trap collected over a period of two weeks. The samples were stored separately and included in the analysis only if the trap and bait was not disturbed or damaged by animals, humans or weather conditions.

Adult carrion beetles were identified to species level following Růžička & Schneider (2004) and stored in 75% ethanol. Selected voucher specimens were dry mounted and are deposited in the author's collection.

A.2.3 Data analysis

Detrended correspondence analysis (DCA) was performed on the species abundance data for each locality to determine the length of the gradient and detect whether some species are co-varying.

To test the effect of environmental factors on carrion beetles we decided to use partial canonical correspondence analysis (CCA) with a randomized block design in which the blocks were defined by covariates (season and region). We chose CCA over RDA because DCA indicated that the length of the gradient is more than 3.7 SD units long and, therefore, we had to use a unimodal type of analysis. Bonferroni correction was applied to adjust for multiple comparisons of the following environmental factors: soil type (chernozem and fluvisol), climatic region (warm – T2, very warm – T4 and mildly warm – MT10), land cover = crop (*Brassica napus*, *Beta vulgaris*, *Carthamus tinctorius*, *Glycine max*, *Helianthus annus*, *Hordeum vulgare*, *Phacelia tanacetifolia*, *Triticum aestivum* and *Zea mays*) and their interactions. Influence of regions was filtered out by using it as a covariate, because we were not interested in that effect.

The diversity of carrion beetles at each location and geographically related region was measured by calculating the Brillouin biodiversity index ($H = 1/N \cdot \ln(N!/n_1!n_2!...n_s!)$) from the total abundance data across all sampling periods (three times two weeks), where N is the total number of individuals caught at a location and n₁, n₂....n_s are the numbers of individuals of all carrion beetles collected at the location (Pielou, 1975). We used this index, because it does not assume randomness of sampling and equal attractiveness of traps as does the commonly used Shannon index (see Magurran, 2004). The number of specimens at each location was averaged over the number of samples, because they differed between locations due to unavoidable adverse events (flooding by rain or destruction of traps).

We used the Wilcoxon rank-sum test with continuity correction to test our hypothesis that abundance of carrion beetles differs in the areas with the two different types of soil. This hypothesis was tested for the whole taxonomic family Silphidae and for each individual species. We chose this nonparametric test because the data were not normally distributed. We also

tested the effect of soil type on the Brillouin biodiversity index using Welch's t-test for two samples.

The significance level was set at 5%. Data management and all analysis was carried out using the Canoco 5 and R statistical programs (ter Braak & Šmilauer, 2012; R Core Team, 2014).

A.3 Results

In total, we obtained 444 samples of silphid communities from 39 different locations (18 on chernozem and 21 on fluvisol soils), the rest was destroyed or did not contain any carrion beetles. In these samples there were 43,856 specimens of 15 carrion beetle species (see Table 1). Three of them are on the Czech Red List of Invertebrates. *Nicrophorus antennatus* (Reitter) and *N. germanicus* (Linnaeus) are considered to be Endangered and *N. sepultor* (Charpentier) Nearly Endangered (Růžička, 2005a).

The whole dataset was dominated by *Thanatophilus sinuatus* (Fabricius) (> 63% of the total catch). This species was also dominant in spring (>73%) and summer (>58%) but not in autumn (12%) when it was the third most abundant after *Nicrophorus vespillo* (Linnaeus) (> 55%) and *Thanatophilus rugosus* (Linnaeus) (> 15%).

DCA showed that species did not cluster according to their percentage abundance on either chernozem or fluvisol soils (see Fig 3). This indicates that other environmental factors could also be involved in determining their occurrence. We tested all the environmental factors included in the CCA analysis, and manual forward selection indicated the following were significant: soil type (chernozem ($p_{adj}=0.038$) and fluvisol ($p_{adj}=0.038$)) and three crops (*Zea mays* ($p_{adj}=0.038$), *Hordeum vulgare* ($p_{adj}=0.038$) and *Helianthus annus* ($p_{adj}=0.038$)) (see Fig 4). The remaining factors appeared to have no significant effect on the composition of the carrion beetles recorded in this study (climatic region (T4, T2 and MT10) and other crops (*Brassica napus*, *Beta vulgaris*, *Carthamus tinctorius*, *Glycine max*, *Phacelia tanacetifolia* and *Triticum aestivum*)).

These finding led us to test the effect of soil on the biodiversity and abundance of carrion beetles. The Brillouin biodiversity index ranged from 0.188 to 1.271 between localities, but

there was not a significant association ($t=1.747$, $p=0.09$) between this index and soil type (mean values of the Brillouin index: chernozem = 0.835 and fluvisol = 0.692).

The carrion beetles as a group were significantly more abundant in areas with a chernozem soil, where the median abundance was 62 ($SD = \pm 157.38$), than on fluvisol soils, where the median abundance was 37 ($SD = \pm 110.867$) ($W=28677.5$, $p>0.001$). At the species level there were significantly higher numbers of specimens of the following species in areas with chernozem soils: *Nicrophorus antennatus* ($W=26118.5$, $p>0.001$), *N. germanicus* ($W=25946.5$, $p=0.029$), *N. interruptus* (Stephens) ($W=26693$, $p=0.03$), *N. sepultor* ($W=31962$, $p>0.001$), *Silpha obscura obscura* (Linnaeus) ($W=31132$, $p>0.001$) and *T. sinuatus* ($W=28514.5$, $p=0.001$). Only in the case of *N. humator* (Gleditsch) ($W=23152.5$, $p=0.005$) were significantly more caught in areas with fluvisol soils. For the rest of the species we did not find any significant association between their abundance and the soil types studied, although we had to exclude some species from the statistical evaluation because they were underrepresented, namely: *N. investigator* (Zetterstedt) ($n=7$), *N. vespilloides* (Herbst) ($n=6$), *Oiceoptoma thoracicum* (Linnaeus) ($n=8$) and *Phosphuga atrata atrata* (Linnaeus) ($n=1$). For an overview of the results, see Fig 5 and Table 1.

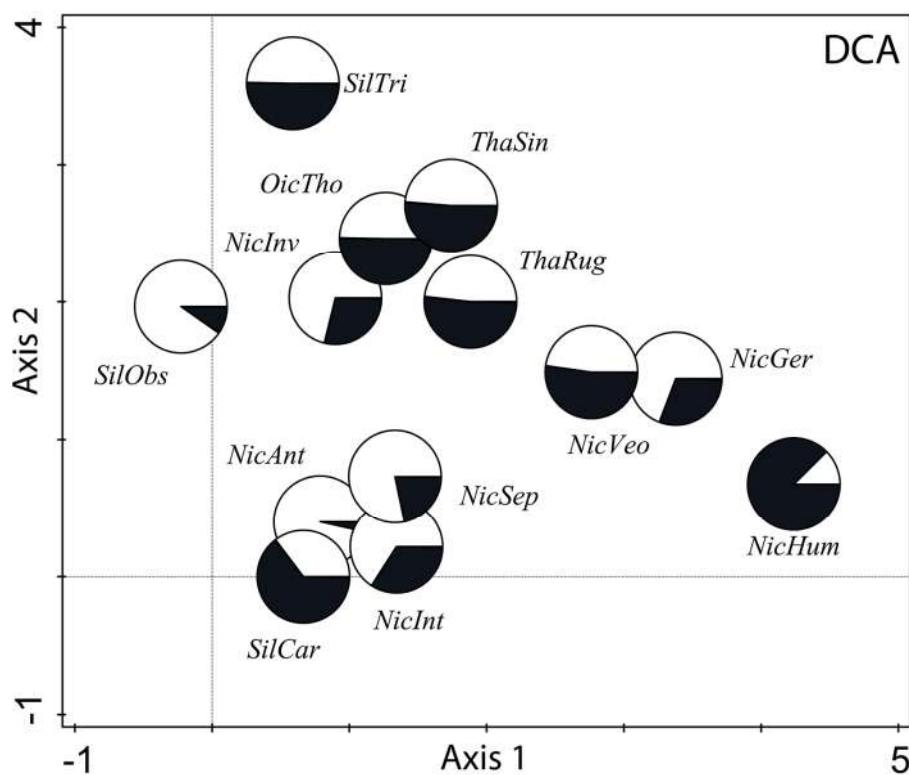


Fig 3. Unconstrained DCA of all species (NicAnt = *N. antennatus*; NicGer = *N. germanicus*; NicHum = *N. humator*; NicInt = *N. interruptus*; NicInv = *N. investigator*; NicSep = *N. sepultor*; NicVeo = *N. vespollo*; NicVes = *N. vespilloides*; OicTho = *O. thoracicum*; SilCar = *S. carinata*; SilObs = *S. obscura obscura*; SilTri = *S. tristis*; ThaRug = *T. rugosus*; ThaSin = *T. sinuatus*) with their percentage abundance in areas with different types of soil (chernozem – black, fluvisol – white) illustrated by pie charts.

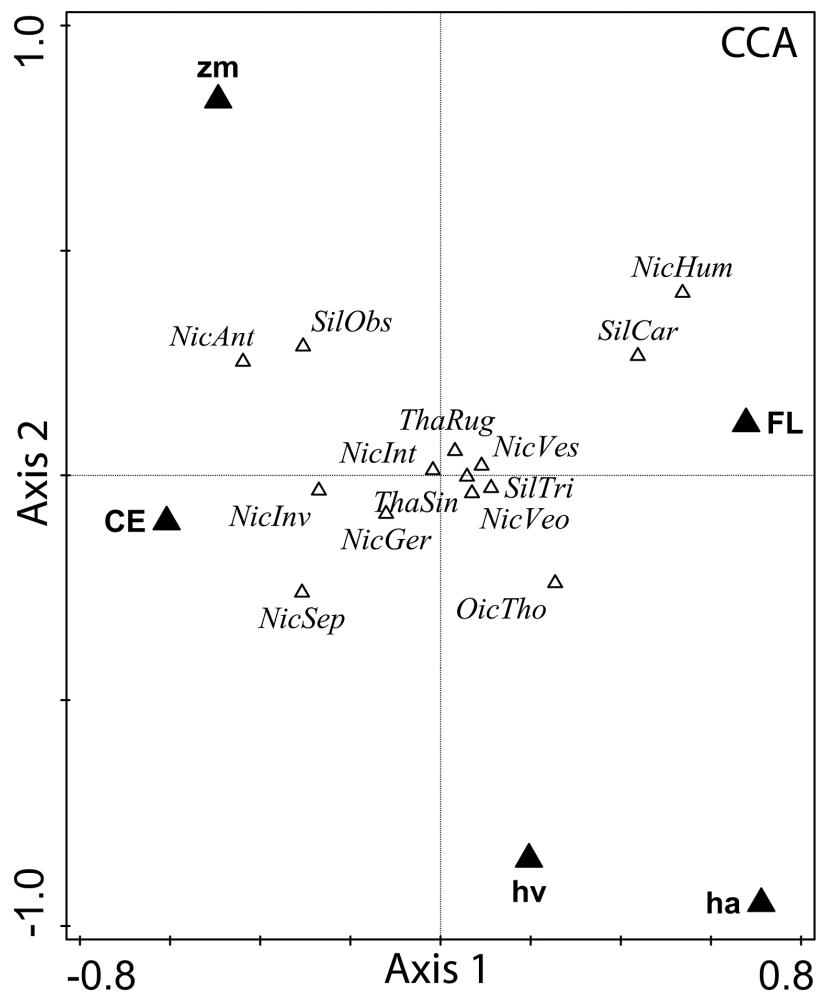


Fig 4. Partial CCA ordination diagram with carrion beetles and statistically significant environmental variables (CE – chernozem, FL – fluvisol, zm – *Zea mays*, hv – *Hordeum vulgare*, ha – *Helianthus annus*).

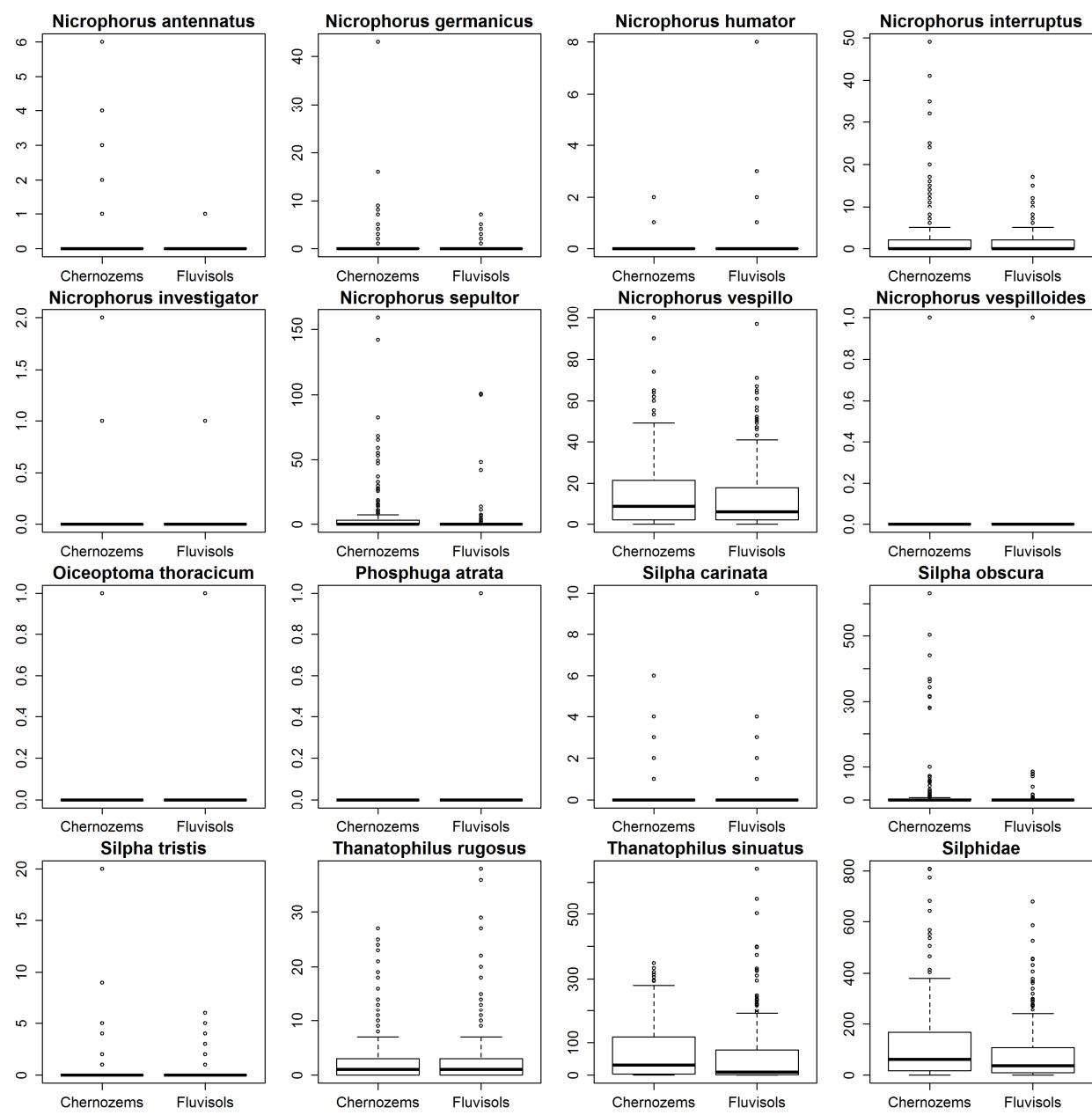


Fig 5. Box plots of all the carrion beetles recorded in the areas with the two types of soil. The thick horizontal lines within the boxes indicate median values. The upper and lower boxes indicate the 75th and 25th percentiles, respectively. Whiskers indicate the values within the 1.5 interquartile ranges. Small circles are outliers.

A.4 Discussion

During the field work we captured and identified 15 species of carrion beetles. Three of which are currently considered as rare and are on the Czech Red List of Invertebrates as Endangered (*N. antennatus* and *N. germanicus*) or Nearly Endangered (*N. sepultor*) (Růžička, 2005a). The last ecological studies on these species in Europe were done almost 50 years ago when they were probably much more common (Novák, 1966; Petruška, 1968). These species deserve much more attention, because they could play a major role in nature conservation as bio-indicators or umbrella species (see Guarisco, 1997; Holloway & Schnell, 1997; Walker & Hoback, 2007; Creighton et al., 2009; Crawford & Hoagland, 2010; Jurzenski et al., 2014).

The most frequent species was *T. sinuatus*, whose dominance was overshadowed by *N. vespillo* and *T. rugosus*, but only in autumn. All these species seem to be very common in open landscape habitats and our findings confirm the earlier observations of Novák (1962, 1965, 1966) and Petruška (1964).

T. sinuatus and *T. rugosus* are considered to be co-occurring species without spatially or temporally differentiated niches (Novák, 1966). The higher abundance of *T. rugosus* in autumn samples could indicate a temporal niche differentiation.

Some of the carrion beetles caught are considered to be forest species (*N. humator*, *N. investigator*, *N. vespilloides* and *O. thoracicum*) by several authors (e.g., Růžička, 1994; Kočárek & Benko, 1997). However, the traps were not set in forested areas, our observations are in line with their findings, because few of these species were caught in this study (in total 32, 7, 6 and 6 specimens, respectively). The more frequent occurrence of *N. humator* was probably due to the greater flight activity of this large and common beetle.

CCA analysis revealed that the factors that are significantly associated with the species composition are both soil types (chernozem and fluvisol) and three crops (*Zea mays*, *Hordeum vulgare* and *Helianthus annus*). As depicted in Fig 4 the positions of these factors are roughly orthogonal, with the exception of *H. vulgare* and *H. annus*, therefore they are probably unrelated.

The association between the abundance of the carrion beetles and these crops is very interesting. We think that it could be due to the microclimatic conditions in fields with these crops. Based on our experience, *Z. mays* provides a much more humid and cooler environment than *H. vulgare* and *H. annus*. Further study is needed to reveal causality.

We were able to show that the abundance of seven of the carrion beetles (*N. antennatus*, *N. germanicus*, *N. humator*, *N. interruptus*, *N. sepultor*, *Silpha obscura obscura* and *T. sinuatus*) differed significantly in areas with chernozem and fluvisol soils, and therefore soil type is an important factor in determining the occurrence of these carrion beetles. Our findings are supported by the results of the CCA analysis and Wilcoxon rank-sum tests.

This association is assumed by many authors, but only for beetles of the subgenus *Nicrophorus* (e.g., Pukowski, 1933; Paulian, 1946; Theodorides & Heerdt, 1952; Novák, 1961, 1962). Heretofore, this phenomenon was empirically proven only for North American species (Muths, 1991; Bishop et al., 2002; Looney et al., 2009), where the association of beetles of the subfamily Silphinae with a particular soil was previously reported by Bishop et al. (2002).

All these findings raise an important question as to what mechanisms drive this phenomenon. Muths (1991) has shown that burying beetles are able to distinguish among different types of soil and choose the best substrate for digging in the laboratory. This experiment was conducted at a small scale (an area with a diameter of 1.5 m) and it is reasonable to think that this type of response occurs only during microhabitat selection. Thus, it does not answer our question. Our goal was to determine if the type of soil could be important in habitat selection. Looney et al. (2009) offers three possible explanations. Beetles are either simply more abundant in areas with a particular type of soil, or they preferentially colonize, or they are more competitive in such areas. From our point of view the last option is the most likely for the following reasons.

It is likely that one of the main factors influencing long range habitat selection by carrion beetles is the presence of food (carrion) (Kalinová et al., 2009). The greater abundance of these beetles in areas with particular types of soil (chernozem or fluvisol in our case) could be caused indirectly.

However, burying beetles are good fliers and can cover long distances they mostly choose to stay close to their original locations (e.g., *Nicrophorus americanus*, which is a relatively large and robust beetle, is capable of flying as far as 7.41 km in a single night, but more typically travels less than 1.6 km/night) (Jurzenksi et al., 2011). Limited mobility coupled with adaptation to local conditions could cause the observed spatial structure rather than individual habitat choice (preferential colonization). This is also in line with general local adaptation hypotheses (Alstad, 1998).

The same reasons might account for our finding in the case of *T. sinuatus*, because it has functional wings (Ikeda et al., 2008), but only a short flight range (Petruška, 1964). Therefore, it has a very similar lifestyle to the burying beetles studied: *N. antennatus*, *N. germanicus*, *N. humator*, *N. interruptus*, *N. investigator*, *N. sepultor*, *N. vespillo* and *N. vespilloides*. This hypothesis is supported by the fact that all these species were recorded in areas with both of the different types of soil and often in large numbers, so they are not closely associated with a particular type of soil (see Table 1).

The biology of *Silpha obscura obscura* is not well known. There is little known about the diet and flight ability of the species in the genus *Silpha* (Ikeda et al., 2007). There is also a strong possibility that this species is not strictly necrophagous. Its preference for areas with a chernozem soil is surprising in this case, but it could be due the spatial structure of the population, which is driven by an adaptation to chernozem soil.

Loess loams are proposed as the preferred soils of many species of burying beetles (*N. antennatus*, *N. germanicus*, *N. interruptus*, *N. vespillo* and *N. sepultor*), but according to Novák (1962) *N. vestigator* prefers sandy soils. This species unfortunately was not recorded in our study despite the fact that we set traps close to locations where it was often recorded by collectors in the past. It is possible that we missed the population peaks of this rare species. Future studies on this species should focus on earlier months in the year (April–May), when it could be more abundant (Novák, 1962; Šustek, 1981).

Our findings are limited to two types of soil (chernozem and fluvisol) and can be extended only to similar types of soil (e.g., Phaeozem and haplic Luvisol). It is also possible that the

abundances of the species studied are different throughout their distribution area, as pointed out by Scott (1998).

This study has revealed more about the distribution and ecology of European carrion beetles, especially the preference of three endangered species (*N. antennatus*, *N. germanicus* and *N. sepultor*) for areas with chernozem soils (see also Jakubec & Růžička, 2012). Our finding that the preferences of some species of carrion beetles are possibly determined by an adaptation to particular types of soil is crucial for the effective conservation of these species, which is currently not a topical issue in the Czech Republic and Europe generally. These beetles are charismatic and could become a widely accepted flagship species for stakeholders and policymakers, as indicated by the public interest in and the vast number of studies on the American burying beetle (*N. americanus*) (e.g., Anderson, 1982b; Lomolino et al., 1995; Amaral et al., 1997; Crawford & Hoagland, 2010).

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A.5 *References*

ALSTAD, D. 1998: Population Structure and Conundrum of Local Adaptation. In *Genetic Structure and Local Adaptation in Natural Insect Populations: Effects of Ecology, Life History and Behavior* (ed. by Mopper, S. & Strauss, S.Y.). Springer-Science+Business Media, B.V., Florence, pp. 3–21.

AMARAL, M., KOZOL, A. & FRENCH, T. 1997: Conservation Status and Reintroduction of the Endangered American Burying Beetle. *Northeastern Naturalist*, **4**, 121–132.

- ANDERSON, R.S. 1982a: Resource partitioning in carrion beetle (Coleoptera: Silphidae) fauna of southern Ontario: ecological and evolutionary considerations. *Canadian Journal of Zoology*, **60**, 1314–1325.
- ANDERSON, R.S. 1982b: On the Decreasing Abundance of *Nicrophorus americanus* Olivier (Coleoptera: Silphidae) in Eastern North America. *The Coleopterists Bulletin*, **36**, 362–365.
- ANDERSON, R.S. & PECK, S.B. 1985: *The Insects and Arachnids of Canada, Part 13: The carrion beetles of Canada and Alaska (Coleoptera: Silphidae and Agyrtidae)*. Agriculture Canada, Ottawa.
- ARCHER, M.S. 2003: Annual variation in arrival and departure times of carrion insects at carcasses: implications for succession studies in forensic entomology. *Australian Journal of Zoology*, **51**, 569–576.
- BISHOP, A.A., HOBACK, W.W., ALBRECHT, M. & SKINNER, K.M. 2002: A Comparison of an Ecological Model and GIS Spatial Analysis to Describe Niche Partitioning Amongst Carrion Beetles in Nebraska. *Transactions in GIS*, **6**, 457–470.
- BRAAK, C.J.F. TER & ŠMILAUER, P. 2012: Canoco reference manual and user's guide software for ordination, version 5.0.
- CENIA. 2008: Czech National Geoportal [WWW Document]. URL <http://geoportal.gov.cz> [accessed on 2008].
- CENIA. 2015: Czech National Geoportal [WWW Document]. URL <http://geoportal.gov.cz> [accessed on 2015].
- CRAWFORD, P.H.C. & HOAGLAND, B.W. 2010: Using Species Distribution Models to Guide Conservation at the State Level: the Endangered American Burying Beetle (*Nicrophorus americanus*) in Oklahoma. *Journal of Insect Conservation*, **14**, 511–521.
- CREIGHTON, J.C., BASTARACHE, R., LOMOLINO, M. V. & BELK, M.C. 2009: Effect of forest removal on the abundance of the endangered American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae). *Journal of Insect Conservation*, **13**, 37–43.
- CREIGHTON, J.C., VAUGHN, C.C. & CHAPMAN, B.R. 1993: Habitat Preference of the Endangered American Burying Beetle (*Nicrophorus americanus*) in Oklahoma. *The Southwestern Naturalist*, **38**, 275–277.
- ESRI. 2008: ArcMap 9.2. ESRI (Environmental Systems Research Institute). Redlands, California, USA.

- GOFF, M.L. 2009: Forensic Entomology. In *Encyclopedia of Insects* (ed. by Resh, V.H. & Cardé, R.T.). Elsevier, London, pp. 381–386.
- GREBENNIKOV, V. V. & NEWTON, A.F. 2012: Detecting the basal dichotomies in the monophylum of carrion and rove beetles (Insecta: Coleoptera: Silphidae and Staphylinidae) with emphasis on the Oxyteline group of subfamilies. *Arthropod Systematics & Phylogeny*, **70**, 133–165.
- GUARISCO, H. 1997: Discovery of the Federally Endangered American Burying Beetle (*Nicrophorus americanus*) in the Chautauqua Hills of Southeastern Kansas Discovery of the Federally Endangered American Burying Beetle (*Nicrophorus americanus*) in the Chautauqua Hills of South. *Transactions of the Kansas Academy of Science*, **100**, 116–122.
- HOCKING, M.D., DARIMONT, C.T., CHRISTIE, K.S. & REIMCHEN, T.E. 2007: Niche variation in burying beetles (*Nicrophorus* spp.) associated with marine and terrestrial carrion. *Canadian Journal of Zoology*, **85**, 437–442.
- HOLLOWAY, A.K. & SCHNELL, G.D. 1997: Relationsip Between Numbers of the Endangered American Burying Beetle *Nicrophorus americanus* Olivier (Coleoptera: Silphidae) and Available Food Resources. *Biological Conservation*, **81**, 145–152.
- IKEDA, H., KAGAYA, T., KUBOTA, K. & ABE, T. 2007: Flight capabilities and feeding habits of silphine beetles: are flightless species really “carrion beetles”? *Ecological Research*, **22**, 237–241.
- IKEDA, H., KAGAYA, T., KUBOTA, K. & ABE, T. 2008: Evolutionary relationships among food habit, loss of flight, and reproductive traits: life-history evolution in the Silphinae (Coleoptera: Silphidae). *Evolution*, **62**, 2065–2079.
- JAKUBEC, P. & RŮŽIČKA, J. 2012: Distribution of open landscape carrion beetles (Coleoptera: Silphidae) in selected lowlands of the Czech Republic. *Klapalekiana*, **48**, 169–189.
- JURZENSKI, J., SNETHEN, D.G., BRUST, M.L. & HOBACK, W.W. 2011: New records of carrion beetles in Nebraska reveal increased presence of the American burying beetle, *Nicrophorus americanus* Olivier (Coleoptera: Silphidae). *Great Plains Research*, **21**, 131–143.
- JURZENSKI, J.D., JORGENSEN, C.F., BISHOP, A., GROSSE, R., RIENS, J. & HOBACK, W.W. 2014: Identifying priority conservation areas for the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae), a habitat generalist. *Systematics and Biodiversity*, **12**, 149–162.
- KALINOVÁ, B., PODSKALSKÁ, H., RŮŽICKA, J., HOSKOVEC, M. & RŮŽIČKA, J. 2009: Irresistible bouquet of death—how are burying beetles (Coleoptera: Silphidae: *Nicrophorus*) attracted by carcasses. *Naturwissenschaften*, **96**, 889–899.

- KOČÁREK, P. 2001: Diurnal activity rhythms and niche differentiation in a carrion beetle assemblage (Coleoptera: Silphidae) in Opava, the Czech Republic. *Biological Rhythm Research*, **32**, 431–438.
- KOČÁREK, P. & BENKO, K. 1997: The occurrence and seasonal activity of Silphidae in Hlučín region (Silesia, Czech Republic). *Časopis Slezského muzea v Opavě*, **46**, 173–179.
- LINGAFELTER, S.W. 1995: Diversity, Habitat Preferences, and Seasonality of Kansas Carrion Beetles (Coleoptera : Silphidae). *Journal of the Kansas Entomological Society*, **68**, 214–223.
- LOMOLINO, M. V., CREIGHTON, J.C., SCHNELL, G.D. & CERTAIN, D.L. 1995: Ecology and Conservation of the Endangered American Burying Beetle (*Nicrophorus americanus*). *Conservation Biology*, **9**, 605–614.
- LOMOLINO, M. V. & CREIGHTON, J.C. 1996: Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus americanus*. *Biological Conservation*, **77**, 235–241.
- LOONEY, C., CALDWELL, B.T. & EIGENBRODE, S.D. 2009: When the prairie varies: the importance of site characteristics for strategising insect conservation. *Insect Conservation and Diversity*, **2**, 243–250.
- MAGURRAN, A.E. 2004: *Measuring Biological Diversity*. Blackwell Science Ltd, Malden. MULLINS, P.L., RILEY, E.G. & OSWALD, J.D. 2013: Identification, distribution, and adult phenology of the carrion beetles (Coleoptera: Silphidae) of Texas. *Zootaxa*, **3666**, 221–251.
- MUTHS, E.L. 1991: Substrate Discrimination in Burying Beetles, *Nicrophorus orbicollis* (Coleoptera: Silphidae). *Journal of the Kansas Entomological Society*, **64**, 447–450.
- NOVÁK, B. 1961: Saisonmässiges Vorkommen von Totengräbern in Feldbiozönosen (Col. Silphidae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **6**, 45–114.
- NOVÁK, B. 1962: Ein Beitrag zur Faunistik und Ökologie der Totengräber (Col. Silphidae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **11**, 263–300.
- NOVÁK, B. 1965: Zur Faunistik und Ökologie der Totengräber in den Feldbiotopen von Haná (Col. Silphidae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **19**, 121–151.
- NOVÁK, B. 1966: Dynamika populací brouků ze skupiny Silphini (Coleoptera). Populationsdynamik der Silphini (Coleoptera)). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **22**, 129–151.

- PAULIAN, R. 1946: Essai de bionomie quantitative sur les nécrophores. *Revue française d'Entomologie*, **13**, 93–98.
- PECK, S.B. & ANDERSON, R.S. 1985a: Taxonomy, phylogeny and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). *Quaestiones Entomologicae*, **21**, 247–317.
- PECK, S.B. & ANDERSON, R.S. 1985b: Seasonal activity and habitat associations of adult small carrion beetles in southern Ontario (Coleoptera: Leiodidae: Cholevinae). *The Coleopterists Bulletin*, **39**, 347–353.
- PETRUŠKA, F. 1964: Beitrag zur Bewegungsaktivität einiger Aaskäfer-Arten (Col. Silphidae et Histeridae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **16**, 159–187.
- PETRUŠKA, F. 1968: The Carrion-Beetles as a Component Part of the Insects Fauna of the Fields in the Uničov Plain. *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **28**, 159–187.
- PIELOU, E.C. 1975: *Ecological diversity*. Wiley-Interscience, New York.
- PUKOWSKI, E. 1933: Oekologische Untersuchungen an Necrophorus F. *Zeitschrift für Morphologie und Oekologie der Tiere*, **27**, 518–186.
- R CORE TEAM. 2014: R: A language and Environment for Statistical Computing.
- RŮŽIČKA, J. 1994: Seasonal activity and habitat associations of Silphidae and Leiodidae: Cholevinae (Coleoptera) in central Bohemia. *Acta Societatis Zoologicae Bohemicae*, **58**, 67–78.
- RŮŽIČKA, J. 2005: Silphidae (mrchožroutovití). Silphidae (carrion beetles). In *Červený seznam ohrožených druhů České republiky. Bezobratlí. Red list of threatened species in the Czech Republic. Invertebrates*. (ed. by Farkač, J., Král, D. & Škorpík, M.). Agentura ochrany přírody a krajiny ČR, Praha, pp. 429–430.
- RŮŽIČKA, J. 2007: Beetles (Coleoptera) in rock debris of Komáří vrch hill, catastre of Nová Ves near Kraslice. In *Příroda Kraslicka 1. [Nature of Kraslice region 1.]*. (ed. by Hejkal, J., Havalová, A. & Michálek, J.). Nakladatelství Jan Farkač, Praha, pp. 83–102.
- RŮŽIČKA, J. & SCHNEIDER, J. 2004: Silphidae. In *Catalogue of Palaearctic Coleoptera, Vol. 2* (ed. by Löbl, I. & Smetana, A.). Apollo Books, Stenstrup, pp. 229–237.
- SCOTT, M.P. 1998: The Ecology and Behavior of Burying Beetles. *Annual Review of Entomology*, **43**, 595–618.

- SIKES, D. 2005: Silphidae Latreille, 1807. In *Handbook of Zoology, Volume IV: Arthropoda: Insecta, Part 38: Coleoptera, Beetles. Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. (ed. by Beutel, R.G. & Leschen, R.A.B.). Walter de Gruyter, Berlin, pp. 288–296.
- SIKES, D. 2008: Carrion beetles (Coleoptera: Silphidae). In *Encyclopedia of Entomology. Volume 1: A - C* (ed. by Capinera, J.L.). Springer, Berlin, pp. 749–758.
- SIKES, D.S. & VENABLES, C. 2013: Molecular phylogeny of the burying beetles (Coleoptera: Silphidae: Nicrophorinae). *Molecular Phylogenetics and Evolution*, **69**, 552–65.
- ŠUSTEK, Z. 1981: Keys to identification of insects 2: Carrion beetles of Czechoslovakia (Coleoptera: Silphidae). *Zprávy Československé Společnosti Entomologické při ČSAV*, **2**, 1–47.
- THEODORIDES, J. & HEERDT, P.F. 1952: Nouvelles recherches écologiques sur les nécrophores (Coleoptera Silphidae); comparison des résultats du terrain avec ceux du laboratoire (thermopreferendum at hygropreferendum). *Physiologia Comparata et Oecologia*, **2**, 297–309.
- WALKER, T.L. & HOBACK, W.W. 2007: Effects of Invasive Eastern Redcedar on Capture Rates of *Nicrophorus americanus* and Other Silphidae. *Environmental entomology*, **36**, 297–307.

B Thermal summation model and instar determination of all developmental stages of *Sciodrepoides watsoni* (Coleoptera: Cholevinae)

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Key words. Coleoptera, Leiodidae, Cholevinae, development, thermal summation model, forensic entomology, instar determination, Holarctic region

Abstract. Necrophagous beetles are underrepresented in forensic entomology studies despite their undeniable utility for the field. In our article we would like to address this problem and provide information regarding developmental biology and instar determination of *Sciodrepoides watsoni* (Spence, 1813), which is very common species occurring across the Holarctic region. We collected adult specimens from several localities across the Czech Republic to establish a laboratory culture with constant temperature regime and long day photoperiod. These adults were divided between five treatments that differed only in temperature (15, 18, 21, 25 and 28°C). Emerging larvae were separated and their individual development was photographically documented every day until adulthood. Parameters of thermal summation models and their standard errors were calculated for each developmental stage. We also propose head width as a new character for larval instar determination together with a new methodology for future studies of size based characters.

B. 1 Introduction

Forensic entomology is a rapidly developing new field of science (Midgley *et al.*, 2010). New methods and models for estimation of minimum post mortem interval (PMI_{min}) are developing at a very rapid pace (e.g., pre-appearance interval, gene expression during larval development, quantile mixed effects models, generalized additive modeling or generalized additive mixed modeling) (Matuszewski, 2011; Tarone & Foran, 2011; Baqué *et al.*, 2015a, 2015b), but even the well-established models lack actual data for their further use and application. A good example is the commonly used thermal summation model (Richards & Villet, 2008). This model, which is based on the assumption that development of immature stages is linear, has been known for several decades (Higley *et al.*, 1986), but it is still not established for the majority of forensically important species of invertebrates, which would be a great contribution to legal investigations.

Currently these models are known for a number of fly species (Diptera) (Nabity *et al.*, 2006; Villet *et al.*, 2006; Richards *et al.*, 2009; Voss *et al.*, 2010a, 2010b, 2014; Tarone *et al.*, 2011; Nassu *et al.*, 2014; Zuhá & Omar, 2014), but because the utility of beetles in forensic entomology was overlooked for a long time (Midgley *et al.*, 2010), there are only three species of beetles with well established thermal summation models (Midgley & Villet, 2009a; Velásquez & Viloria, 2009; Ridgeway *et al.*, 2014).

Although using beetles for PMI_{min} estimation has several benefits compared to flies. Beetles tend to have longer development therefore they can be found on and around the carrion for a longer period of time (Villet, 2011). They also do not form a maggot ball like flies and they can be reared individually so they are easier to handle in laboratory conditions (Midgley *et al.*, 2010). However, we think that the biggest advantage is the possibility of cross validating PMI_{min} estimates between species and groups, such as flies and mites. This is important mainly in cases when one of these groups or species could have been affected by external factors (restricted access to body, temperature too high or low, etc.) and give biased estimate (H. Šuláková 2014, pers. comm.).

As mentioned above, statistically robust thermal summation models are only known for three species of necrophagous beetles, all of them belonging to the family Silphidae. These are

Thanatophilus micans (Fabricius, 1794) (Ridgeway *et al.*, 2014), *T. mutilatus* (Castelnau, 1840) (Ridgeway *et al.*, 2014) and *Oxelytrum discicolle* (Brullé, 1840) (Velásquez & Viloria, 2009). *T. micans* occurs mainly in Africa and extends to Yemen on the Arabian Peninsula (Schawaller, 1981; Růžička & Schneider, 2004), *T. mutilatus* has a geographical distribution restricted to South Africa region (Schawaller, 1981, 1987) and *O. discicolle* inhabits Central and South America (Peck & Anderson, 1985a). This leaves North America, Europe and most of Asia without a single beetle species with a known thermal summation model.

Models alone are not sufficient to make a species available for use in legal investigation. There are other criteria to be fulfilled. Any forensic entomologist has to be able to identify those species in every stage of development and discriminate between larval instars. Without reliable instar determination it is not possible to expect reliable PMI_{min} estimates. But this is sometimes complicated, because beetle larvae often lack any morphological characters, which would allow such identification. Therefore size based models were developed instead (Midgley & Villet, 2009b; Velásquez & Viloria, 2010; Fratzak & Matuszewski, 2014), but larval instars of only two European species can be identified in this way, namely *Necrodes littoralis* (Linnaeus, 1758) (Silphidae) and *Creophilus maxillosus* (Linnaeus, 1758) (Staphylinidae) (Fratzak & Matuszewski, 2014).

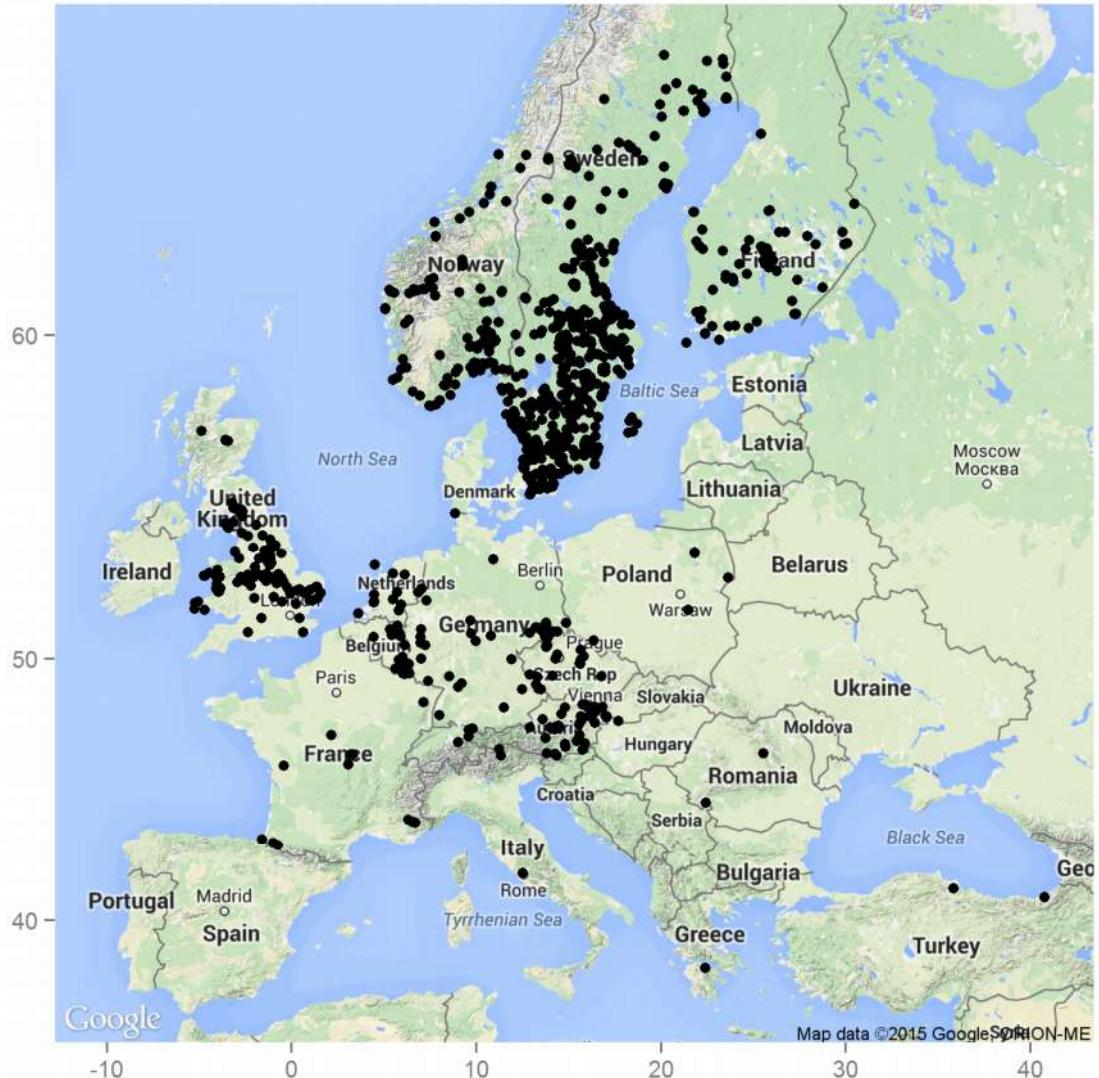


Fig. 1: Occurrence of *S. watsoni* in Europe based on our own observations and records from the GBIF database (GBIF, 2015). Underlying map generated by package ggmap (Kahle & Wickham, 2013).

Sciodrepoides watsoni (Spence, 1813) is one of the most widespread and abundant species of necrophagous beetles in the Holarctic region (Peck & Cook, 2002; Perreau, 2004). Robust occurrence data are available especially for Europe (see Fig. 1). This saprophagous beetle belongs to subfamily Cholevinae (Leiodidae) and is rather inconspicuous, because the whole

body is brown and about 3 millimeters long (Szymczakowski, 1961; Perreau, 2004) (see Fig. 2). Adults can be fairly easily distinguished from the other European species of genus *Sciodrepoides* by the shape of the antennal segments (Szymczakowski, 1961). The main peak of activity is during the warmer parts of the year (late spring and summer) (Růžička, 1994). All stages can be found on decaying corpses of vertebrates in various types of habitats where they feed and develop (Růžička, 1994; Peck & Cook, 2002; Topp, 2003).



Fig. 2: Habitus of the *S. watsoni* male from dorsal view.

Egg, all larval instars and pupae of this beetle were properly described recently by Kilian & Mądra (2015) and also DNA barcode for possible validation is available (Schilthuizen *et al.*, 2011). Therefore identification of this species in every stage of development is not an issue.

Instar determination of *S. watsoni* larvae is also partially possible thanks to Kilian & Mądra (2015), but they found morphological differences only between the first and second instar, which is not enough for future application for PMI_{min} estimation.

We would like to improve the utility of *S. watsoni* for PMI_{min} estimation by finding the parameters of its thermal summation model and also offering a new method for identifying larval stages based on combination of morphological features mentioned by Kilian & Mądra (2015) and the size based characters.

B.2 Material and Methods

A laboratory colony was started with adults of *S. watsoni*, which were collected in spring of 2012 and/or 2013 from five localities in the Czech Republic (Prague – Suchdol (15 May – 12 April 2012, 15 May – 12 April 2013), Běstvina (7 – 11 April 2012, 6 – 10 April 2013), Domažlice (28 May – 12 April 2013) and Klatovy (14 – 28 May 2013)).

Beetles were collected using 10 baited pitfall traps, placed at each locality. The traps composed of 1,080 ml plastic buckets (opening of 103 mm and 117 mm deep). These buckets were embedded in substrate up to the rim to eliminate any obstructions which could deter beetles from entering. As protection against rain we put metal roofs (150x150 mm) over the traps. The roof was supported by four 100 mm nails, one in each corner, and placed approximately two centimeters above the surface. The bait, ripened cheese (Romadur) and fish meat (*Scomber scombrus* Linnaeus, 1758), was placed directly inside the bucket on a shallow layer of moist soil. This created good conditions for survival of the trapped beetles between servicing, which was usually done once a week.

After transport to our laboratory we confirmed identification and sexed the beetles under binocular microscope (Olympus SZX7). Most of the beetles were than randomly assigned to

form breeding groups of at least four individuals (2 males and 2 females). Specimens from the same locality were kept together regardless of capture date to eliminate cross-breeding of different populations. These groups were formed to produce new progeny, which we than observed throughout of their development (breeding experiment).

These groups were kept in Petri dishes with the layer of soil and small piece (approx. 5x5 mm) of fish meat (*Scomber scombrus*) as a food source. The content of the dish was lightly sprayed with tap water every day and food was provided *ad libitum* and changed if we spotted any sign of fungal growth.

The dishes were randomly placed in one of six climatic chambers (custom made by CIRIS s.r.o.). The chambers were set up at constant temperature (15, 18, 21, 25 or 28°C) and 16 hours of light and 8 hours of dark photoperiod regime, maintained by fluorescent light (Osram L 8W/640). We tried to have a similar number of breeding groups from the same locality in each chamber. We accomplished that in case of beetles from Praha and Běstvina, but it was not possible for beetles from Domažlice and Klatovy, because of a low number of adults obtained. Therefore we kept them together in one treatment (18°C).

We also started an observation study of their natural behavior. The study was conducted in a small plastic box (15x6x2 centimeters) with 12 adult individuals (7 females and 5 males) from Prague population. In this colony we did not separate larvae from adults or each other, but we allowed them to interact freely and without our intervention. The box itself was placed in 18°C treatment and its inhabitants were attended in the same way as the specimens in the breeding experiment (regular water spray and meat replaced if we saw a sign of fungal growth).

In the breeding experiment we slightly changed our method of handling eggs and first instar between the years to improve accuracy of our observations. During the first year of experiment (2012) we searched the dishes for eggs and then we transferred them individually to separate dish. But due to the fact that eggs of *S. watsoni* are very small and adults tended to hide them in the substrate, we struggled to find them right after laying. Due to that our estimation of egg and L1 development for the first year were inconsistent and we did not use them for models.

To minimize this error we chose different approach for the second year (2013). We instead transferred the whole breeding group to a new Petri dish every day. The old dishes were marked and kept in the same climatic chamber as the parents. We checked them every day for emergence of the first instar larvae that were further separated into their own dishes. The time when the eggs were laid, was estimated as a half-time between the transfers of the breeding group.

Every larva from the second year (2013) breeding experiment was photographed every day, starting with their occurrence as the first instar larvae and we continued until pupation. In this way we documented morphological changes during their development. The whole process of finding the larva and taking a picture did not usually take more than 1 minute in total. Key developmental stages of each larva with the accurate date and time could be distinguished based on those photographs simply by keeping track of the change in the width of their head capsule, because its size expand after each molt.

It happened sometimes that we were unable to find some larva in the Petri dish. In that case we treated the dish as full and put it back into its treatment and tried another day. If the larvae changed instars before we found it, we counted both instars as NAs and we tried to keep track of it all the time in the next stage.

We also used obtained photographs for the instar determination. Because, the dorsal side of all the larvae was photographed daily, we had plenty of characters to choose from. However, the thorax and abdomen of the *S. watsoni* larvae are not strongly sclerotized (see Fig. 3), so we omitted these parts, and also the body length, as good characters for instar determination. Measuring of some smaller parts such as urogomphi or antennae was impractical, because our camera had low resolution and those parts would be very challenging to measure accurately.



Fig.3: Dorsal (A), lateral (B) and ventral (C) side of the third larval instar of *S. watsoni*. Point, where the measurement of the head width was done, is shown (a).

The most stable and reliable feature for the instar determination of *S. watsoni* larvae appears to be the head capsule. This part of the body is strongly sclerotized, therefore it is not affected by water or food content, but it changes its size after each molt so it is tightly linked with individual growth. Also the head does not change its size in different fixation media or even after desiccated, thus the instar can be identified even for very poorly handled and long dead specimens. Ultimately, we chose the head width over its length for a practical reason. Head

width of living larvae do not change on the pictures captured from above, but length varies a lot.

For estimating the mean and standard deviation of the head capsule width we used all photographs where the head was clearly visible and was sharp enough to make a precise measurement. All measurements were done with graphical program EidosMicro calibrated by precise ruler.

Parameters of thermal summation model (lower developmental threshold (t) and sum of effective temperatures (k)) were estimated for each developmental stage using the major axis regression method ($(DT) = k + tD$) where D is duration of development, T is environmental temperature ($^{\circ}\text{C}$). This formula was developed by (Ikemoto & Takai, 2000) and is commonly used for estimation of thermal summation parameters and their standard errors in forensic entomology (e.g., Midgley & Villet, 2009a; Ridgeway *et al.*, 2014). Ikemoto & Takai (2000) method is based on standard linearized formula ($1/D = - (t/k) + (1/k)T$), but it weights out the data points in lower and upper part of the temperature range to obtain more reliable estimates of the parameters.

Normality of all the data was confirmed by evaluation of the qqplots and histograms. The significance level was set at 5%. Data management and all analysis were carried out using R statistical program (R Core Team, 2015). Graphical outputs were handled by ggplot2 and ggmap R packages (Wickham, 2009; Kahle & Wickham, 2013).

B.3 Results

In total, we were able to catch 81 adult specimens of *S. watsoni* and they produced 399 first instar larvae (Prague – 174, Běstvina - 178, Klatovy - 19, Domažlice - 28) for the breeding experiment. Because we obtained only twelve adults from Klatovy and six from Domažlice, it was impossible to split them between all our treatments. Therefore we decided to keep them all at 18°C .

In the breeding experiment we observed, directly or indirectly, and recorded duration of the development of all *S. watsoni* stages, namely egg, three larval instars (L1, L2 and L3) and pupae. These observations were made on 399 specimens in total starting with the first instar larvae.

Higher temperatures (25 and 28°C) were probably limiting to breeding activity of our beetles in the experiment. Ultimately we did not obtain any larvae from the 28°C treatment. Mortality in the other treatments was also quite high especially for the third instar and pupae (see Fig. 4) and only 23 individuals developed until adulthood.

The development times differed between stages (Fig. 5) and the mean development time decreased with increasing temperature (Fig. 6), except for L2 and L3 instars in 25°C treatment. The sum of effective temperatures (k) and lower developmental threshold (t) values were calculated for all developmental stages of *S. watsoni* with their expected errors (see Table 1 and Fig. 7).

Table 1: Summary of development constants for *S. watsoni* for five developmental stages. Sum of effective temperatures (k) and lower developmental threshold (t) shown as means with the standard errors.

Temperature						
Stage	range	R2	Df	p value	k	t
egg	15-25	0.8134	220	2.20E-16	929.354 ±49.111	11.400 ±0.368
L1	15-25	0.9375	171	2.20E-16	233.683 ±27.031	15.437 ±0.305
L2	15-25	0.8768	206	2.20E-16	243.945 ±45.301	15.689 ±0.410
L3	15-25	0.8199	27	1.49E-11	2602.996 ±297.464	9.375 ±0.846
Pupae	15-21	0.8563	10	1.61E-05	1207.431 ±489.288	12.535 ±1.624

Mortality of the specimens in the observation study could not be measured, but the colony itself prospered very well and number of adults increased steadily, which is in contrast with what we observed in the breeding experiment. The observed females tended to hide their eggs in small holes or crevices in the substrate. Newly hatched larvae could be found mostly around the food source. The third instar larvae after few days of feeding dug underground and created small chamber where they pupate. No cannibalism or hostility of any kind between individuals was recorded.

For the instar determination measurements we made 2,104 photographs, but only 1,731 were good enough to allow precise measurements of the head width. Those pictures covered all three larval instars (L1 = 591, L2 = 500 and L3 = 640 pictures). The bias in number of pictures between different stages was caused by difference in the duration of development of these instars (lower stages of development are shorter in duration) and it was also much more challenging to take a usable picture of the first or second instar larvae.

The mean width of the head appears to be a good character for the instar determination (see Table 2 and Fig. 8). Standard deviations are well separated and there is only a small overlap between 75th and 25th quintiles across all instars. We recorded some extreme values on the both sides of the spectrum, but these were very rare.

Table 2: The head widths (in millimeters) of all three larval instars of *S. watsoni*.

Instar	max.	min.	mean	stand. dev.
L1	0.392	0.270	0.329	0.017
L2	0.479	0.350	0.421	0.021
L3	0.582	0.451	0.522	0.021

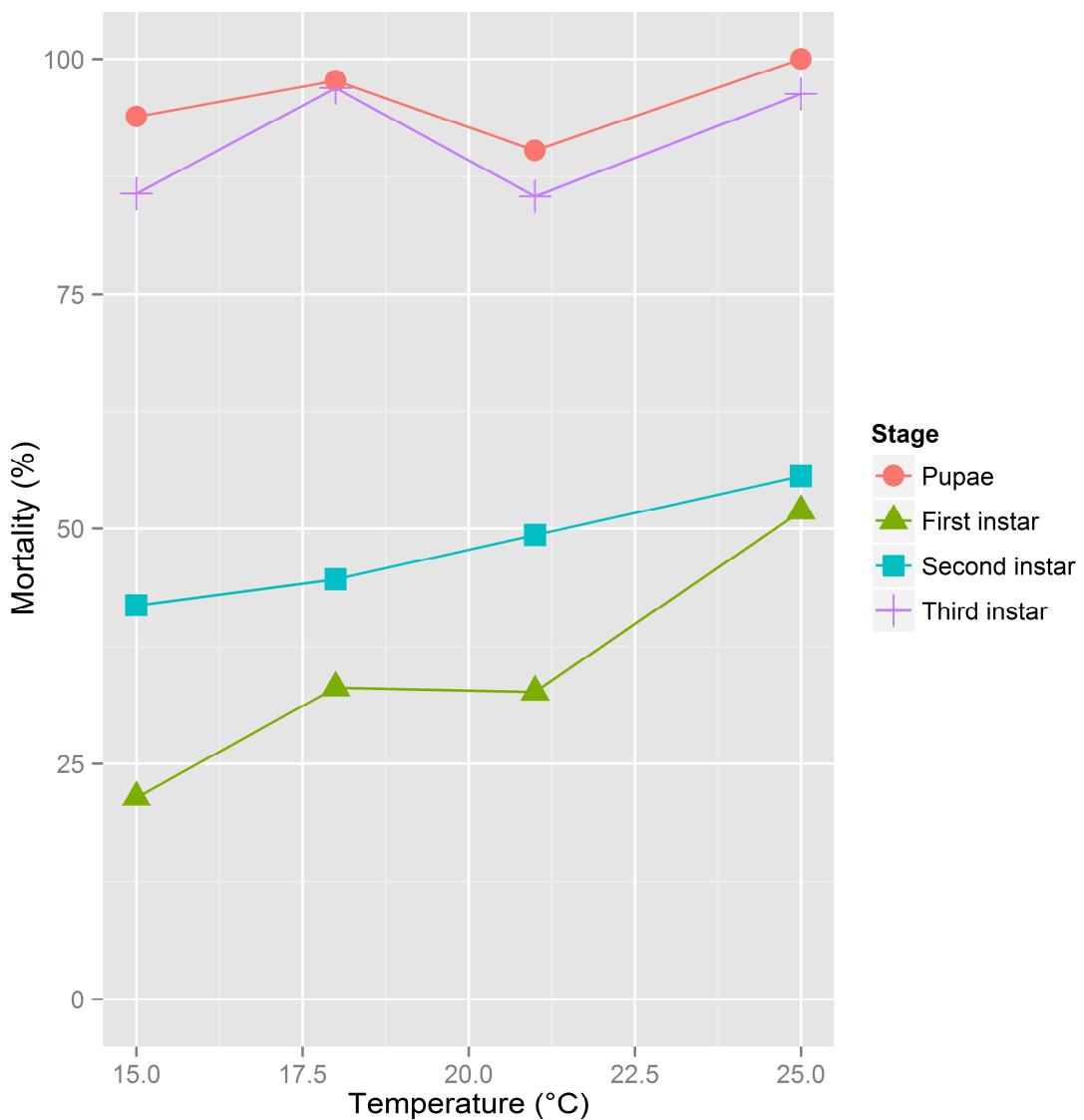


Fig. 4: Mortality rates between developmental stages of *S. watsoni*. The 28°C treatment is not shown, because breeding did not occur.

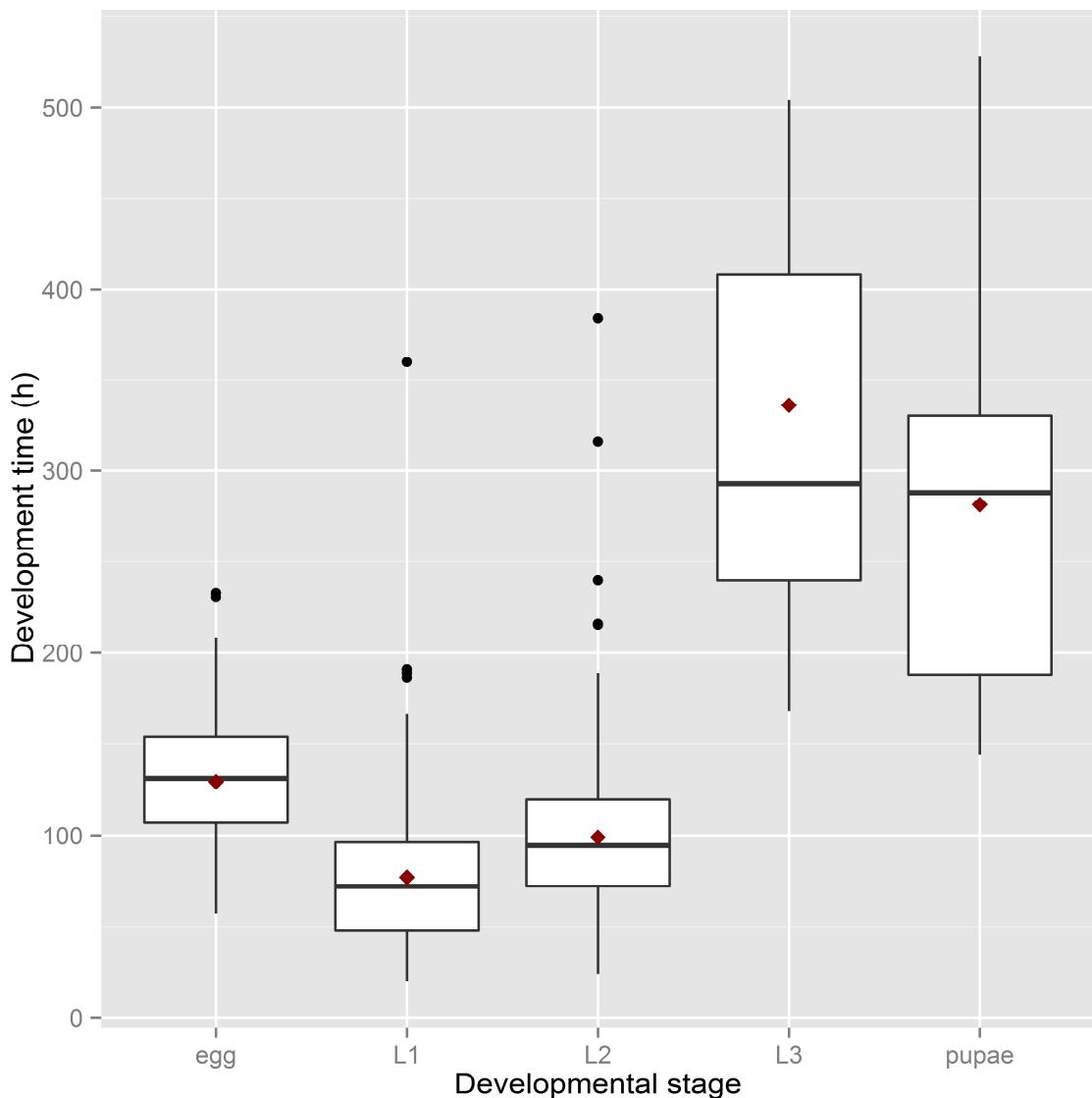


Fig. 5: Observed range of development times of *S. watsoni* over four experimental treatments (15, 18, 21, 25 °C) for each developmental stage (2012 data were excluded for egg and L1). The horizontal lines within the boxes indicate median values. The upper and lower boxes indicate the 75th and 25th percentiles, respectively. Whiskers indicate the values with the 1.5 interquartile ranges. Small, black dots are outliers. Small red dots are the mean values of development time.

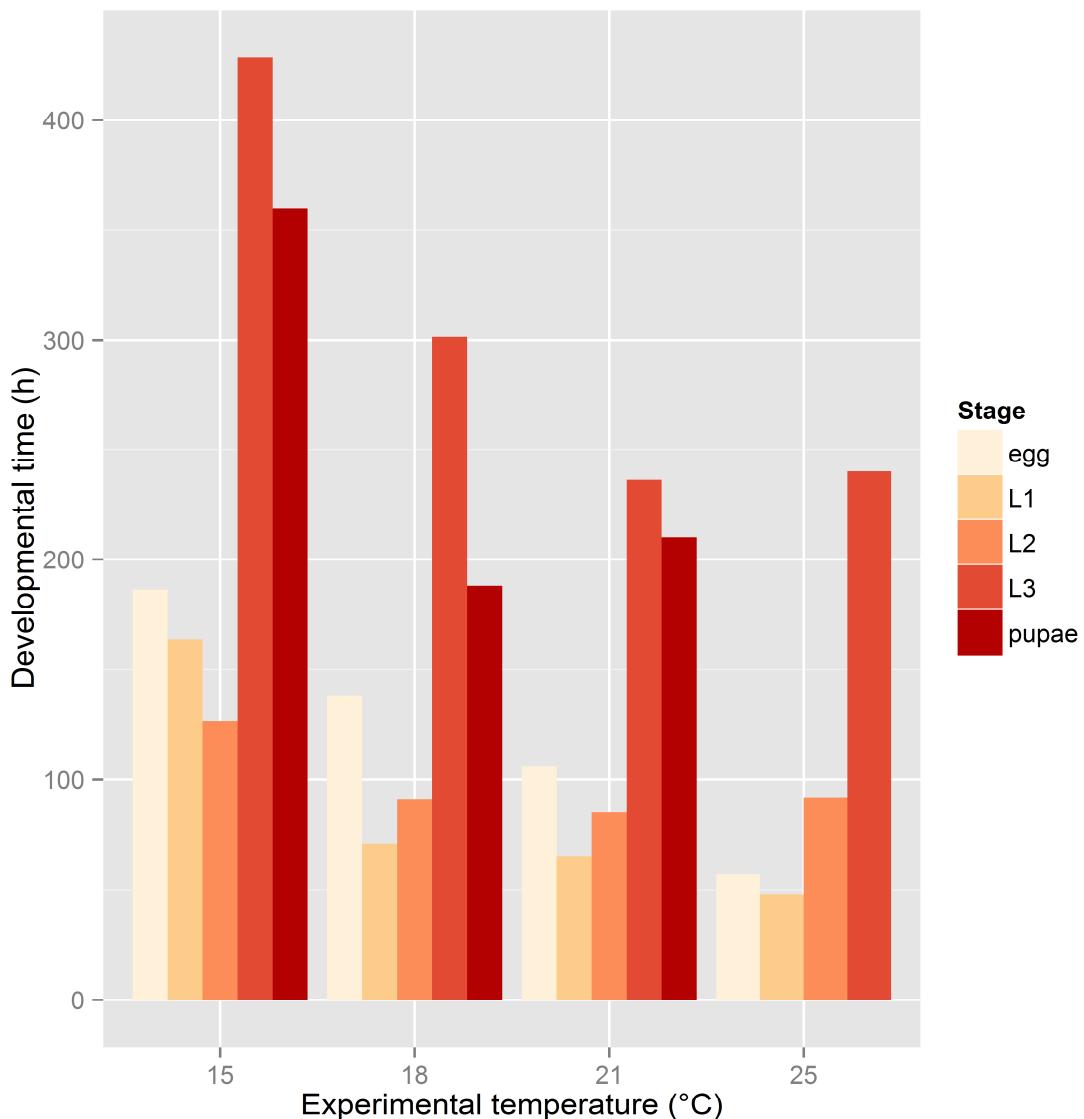


Fig. 6: Bar plot of mean development time (in hours) of all observed stages (2012 data were excluded for egg and L1) of *S. watsoni* over the whole range of experimental temperature except the 28°C, where beetles did not breed successfully.



Fig. 7: Major axis regression for all stages of development in *S. watsoni*. Black line shows median and grey area around is standard error. DT is the time in days to reach the stage multiplied by the constant rearing temperature. 2012 data were excluded for egg and L1.

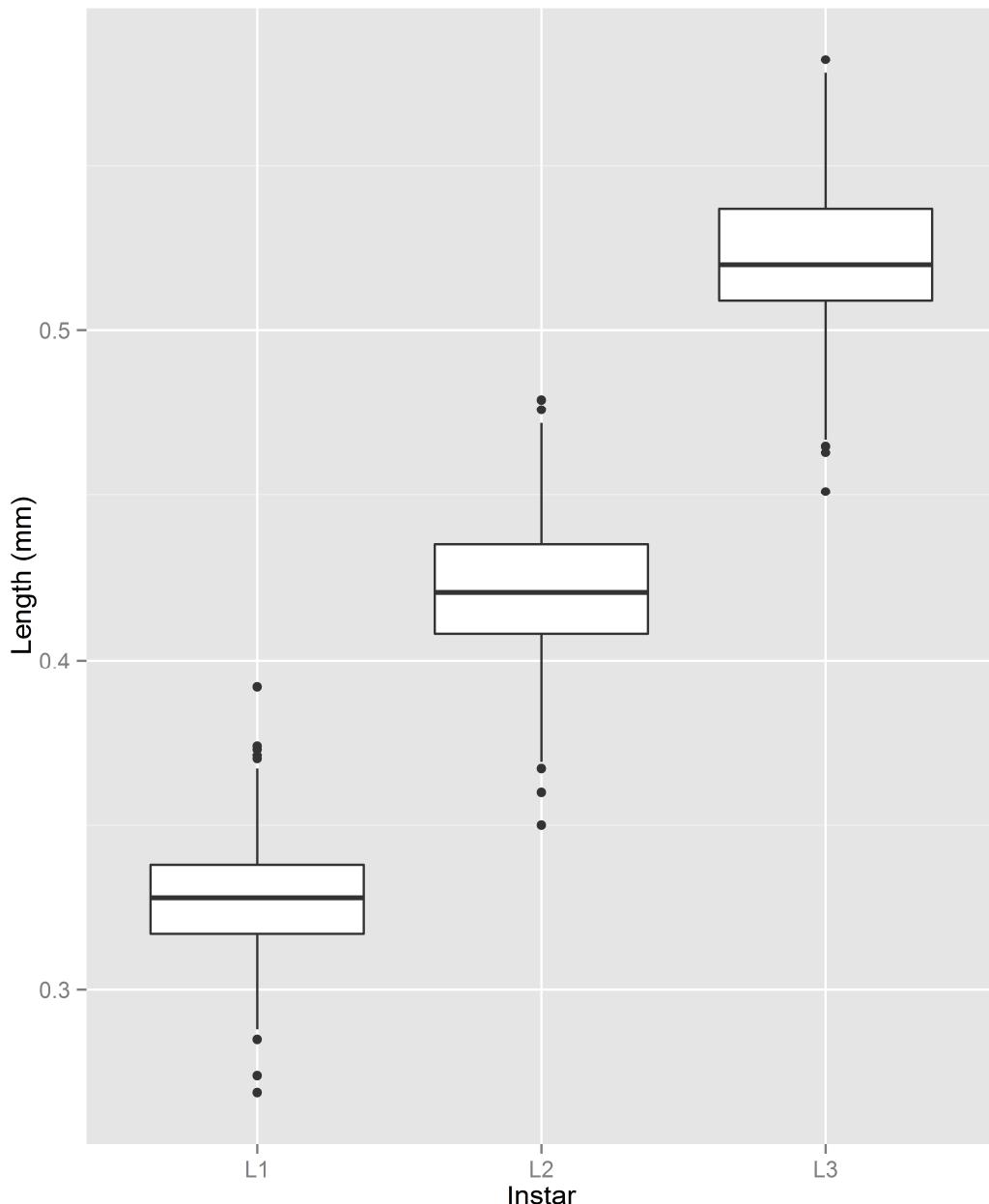


Fig. 8: Box plot graph of lengths of all three instars (L1, L2 and L3) of the *S. watsoni* larvae. The horizontal lines within the boxes indicate median values. The upper and lower boxes indicate the 75th and 25th percentiles, respectively. Whiskers indicate the values with the 1.5 interquartile ranges. Small, black dots are outliers.

B.4 Discussion

We did not obtain any larvae from the 28°C treatment probably because adults did not oviposit in this temperature or egg mortality was too high. The second claim is little bit more likely from our point of view, because we did not find any eggs. But as we mentioned in the methodology section, eggs of *S. watsoni* are tiny and we could simply overlook them during our controls in the Petri dish's substrate even under the binocular microscope.

Mortality of our specimens in the breeding experiment was very high over the all treatments especially in the later stages (L3 and pupae). This was in a sharp contrast with what we saw in the observation study. The whole colony in the observation study prospered and even increased in the number of adult over time. Only difference between these two was that we did not separate individuals and we also did not have to handle the larvae for photo documentation.

We did not observe any hostility between specimens in the observation study or signs of cannibalism between individuals as reported by Kilian & Mądra (2015), but it is possible that we missed it, because the estimated number of individuals in the box was close to one hundred.

We think that photographing process was not so intrusive to be responsible for such high mortality rates thus it is more likely that separation from other larvae and adults was the reason for that. Peck (1975) mentioned that *Ptomaphagus hirtus* (Tellkampf, 1844) (Leiodidae: Cholevinae: Ptomaphagini) needed soil from its cave of origin to successfully complete the development. Soil bacteria probably play some part in this process, because specimens did not develop on autoclaved soil. It is possible that adults feeding along with larvae could have provided such bacteria in our case. Another explanation could be that feeding of multiple individuals is much more effective or improves the quality of the food source.

We had to change our methodology of egg extraction for the second year due to the fact that eggs could be easily overlooked in the substrate and beetles refused to lay their eggs in offered damp cotton wool balls or small pieces of paper. To prevent bias in recorded time we introduced dish rotation methodology and adults stayed in the same dish only one day and then were moved to another. Those used dishes were then regularly searched for emerging larvae.

The main issue with this approach (dish rotation) is that we could not measure egg mortality, because we could not count the original number of eggs.

The mean development time decreased with increasing temperature (Fig. 6), except for L2 and L3 instars in the 25°C treatment. This might indicate that between 21°C and 25°C should be an optimal temperature for the development of these two stages. Optimal temperatures for lower stages are probably even higher. This agrees with findings of Engler (1981), who reported *S. watsoni* as warm season species in contrast to some species of *Choleva* and *Catops* that prefers to breed during the winter season and their optimal temperatures for development were below 16°C.

As you can see in Table 1, we had low number repeats for L3 and pupae. This was caused by high mortality rates of both instars. Measuring development time for pupae was even more challenging and we had difficulties measuring it precisely due to the fact that they did not pupate close to the wall of Petri dish. Therefore we had to search for them. This was sometimes unsuccessful and some specimens surprised us after time when they appeared as adults, because they had been missing and presumed dead.

Our methodology of measuring the size of the instars was based on continual observation of individuals from egg until pupation. This approached differs from other studies with similar goals (see Velásquez & Viloria, 2010; Fratzczak & Matuszewski, 2014), where authors tried to estimate the stage of development based on the size of selected characters without prior knowledge of the true stage of the specimen. This approach is from our point of view a little bit problematic, because those measured characters are correlated, therefore bigger larvae could be misidentified as higher instar than they really are. This bias would probably not affect the obtained mean values, but it would give a distorted picture of variation.

As can be seen on Fig. 8 and Table 3, all instars have some overlap in the head widths. This is especially true for the first and second instar. It would not help to measure more characters, because they are correlated, but we offer a different solution. A first instar larva has only primary setae on its body, but after molting to the second instar a secondary set of setae will emerge and they are also present unchanged on the third instar larvae. Thus chaetotaxy can be

used for the discrimination of the first and second instar larvae. For additional differential diagnosis of those morphological characters, see Kilian & Mądra (2015).

We established developmental parameters for *Sciodrepoides watsoni* together with the new and reliable character for instar determination. This species is so far the smallest necrophagous beetle with a known thermal summation model. The developmental characteristics provided in this study will help to estimate the PMImin in cases where it was not possible before. The instar determination is the integral part of the PMImin estimation, because without accurate determination of instar we could not reach the right conclusion. We strongly encourage other authors to adopt our methodology for establishing size based instar characteristics, because it provides an accurate picture of its variability.

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B.5 *References*

BAQUÉ, M., AMENDT, J., VERHOFF, M.A. & ZEHNER, R. 2015a: Descriptive analyses of differentially expressed genes during larval development of *Calliphora vicina* (Diptera: Calliphoridae). *International Journal of Legal Medicine*, **129**, 891–902.

BAQUÉ, M., FILMANN, N., VERHOFF, M.A. & AMENDT, J. 2015b: Establishment of developmental charts for the larvae of the blow fly *Calliphora vicina* using quantile regression. *Forensic Science International*, **248**, 1–9.

- ENGLER, I. 1981: Vergleichende Untersuchungen zur jahreszeitlichen Einpassung von Catopiden (Col.) in ihren Lebensraum. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, **109**, 399–432.
- FRATCZAK, K. & MATUSZEWSKI, S. 2014: Instar determination in forensically useful beetles *Necrodes littoralis* (Silphidae) and *Creophilus maxillosus* (Staphylinidae). *Forensic Science International*, **241**, 20–26.
- GBIF. 2015: *Sciodrepoides watsoni* [WWW Document]. URL <http://www.gbif.org/species/4445042> [accessed on 2015].
- HIGLEY, L.G., PEDIGO, L.P. & OSTLIE, K.R. 1986: Degday: A Program for Calculating Degree-days, and Assumptions Behind the Degree-day Approach. *Environmental Entomology*, **15**, 999–1016.
- IKEMOTO, T. & TAKAI, K. 2000: A New Linearized Formula for the Law of Total Effective Temperature and the Evaluation of Line-Fitting Methods with Both Variables Subject to Error. *Environmental Entomology*, **29**, 671–682.
- KAHLE, D. & WICKHAM, H. 2013: ggmap : Spatial Visualization with. *The R Journal*, **5**, 144–161.
- KILIAN, A. & MĄDRA, A. 2015: Comments on the biology of *Sciodrepoides watsoni* watsoni (Spence, 1813) with descriptions of larvae and pupa (Coleoptera: Leiodidae: Cholevinae). *Zootaxa*, **3955**, 45–61.
- MATUSZEWSKI, S. 2011: Estimating the pre-appearance interval from temperature in *Necrodes littoralis* L. (Coleoptera: Silphidae). *Forensic Science International*, **212**, 180–188.
- MIDGLEY, J.M., RICHARDS, C.S. & VILLET, M.H. 2010: The Utility of Coleoptera in Forensic Investigations. In *Current Concepts in Forensic Entomology* (ed. by Amendt, J., Goff, M.L., Campobasso, C.P. & Grassberger, M.). Springer Netherlands, Dordrecht, pp. 57–68.
- MIDGLEY, J.M. & VILLET, M.H. 2009a: Development of *Thanatophilus micans* (Fabricius 1794) (Coleoptera: Silphidae) at constant temperatures. *International Journal of Legal Medicine*, **123**, 285–292.
- MIDGLEY, J.M. & VILLET, M.H. 2009b: Effect of the killing method on post-mortem change in length of larvae of *Thanatophilus micans* (Fabricius 1794) (Coleoptera: Silphidae) stored in 70% ethanol. *International Journal of Legal Medicine*, **123**, 103–8.
- NABILITY, P.D., HIGLEY, L.G. & HENG-MOSS, T.M. 2006: Effects of temperature on development of *Phormia regina* (Diptera: Calliphoridae) and use of developmental data in determining time intervals in forensic entomology. *Journal of Medical Entomology*, **43**, 1276–86.

- NASSU, M.P., THYSSEN, P.J. & LINHARES, A.X. 2014: Developmental rate of immatures of two fly species of forensic importance: *Sarcophaga* (*Liopygia*) *ruficornis* and *Microcerella halli* (Diptera: Sarcophagidae). *Parasitology Research*, **113**, 217–22.
- PECK, S. 1975: The life cycle of a Kentucky cave beetle, *Ptomaphagus hirtus*, (Coleoptera; Leiodidae; Catopinae). *International Journal of Speleology*, **7**, 7–17.
- PECK, S. & ANDERSON, R. 1985: Taxonomy, phylogeny and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). *Quaestiones Entomologicae*, **21**, 247–317.
- PECK, S.B. & COOK, J. 2002: Systematics, distributions, and bionomics of the small carrion beetles (Coleoptera: Leiodidae: Cholevinae: Cholevini) of North America. *The Canadian Entomologist*, **134**, 723–787.
- PERREAU, M. 2004: Family Leiodidae Fleming, 1821. In *Catalogue of Palaearctic Coleoptera Hydrophiloidea Histeroidea Staphylinoidea* (ed. by Löbl, I. & Smetana, A.). Apollo Books, Steensrup, pp. 133–203.
- R CORE TEAM. 2015: R: A Language and Environment for Statistical Computing.
- RIDGEWAY, J. A., MIDGLEY, J.M., COLLETT, I.J. & VILLET, M.H. 2014: Advantages of using development models of the carrion beetles *Thanatophilus micans* (Fabricius) and *T. mutilatus* (Castelnau) (Coleoptera: Silphidae) for estimating minimum post mortem intervals, verified with case data. *International Journal of Legal Medicine*, **128**, 207–220.
- RICHARDS, C.S., CROUS, K.L. & VILLET, M.H. 2009: Models of development for blowfly sister species *Chrysomya chloropyga* and *Chrysomya putoria*. *Medical and Veterinary Entomology*, **23**, 56–61.
- RICHARDS, C.S. & VILLET, M.H. 2008: Factors affecting accuracy and precision of thermal summation models of insect development used to estimate post-mortem intervals. *International Journal of Legal Medicine*, **122**, 401–408.
- RŮŽIČKA, J. 1994: Seasonal activity and habitat associations of Silphidae and Leiodidae: Cholevinae (Coleoptera) in central Bohemia. *Acta Societatis Zoologicae Bohemoslovicae*.
- RŮŽIČKA, J. & SCHNEIDER, J. 2004: Family Silphidae Latreille, 1807. In *Catalogue of Palaearctic Coleoptera, Vol. 2: Hydrophiloidea - Histeroidea - Staphylinoidea* (ed. by Löbl, I. & Smetana, A.). Apollo Books, Steensrup, pp. 229–237.
- SCHAWALLER, W. 1981: Taxonomie und Faunistik der Gattung *Thanatophilus* (Coleoptera: Silphidae). *Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie)*, **351**, 1–21.

- SCHAWALLER, W. 1987: Faunistische und systematische Daten zur Silphidae-Fauna Südafrikas (Coleoptera: Silphidae). *Entomofauna*, **8**, 277–285.
- SCHILTHUIZEN, M., SCHOLTE, C., WIJK, R.E.J. VAN, DOMMERSHUIZEN, J., HORST, D. VAN DER, ZU SCHLOCHTERN, M.M., ET AL. 2011: Using DNA-barcoding to make the necrobiонт beetle family Cholevidae accessible for forensic entomology. *Forensic Science International*, **210**, 91–95.
- SZYMCAKOWSKI, W. 1961: *Klucze do oznaczania owadów Polski, Część XIX Chrząszcze - Coleoptera, Zeszyt 13 Catopidae. [Keys to identification of Poland insects, Part XIX Beetles - Coleoptera, Issue 13 Small carrion beetles - Catopidae]]*. Państwowe wydawnictwo naukowe, Warszawa.
- TARONE, A.M. & FORAN, D.R. 2011: Gene expression during blow fly development: improving the precision of age estimates in forensic entomology. *Journal of Forensic Sciences*, **56**, S112–22.
- TARONE, A.M., PICARD, C.J., SPIEGELMAN, C. & FORAN, D.R. 2011: Population and Temperature Effects on *Lucilia sericata* (Diptera: Calliphoridae) Body Size and Minimum Development Time. *Journal of Medical Entomology*, **48**, 1062–1068.
- TOPP, W. 2003: Phenotypic plasticity and development of cold-season insects (Coleoptera: Leiodidae) and their response to climatic change. *European Journal of Entomology*, **100**, 233–243.
- VELÁSQUEZ, Y. & VILORIA, A.L. 2009: Effects of temperature on the development of the Neotropical carrion beetle *Oxelytrum discicolle* (Brullé, 1840) (Coleoptera: Silphidae). *Forensic Science International*, **185**, 107–109.
- VELÁSQUEZ, Y. & VILORIA, A.L. 2010: Instar determination of the neotropical beetle *Oxelytrum discicolle* (Coleoptera: Silphidae). *Journal of Medical Entomology*, **47**, 723–726.
- VILLET, M. 2011: African carrion ecosystems and their insect communities in relation to forensic entomology. *Pest Technol.*
- VILLET, M.H., MACKENZIE, B. & MULLER, W.J. 2006: Larval development of the carrion-breeding flesh fly, *Sarcophaga* (*Liosarcophaga*) *tibialis* Macquart (Diptera : Sarcophagidae), at constant temperatures. *African Entomology*, **14**, 357–366.
- Voss, S.C., COOK, D.F., HUNG, W.-F. & DADOUR, I.R. 2014: Survival and development of the forensically important blow fly, *Calliphora varifrons* (Diptera: Calliphoridae) at constant temperatures. *Forensic Science, Medicine, and Pathology*, **10**, 314–21.
- Voss, S.C., SPAFFORD, H. & DADOUR, I.R. 2010a: Temperature-dependent development of the parasitoid *Tachinaephagus zealandicus* on five forensically important carrion fly species. *Medical and Veterinary Entomology*, **24**, 189–98.

Voss, S.C., SPAFFORD, H. & DADOUR, I.R. 2010b: Temperature-dependant development of *Nasonia vitripennis* on five forensically important carrion fly species. *Entomologia Experimentalis et Applicata*, **135**, 37–47.

WICKHAM, H. 2009: ggplot2: elegant graphics for data analysis.

ZUHA, R.M. & OMAR, B. 2014: Developmental rate, size, and sexual dimorphism of *Megaselia scalaris* (Loew) (Diptera: Phoridae): its possible implications in forensic entomology. *Parasitology Research*, **113**, 2285–94.

C Distribution of open landscape carrion beetles (Coleoptera: Silphidae) in selected lowlands of the Czech Republic

Rozšíření mrchožroutovitých brouků (Coleoptera: Silphidae) otevřené krajiny ve vybraných nížinných oblastech České republiky

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Abstract. Beetles of the family Silphidae are an important but imperfectly understood part of Palaearctic ecosystems. Our team studied the ecology of open-landscape silphids around Louny, Kutná Hora, Zábřeh and Židlochovice in 2008 and 2009. We used 420 baited pitfall traps and, at 84 localities, we collected 71 234 specimens of 15 silphid species. Distribution data for all species are provided here. We found three endangered carrion beetle species listed on the Czech Red List of Invertebrates. Two are vulnerable thermophilic species of open landscapes, *Nicrophorus antennatus* (Reitter, 1884) (collected around Louny and Židlochovice) and *Nicrophorus germanicus* (Linnaeus, 1758) (Louny, Zábřeh and Židlochovice). The third is the near threatened species, *Nicrophorus sepulcralis* Charpentier, 1825 (collected around Louny, Kutná Hora, Zábřeh and Židlochovice), which also prefers open landscapes.

C.1 Úvod

Čeleď *Silphidae* je druhově poměrně malá, celosvětově obsahuje 186 dosud popsaných druhů ve dvou podčeledích, *Nicrophorinae* a *Silphinae*, přičemž největší diverzita této skupiny je soustředěna v holarktické oblasti (Sikes, 2008; Grebennikov & Newton, 2012). V České republice se prokazatelně vyskytuje 23 druhů (Růžička, 2005b).

Z ekologického hlediska je čeleď *Silphidae* zajímavá tím, že většina druhů je nekrofágů, ale potravní nároky jejich zástupců mohou být poměrně různorodé – od čistě karnivorních druhů, přes saprofágy až po fytofágy (Sikes, 2005). Stejně různorodé jsou i jejich biotopové preference, kdy část druhů preferuje otevřené biotopy a jiní jsou zase častěji nacházeni v lesích (Anderson, 1982; Růžička, 1994).

Rozšíření čeledi *Silphidae* v rámci ČR nebylo nikdy zpracováno jako celek, jedinou ucelenější faunistickou prací jsou údaje Vysokého (2007) pro Ústecký kraj. Protože zejména nekrofágové zástupci se dají dobře sbírat pomocí zemních pastí s návnadou, jednotlivé další záznamy z dalších oblastí ČR jsou roztríštěny v lokálních faunistických a ekologických pracích, často obecně věnovaných inventarizaci brouků (z těch současnějších např. Kočárek (1997), Kočárek & Benko (1997), Kočárek & Roháčová (1997), Růžička (1999, 2000, 2007), Bocáková (2003), Hamet & Vancl (2005), Nakládal (2008, 2011a, b), Boháč & Matějíček (2009), Háva (2009), Rébl (2010), Hamet et al. (2012)).

Starší i novější ekologické práce ze severní Moravy obsahují velmi zajímavé údaje o preferenci biotopů, sezónní dynamice a pohyblivosti druhů mrchožroutů polních ekosystémů (Novák, 1961, 1962, 1965, 1966; Petruška, 1964) a o cirkadiánní aktivitě a sukcesi mrchožroutů při dekompozici mršiny (Kočárek, 2001, 2002a, 2002b).

Tato práce vznikla v letech 2008 a 2009 za účelem poznání ekologických preferencí nekrofágů mrchožroutů žijících v otevřené krajině, jejím účelem je navázat na výše zmíněné práce Nováka a Petrušky. Sběr a determinace materiálu proběhl v rámci dvou bakalářských a čtyř diplomových prací vedených Janem Růžičkou. Ekologické výsledky budou zpracovány

samostatně, zde chceme shrnout a komentovat nashromážděná faunistická data, včetně údajů o vzácnější sbíraných druzích mrchožroutovitých brouků, zejména hrobaříků.

C.2 Materiál a metodika

Studovaná území se nacházela poblíž Loun (faunistické čtverce: 5648, 5649, 5650, 5749), Kutné Hory (5957, 6057, 6058), Zábřehu na Moravě (dále v textu označovaný jako Zábřeh) (6067, 6167, 6267) a v oblasti mezi Brnem a Břeclaví s centrem okolo Židlochovic (dále v textu označeno jako Židlochovice) (7064, 6865, 6965, 7065, 7066, 7167, 7267). Lokality byly vybrány v nížinných oblastech Čech i Moravy (obr. 1). Pasti byly vždy položené v otevřené krajině, nejčastěji na poli, vzdáleném min. 50 m od okraje biotopu včetně nejbližšího lesního fragmentu.

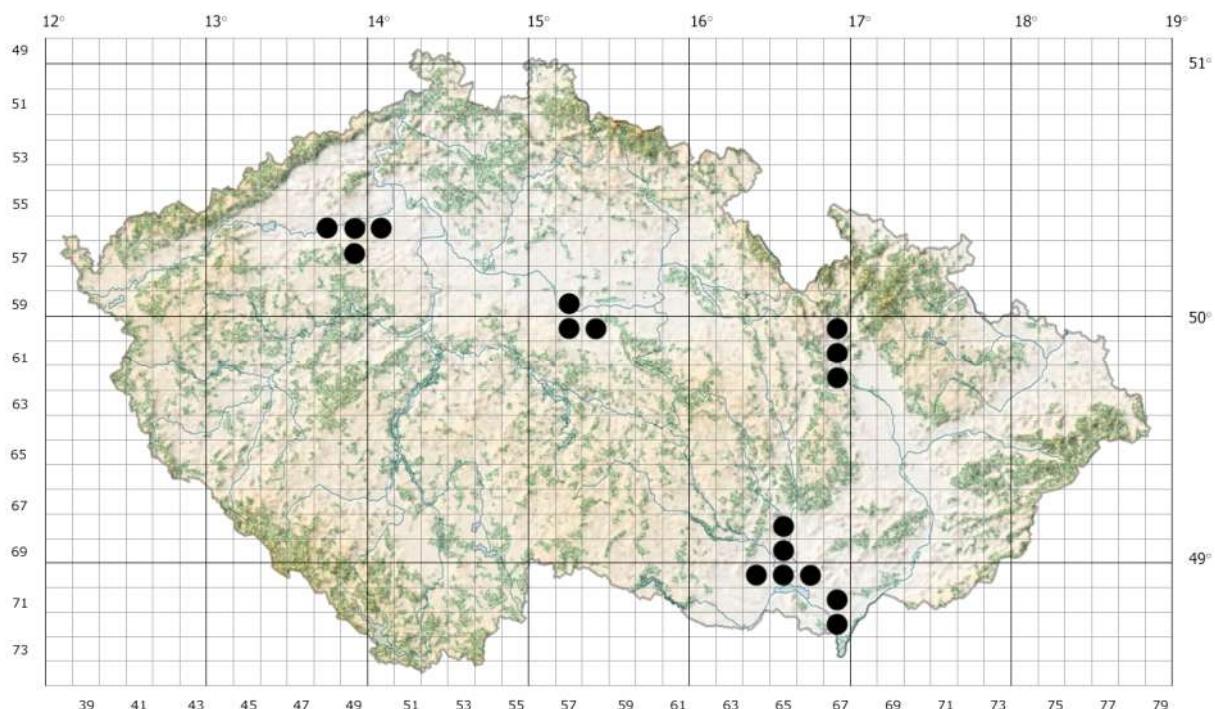
K odchytu mrchožroutů byly použity padací pasti s návnadou ze zrajícího sýra a rybího masa. Jako fixáž byla použita směs etylenglyku a vody v poměru 1:1.

Pasti byly zakopány na každé lokalitě v linii po pěti se vzdáleností 20 m mezi sebou, dále v textu je udán součet jedinců z celé pětice pastí. Exponované byly většinou po dobu 14 dnů. Jedinou výjimku tvořilo jarní období roku 2008, kdy byla expozice prodloužena z důvodu nepříznivého chladného počasí na tři týdny. Odběry probíhaly pouze ve třech úsecích během roku, v jarním, letním a podzimním období.

V okolí Loun a Kutné Hory byly pasti instalovány v letech 2008 a 2009, v Zábřehu na Moravě a v Židlochovicích pouze v roce 2009.

O sběr i determinaci se v každé oblasti starala vždy jedna osoba. Na Lounsku to byla Lucia Lvová, Židlochovice zpracovala Kateřina Štefúnová, Zábřeh Helena Šifrová a Kutnou Horu Pavel Jakubec.

Determinace byla prováděna na základě srovnání s klíčem Šustka (1981). Problematické kusy revidoval Jan Růžička. Dokladové kusy ze všech lokalit jsou uloženy v jeho sbírce s výjimkou materiálu z okolí Kutné Hory, který je uložen ve sbírce Pavla Jakubce.



Obr. 1. Přehled studovaných lokalit v ČR, schematicky vyjádřených pomocí faunistických čtverců (mapový podklad AOPK, Praha).

Fig. 1. Studied localities within the Czech Republic, schematically represented by dots on faunistic grid map (map base provided by AOPK, Praha).

C.2.1 Termíny expozice zemních pastí

Kutná Hora 2008 – jaro 2008: 3.V.–24.V.2008, léto 2008: 29.VI.–13.VII.2008, podzim 2008: 14.IX.–28.IX. 2008.

Kutná Hora 2009 – jaro 2009: 17.V.–31.V.2009, léto 2009: 5.VII.–19.VII.2009, podzim 2009: 13. IX.–27.IX. 2009.

Louny 2008 – jaro 2008: 10.V.–31.V.2008, léto 2008: 4.VII.–6.VII.2008, podzim 2008: 16.IX.– 29.IX.2008.

Louny 2009 – jaro 2009: 16.V.–30.V.2009, léto 2009: 1.VII.–12.VII.2009, podzim 2009: 17.IX.– 3.X.2009.

Židlochovice 2009 – jaro 2009: 15.V.–29.V.2009, léto 2009: 11.VII.–25.VII.2009, podzim 2009: 11.IX.–25. IX.2009.

Zábřeh 2009 – jaro 2009: 17.V.–31.V.2009, léto 2009: 5.VII.–19.VII.2009, podzim 2009: 13.IX.–27.IX.2009.

C.2.2 Popis lokalit

Následující sekce obsahuje bližší údaje o lokalitách, které jsou rozděleny do jednotlivých oblastí a let, kdy probíhal sběr. Tyto lokality jsou vždy označeny pořadovým číslem, názvem nejbližší obce, čtvercem faunistického mapování, GPS souřadnicemi středu linie pastí a vědeckým názvem pěstované plodiny v okolí pasti.

Kutná Hora 2008

1 – Církvice (6058c), 49°56'48,183"N, 15°20'47,287"E, *Zea mays*. **2** – Kalabousek (6058c), 49°55'39"N, 15°23'6,542"E, *Hordeum vulgare*. **3** – Žleby (6058d), 49°54'2,786"N, 15°29'30,715"E, *Triticum aestivum*. **4** – Vrdy I. (6058d), 49°55'12,946"N, 15°28'51,636"E, *Zea mays*. **5** – Horní Bučice (6058d), 49°56'8,593"N, 15°26'58,012"E, *Hordeum vulgare*. **6** – Bojmany (6058d), 49°57'16,818"N, 15°26'7,632"E, *Brassica napus*. **7** – Kolín (5957c), 4950°1'46,826"N, 15°13'26,68"E, *Brassica napus*. **8** – Starý Kolín I. (5957d), 50°0'5,501"N, 15°17'46,691"E, *Triticum aestivum*. **9** – Červený domek (6057b), 49°59'12,954"N, 15°19'26,96"E, *Brassica oleracea* convar. *capitata* var. *alba*. **10** – Nové Dvory I. (6058a), 49°57'59,871"N, 15°20'31,841"E, *Beta vulgaris* var. *rapacea*. **11** – Malín I. (6057a), 49°58'28,99"N, 15°18'5,774"E, *Triticum aestivum*. **12** – Skalka (6057a), 49°59'47,749"N, 15°14'51,083"E, *Beta vulgaris* var. *rapacea*.

Kutná Hora 2009

13 – Hluboký důl (5957c), 50°0'32.79"N, 15°15'52.48"E, *Triticum aestivum*. **14** – Starý Kolín II. (5957b), 50°0'32.79"N, 15°15'52.48"E, *Zea mays*. **15** – Libenice (6057b), 49°59'26.27"N,

15°15'55.35"E, *Beta vulgaris* var. *rapacea*. **16** – Hlízov (6057b), 49°59'32.44"N, 15°18'15.89"E,
Triticum aestivum. **17** – Nové Dvory II. (6057b), 49°57'31.46"N, 15°19'29.81"E, *Zea mays*. **18** –
Chotusice – letiště (6058a), 49°57'26.98"N, 15°21'26.72"E, *Triticum aestivum*. **19** – Chotusice
(6058a), 49°57'6.79"N, 15°24'19.85"E, *Hordeum vulgare*. **20** – Druhanice (6058d),
49°56'36.97"N, 15°25'12.53"E, *Glycine max*. **21** – Výčapy (6058d), 49°56'35.10"N, 15°27'28.13"E,
Triticum aestivum. **22** – Vrdy II. (6058d), 49°54'48.86"N, 15°27'53.30"E, *Hordeum vulgare*. **23** –
Vinice (6058d), 49°54'45.96"N, 15°29'31.00"E, *Triticum aestivum*. **24** – Malín II. (6057b),
49°58'15.74"N, 15°18'38.02"E, *Triticum aestivum*.

Louny 2008

25 – Pozdeň I. (5749d), 50°14'44,340"N 013°56'10,104"E, *Triticum aestivum*. **26** – Pozdeň II.
(5749b), 50°15'08,640"N 013°57'12,204"E, *Hordeum vulgare*. **27** – Hořešovice I. (5749b),
50°15'41,400"N 013°56'53,196"E, *Triticum aestivum*. **28** – Hořešovice II. (5749b),
50°15'43,056"N 013°57'20,988"E, *Triticum aestivum*. **29** – Hořešovice III. (5749b),
50°16'05,484"N 013°56'56,580"E, *Beta vulgaris* var. *rapacea*. **30** – Klobuky (5749b),
50°17'28,752"N 013°58'08,724"E, *Medicago sativa*.

Louny 2009

31 – Skupice I. (5648c), 50°19'51.8"N 13°41'41.61"E, *Zea mays*. **32** – Skupice II. (5648c),
50°20'50.86"N 13°42'10.96"E, *Hordeum vulgare*. **33** – Malnice (5648c), 50°20'15.86"N
13°43'19.41"E, *Phacelia tanacetifolia*. **34** – Postoloprty (5648a), 50°22'26.05"N, 13°42'59.19"E,
Triticum aestivum. **35** – Březno (5648a), 50°21'27.47"N 13°44'41.13"E, *Hordeum vulgare*. **36** –
Louny I. (5648b), 50°21'3.42"N 13°46'33.91"E, *Triticum aestivum*. **37** – Louny II. (5648b),
50°22'2.22"N 13°49'5.63"E, *Hordeum vulgare*. **38** – Veltěže (5649c), 50°20'54.16"N
13°52'45.63"E, *Hordeum vulgare*. **39** – Počedělice (5649a), 50°22'29.56"N 13°53'25.33"E,
Hordeum vulgare. **40** – Slavětín (5649a), 50°21'46"N 13°54'50.15"E, *Hordeum vulgare*. **41** –
Stradonice (5649b), 50°23'3.25"N 13°58'10.69"E, *Hordeum vulgare*. **42** – Křesín (5650a),
50°23'49.51"N 14°0'19.94"E, *Triticum aestivum*.

Židlochovice 2009

43 – Rebešovice (6865d), 49°6'3.309"N, 16°39'5.433"E, *Triticum aestivum*. **44** – Modřice (6865d), 49°7'5.7"N, 16°37'30.601"E, *Helianthus annus*. **45** – Holasice (6965b), 49°4'48.925"N, 16°37'13.974"E, *Triticum aestivum*. **46** – Vojkovice (6965b), 49°3'48.377"N, 16°35'2.289"E, *Triticum aestivum*. **47** – Medlov (6965c), 49°2'16.205"N, 16°32'11.277"E, *Carthamus tinctorius*. **48** – Kupařovice (6965c), 49°2'15.633"N, 16°30'7.352"E, *Hordeum vulgare*. **49** – Odrovice (6965c), 49°1'1.315"N, 16°31'12.008"E, *Brassica napus*. **50** – Cvrčovice (6965c), 49°0'9.305"N, 16°30'20.279"E, *Zea mays*. **51** – Pohořelice (7064a), 48°59'38.058"N, 16°32'0.136"E, *Zea mays*. **52** – Přibice (7065a), 48°59'10.534"N, 16°34'35.124"E, *Hordeum vulgare*. **53** – Vranovice (7065b), 48°59'1.514"N, 16°36'50.803"E, *Zea mays*. **54** – Přísnotice (7065b), 48°59'39.925"N, 16°37'45.159"E, *Zea mays*. **55** – Nosislav (6965d), 49°1'4.694"N, 16°37'35.941"E, *Hordeum vulgare*. **56** – Velké Němčice I. (7065b), 48°59'12.34"N, 16°38'58.002"E, *Triticum aestivum*. **57** – Velké Němčice II. (7066a), 48°58'41.388"N, 16°40'28.065"E, *Zea mays*. **58** – Uherčice (7065b), 48°57'38.568"N, 16°38'48.09"E, *Zea mays*. **59** – Ladná I. (7167c), 48°48'35.362"N, 16°51'56.754"E, *Helianthus annus*. **60** – Ladná II. (7267a), 48°47'55.264"N, 16°53'40.959"E, *Zea mays*.

Zábřeh 2009

61 – Sudkov (6067d), 49°55'10.79"N, 16°57'04.68"E, *Beta vulgaris* var. *rapacea*. **62** – Kolšov (6067d), 49°54'01.33"N, 16°56'43.62"E, *Hordeum vulgare*. **63** – Lesnice (6167b), 49°53'14.36"N, 16°56'21.08"E, *Beta vulgaris* var. *rapacea*. **64** – Zábřeh – sever (6167a), 49°53'33.19"N, 16°52'45.99"E, *Hordeum vulgare*. **65** – Zábřeh – západ (6167a), 49°53'14.53"N, 16°51'09.84"E, louka (pastvina). **66** – Rájec (6167a), 49°51'31.83"N, 16°53'44.99"E, *Hordeum vulgare*. **67** – Zvole (6167c), 49°49'49.81"N, 16°54'25.36"E, *Triticum aestivum*. **68** – Vlachov (6167c), 49°48'52.20"N, 16°54'23.69"E, *Triticum aestivum*. **69** – Libivá (6267a), 49°47'29.77"N, 16°54'57.98"E, *Triticum aestivum*. **70** – Mohelnice (6267b), 49°46'12.85"N, 16°56'02.84"E, *Triticum aestivum*. **71** – Třeština (6267b), 49°47'57.99"N, 16°58'31.31"E, *Zea mays*. **72** – Dubicko (6167d),

49°49'31.25"N, 16°58'12.18"E, *Hordeum vulgare*. **73** – Sudkov – jih (6067d), 49°54'39.64"N, 16°55'55.31"E, *Zea mays*. **74** – Nový Dvůr (6167b), 49°53'44.24"N, 16°55'10.09"E, *Medicago sativa*. **75** – Leština (6167b), 49°52'31.60"N, 16°55'43.29"E, *Medicago sativa*. **76** – Leština – západ (6167a), 49°52'18.42"N, 16°54'42.74"E, *Triticum aestivum*. **77** – Zábřeh – východ (6167a), 49°52'51.07"N, 16°53'39.48"E, louka (pastvina). **78** – Zábřeh (6167a), 49°52'23.44"N, 16°52'41.98"E, louka (pastvina). **79** – Zvole – sever (6167d), 49°50'48.53"N, 16°55'06.03"E, *Medicago sativa*. **80** – Lukavice (6167d), 49°49'34.29"N, 16°55'46.54"E, *Medicago sativa*. **81** – Libivá – východ (6167d), 49°48'15.24"N, 16°55'24.99"E, *Beta vulgaris* var. *rapacea*. **82** – Mohelnice – sever (6267b), 49°46'59.92"N, 16°55'09.30"E, louka (pastvina). **83** – Mohelnice – východ (6267b), 49°46'50.83"N, 16°57'10.56"E, *Triticum aestivum*. **84** – Třeština – severozápad (6167d), 49°48'00.28"N, 16°57'21.16"E, *Zea mays*.

C.3 Výsledky

V rámci této práce bylo sebráno 15 druhů mrchožroutovitých brouků (Coleoptera: Silphidae) v 71 234 exemplářích na 84 lokalitách ve čtyřech oblastech ČR.

Tabulka 1. Počet exemplářů jednotlivých druhů mrchožroutů ve čtyřech sledovaných oblastech České republiky.

Table 1. Number of specimens of carrion beetles in four studied areas of the Czech Republic.

	Louny (2008/09)	Kutná Hora (2008/09)	Zábřeh (2009)	Židlochovice (2009)
<i>Nicrophorus antennatus</i>	51	0	0	4
<i>Nicrophorus germanicus</i>	76	0	1	159
<i>Nicrophorus humator</i>	9	31	2	12
<i>Nicrophorus interruptus</i>	603	369	46	328
<i>Nicrophorus investigator</i>	1	2	0	7
<i>Nicrophorus sepultor</i>	1333	433	2	482
<i>Nicrophorus vespillo</i>	5261	6556	726	1185
<i>Nicrophorus vespilloides</i>	5	153	1	0
<i>Oiceoptoma thoracicum</i>	8	47	5	2

<i>Phosphuga atrata atrata</i>	0	2	0	1
<i>Silpha carinata</i>	71	0	2	44
<i>Silpha obscura obscura</i>	4460	19	70	732
<i>Silpha tristis</i>	78	90	63	49
<i>Thanatophilus rugosus</i>	879	441	22	392
<i>Thanatophilus sinuatus</i>	18617	18627	2769	5906

Výzkum byl prováděn v biologicky poměrně nezajímavém prostředí polních monokultur, ale přesto se nám podařilo odchytit dva ohrožené druhy hrobaříků (*Nicrophorus antennatus* (Reitter, 1884) a *N. germanicus* (Linnaeus, 1758)) a jeden druh téměř ohrožený (*N. sepultor* Charpentier, 1825) dle Červeného seznamu (Růžička, 2005).

V následujícím abecedně uspořádaném přehledu je u každého druhu uveden očíslovaný seznam lokalit s faunistickým čtvercem, obdobím sběru, počtem kusů a případně i pohlavím.

C.3.1 Seznam nálezů a komentáře k jednotlivým druhům

podčeleď Nicrophorinae

***Nicrophorus antennatus* (Reitter, 1884)**

Studovaný materiál. Bohemia: Louny: 28 – Hořešovice II. (5749b), jaro 2008, 2 ex.; 29 – Hořešovice III. (5749b), jaro 2008, 1 ex.; 30 – Klobuky (5749b), jaro 2008, 2 ex., léto 2008, 21 ex.; 34 – Postolopry (5648a), léto 2009, 16 ex., podzim 2009, 3 ex.; 35 – Březno (5648a), léto 2009, 1 ex.; 38 – Veltěže (5649c), léto 2009, 3 ex., podzim 2009, 1 ex.; 42 – Křesín (5650a), léto 2009, 1 ex.; Moravia: Židlochovice: 43 – Rebešovice (6865d), jaro 2009, 1 ex.; 50 – Cvrčovice (6965c), jaro 2009, 1ex., podzim 2009, 2 ex.

Rozšíření a ekologie. Palearktický druh, rozšířený ve většině Evropy, krom severských států a Velké Británie, v Asii se vyskytuje od Turecka až po Kašmír a severozápadní Čínu (Růžička & Schneider, 2004). U nás jen jednotlivé starší nálezy z Čech i Moravy (J. Růžička, nepubl.). Hojný výskyt u Nákla (6368) a Drahanovic (6468) a jen velmi vzácný u Chválkovic (6369) v okolí Olomouce uvádí z přelomu 50. a 60. let Novák (1961, 1965). Recentně také početně nalezen v Čechách, v lučních ekosystémech severně od Žabovřesk nad Ohří (5550) (J. Růžička, nepubl.). Na červeném seznamu je tento druh v ČR uveden v kategorii ohrožený (Růžička, 2005). Novák (1962) uvádí jeho hojný výskyt v otevřených biotopech s vazbou na sprašové půdy. Nalézán jen ve dvou námi studovaných oblastech, většinou jednotlivě.

***Nicrophorus germanicus* (Linnaeus, 1758)**

Studovaný materiál. **Bohemia:** *Louny*: 27 – Hořešovice I. (5749b), jaro 2008, 1 ex.; 28 – Hořešovice II. (5749b), jaro 2008, 2 ex.; 29 – Hořešovice III. (5749b), jaro 2008, 4 ex.; 30 – Klobuky (5749b), jaro 2008, 9 ex., léto 2008, 3 ex.; 36 – Louny I. (5648b), jaro 2009, 1 ex.; 38 – Veltěže (5649c), jaro 2009, 2 ex., léto 2009, 21 ex.; 40 – Slavětín (5649a), jaro 2009, 4 ex.; 41 – Stradonice (5649b), jaro 2009, 14 ex.; 42 – Křesín (5650a), jaro 2009, 4 ex., léto 2009, 5 ex.; 39 – Poředělice (5649a), léto 2009, 4 ex.; 41 – Stradonice (5649b), podzim 2009, 2 ex.; **Moravia:** *Židlochovice*: 43 – Rebešovice (6865d), jaro 2009, 1 ex.; 44 – Modřice (6865d), jaro 2009, 14 ex., léto 2009, 3 ex., podzim 2009, 1 ex.; 46 – Vojkovice (6965b), jaro 2009, 1 ex., léto 2009, 1 ex.; 47 – Medlov (6965c), jaro 2009, 6 ex., léto 2009, 1 ex.; 48 – Kupařovice (6965c), jaro 2009, 2 ex.; 49 – Odrovice (6965c), jaro 2009, 1 ex., léto 2009, 1 ex.; 50 – Cvrčovice (6965c), jaro 2009, 45 ex., léto 2009, 1 ex., podzim 2009, 48 ex.; 51 – Pohořelice (7064a), jaro 2009, 14 ex., léto 2009, 1 ex.; 52 – Přibice (7065a), jaro 2009, 3 ex., léto 2009, 4 ex.; 53 – Vranovice (7065b), jaro 2009, 1 ex., podzim 2009, 1 ex.; 58 – Uherčice (7065b), jaro 2009, 4 ex.; 59 – Ladná I. (7167c), jaro 2009, 1 ex.; 56 – Velké Němčice I. (7065b), léto 2009, 4 ex.; **Zábřeh**: 71 – Třeština (6267b), léto 2009, 1 ex.

Rozšíření a ekologie. Západopalearktický druh, rozšířený od Evropy přes Turecko, jižní Rusko a Irán až do Turkmenistánu (Růžička & Schneider, 2004). U nás jsou početné starší nálezy z Čech i z Moravy (J. Růžička, nepubl.). Hojný výskyt u Nákla (6368), Chválkovic (6369), Drahonovic (6468), a méně hojný u Lhoty nad Moravou (6368) v okolí Olomouce uvádí z přelomu 50. a 60. let Novák (1961, 1962, 1965). V současnosti mnohem vzácněji nalézán, ale známe nejméně dvě další lokality s recentním hojným výskytem – v Čechách severně od Žabovřesk nad Ohří (5550) a na Moravě v okolí Kyjova (7068). V obou případech se jedná o luční ekosystémy (J. Růžička, nepubl.). Stejně jako *N. antennatus* je veden v červeném seznamu ČR jako druh v kategorii ohrožený (Růžička, 2005). Druh otevřené krajiny, s vazbou na teplejší lokality s výskytem sprašových půd (Novák, 1962). Ve dvou studovaných oblastech početněji, v okolí Zábřehu jen ojedinělý nález.

***Nicrophorus humator* (Gleditsch, 1767)**

Studovaný materiál. **Bohemia:** **Louny:** 26 – Pozdeň II. (5749b), jaro 2008, 3 ex.; 27 – Hořešovice I. (5749b), jaro 2008, 1 ex.; 28 – Hořešovice II. (5749b), jaro 2008, 1 ex.; Skupice, léto 2009, 1 ex.; 34 – Postoloprty (5648a), léto 2009, 1 ex.; 41 – Stradonice (5649b), podzim 2009, 2 ex.; **Kutná Hora:** 3 – Žleby (6058d), jaro 2008, 3 m*m*, 1 f*; 4 – Vrdy I. (6058d), jaro 2008, 1 m*; 9 – Červený domek (6057b), jaro 2008, 2 m*m*, 2 f*f*, léto 2008, 1 m*, 1 f*; 2 – Kalabousek (6058c), podzim 2008, 1 f*; 6 – Bojmany (6058d), podzim 2008, 1 m*.; 15 – Libenice (6057b), léto 2009, 2 f*f*; 16 – Hlízov (6057b), podzim 2009, 5 m*m*, 6 f*f*; 17 – Nové Dvory II. (6057b), podzim 2009, 1 f*, 18 – Chotusice – letiště (6058a), léto 2009, 1 f*, podzim 2009, 1 f*, 21 – Výčapy (6058d), jaro 2009, 1 m*, podzim 2009, 1 m*; **Moravia:** **Židlochovice:** 44 – Modřice (6865d), léto 2009, 1 ex.; 45 – Holasice (6965b), léto 2009, 3 ex.; 46 – Vojkovice (6965b), léto 2009, 1 ex.; 51 – Pohořelice (7064a), léto 2009, 4 ex.; 57 – Velké Němčice II. (7066a), léto 2009, 1 ex., podzim 2009, 1 ex.; 59 – Ladná I. (7167c), léto 2009, 1 ex.; **Zábřeh:** 74 – Nový Dvůr (6167b), jaro 2009, 1 ex.; 75 – Leština (6167b), léto 2009, 1 ex.

Rozšíření a ekologie. Široce rozšířený palearktický druh, známý od Evropy a severní Afriky na východní Sibiř a do severozápadní Číny (Růžička & Schneider, 2004). U nás obecně rozšířený, jeden z běžných druhů hrobaříků (např. Vysoký 2007), preferující lesní biotopy (Růžička, 1994). Ve studovaných otevřených biotopech byl zachycen jen jednotlivě.

***Nicrophorus interruptus* Stephens, 1830**

Studovaný materiál. **Bohemia:** Louny: 29 – Hořešovice III. (5749b), jaro 2008, 1 ex.; 26 – Pozdeň II. (5749b), léto 2008, 42 ex., podzim 2009, 2 ex.; 28 – Hořešovice II. (5749b), léto 2009, 40 ex., podzim 2009, 9 ex.; 30 – Klobuky (5749b), léto 2009, 41 ex.; 25 – Pozdeň I. (5749d), podzim 2009, 13 ex.; 32 – Skupice II. (5648c), jaro 2009, 2 ex., léto 2009, 15 ex.; 34 – Postolopryty (5648a), jaro 2009, 5 ex., léto 2009, 90. ex., podzim 2009, 11 ex.; 40 – Slavětín (5649a), jaro 2009, 1 ex., léto 2009, 83 ex.; 41 – Stradonice (5649b), jaro 2009, 2 ex., podzim 2009, 8 ex.; 31 – Skupice I. (5648c), léto 2009, 16 ex.; 35 – Březno (5648a), léto 2009, 12 ex., podzim 2009, 2 ex.; 36 – Louny I. (5648b), léto 2009, 16 ex.; 37 – Louny II. (5648b), léto 2009, 2 ex., podzim 2009, 1 ex.; 38 – Veltěže (5649c), léto 2009, 48 ex.; 39 – Počedělice (5649a), léto 2009, 9 ex.; 42 – Křesín (5650a), léto 2009, 130 ex.; 33 – Malnice (5648c), podzim 2009, 2 ex.; **Kutná Hora:** 1 – Církvice (6058c), jaro 2008, 1 m*, 2 f*f*; 2 – Kalabousek (6058c), jaro 2008, 2 m*m*, 1 f*, léto 2008, 15 m*m*, 15 f*f*, podzim 2008, 1 m*, 1 f*; 3 – Žleby (6058d), jaro 2008, 2 m*m*, 2 f*f*, léto 2008, 6 m*m*, 5 f*f*; 4 – Vrdy I. (6058d), jaro 2008, 4 f*f*, léto 2008, 3 m*m*, podzim 2008, 2 f*f*; 5 – Horní Bučice (6058d), jaro 2008, 3 m*m*, 3 f*f*, léto 2008, 11 m*m*, 8 f*f*, podzim 2008, 2 m*m*, 5 f*f*; 6 – Bojmany (6058d), jaro 2008, 3 m*m*, 7 f*f*, léto 2008, 2 m*m*, podzim 2008, 5 m*m*, 2 f*f*; 7 – Kolín (5957c), jaro 2008, 1 f*; 8 – Starý Kolín I. (5957d), jaro 2008, 6 m*m*, 13 f*f*; 9 – Červený domek (6057b), jaro 2008, 10 m*m*, 11 f*f*, léto 2008, 1 f*, podzim 2008, 2 f*f*; 10 – Nové Dvory I. (6058a), jaro 2008, 1 m*, 2 f*f*, léto 2008, 16 m*m*, 12 f*f*, podzim 2008, 2 f*f*; 11 – Malín I. (6057a), jaro 2008, 6 m*m*, 6 f*f*, podzim 2008, 7 m*m*, 5 f*f*; 12 – Skalka (6057a), jaro 2008, 5 m*m*, 2 f*f*, podzim 2008, 1 f*; 13 – Hluboký důl (5957c), jaro 2009, 1 m*, 1 f*, léto 2009, 10 m*m*, 4 f*f*, podzim 2009, 1 f*; 14 – Starý

Kolín II. (5957b), jaro 2009, 1 m*, léto 2009, 2 m*m*, 1 f*, podzim 2009, 4 m*m*, 5 f*f*; 15 – Libenice (6057b), léto 2009, 10 m*m*, 12 f*f*; 16 – Hlízov (6057b), jaro 2009, 3 m*m*, 5 f*f*, podzim 2009, 2 f*f*; 17 – Nové Dvory II. (6057b), léto 2009, 16 m*m*, 11 f*f*, podzim 2009, 3 m*m*, 1 f*; 18 – Chotusice – letiště (6058a), léto 2009, 3 m*m*, 1 f*, podzim 2009, 3 m*m*, 5 f*f*; 19 – Chotusice (6058a), léto 2009, 6 m*m*, 13 f*f*, podzim 2009, 2 f*f*; 20 – Druhanice (6058d), léto 2009, 4 m*m*, 3 f*f*; 21 – Výčapy (6058d), léto 2009, 1 m*, podzim 2009, 4 f*f*; 22 – Vrdy II. (6058d), jaro 2009, 1 m*, léto 2009, 4 m*m*, 4 f*f*; **Moravia: Židlochovice:** 43 – Rebešovice (6865d), jaro 2009, 2 ex., léto 2009, 1 ex., podzim 2009, 1 ex.; 46 – Vojkovice (6965b), jaro 2009, 3 ex., léto 2009, 27. ex., podzim 2009, 4 ex.; 47 – Medlov (6965c), jaro 2009, 1 ex., léto 2009, 9 ex.; 48 – Kupařovice (6965c), jaro 2009, 3 ex., léto 2009, 6 ex., podzim 2009, 21 ex.; 50 – Cvrčovice (6965c), jaro 2009, 9 ex., léto 2009, 6 ex., podzim 2009, 34 ex.; 51 – Pohořelice (7064a), jaro 2009, 3 ex., léto 2009, 4 ex., podzim 2009, 14 ex.; 52 – Přibice (7065a), jaro 2009, 4 ex., léto 2009, 17 ex., podzim 2009, 17 ex.; 53 – Vranovice (7065b), jaro 2009, 8 ex., podzim 2009, 10 ex.; 54 – Přísnice (7065b), jaro 2009, 1 ex., léto 2009, 1 ex., podzim 2009, 3 ex.; 56 – Velké Němčice I. (7065b), jaro 2009, 2 ex., léto 2009, 16 ex., podzim 2009, 8 ex.; 60 – Ladná II. (7267a), jaro 2009, 8 ex., léto 2009, 3 ex.; 44 – Modřice (6865d), léto 2009, 6 ex., podzim 2009, 4 ex.; 45 – Holasice (6965b), léto 2009, 3 ex., podzim 2009, 4 ex.; 49 – Odrovice (6965c), léto 2009, 1 ex., podzim 2009, 10 ex.; 55 – Nosislav (6965d), léto 2009, 7 ex., podzim 2009, 1 ex.; 58 – Uherčice (7065b), léto 2009, 1 ex.; 57 – Velké Němčice II. (7066a), léto 2009, 3 ex., podzim 2009, 24 ex.; 59 – Ladná I. (7167c), léto 2009, 1 ex., podzim 2009, 17 ex.; **Zábřeh:** 81 – Libivá – východ (6167d), jaro 2009, 1 ex.; 72 – Dubicko (6167d), léto 2009, 5 ex., podzim 2009, 5 ex.; 75 – Leština (6167b), léto 2009, 1 ex.; 76 – Leština – západ (6167a), léto 2009, 4 ex.; 83 – Mohelnice – východ (6267b), léto 2009, 2 ex., podzim 2009, 2 ex.; 61 – Sudkov (6067d), podzim 2009, 1 ex.; 68 – Vlachov (6167c), podzim 2009, 5 ex.; 73 – Sudkov – jih (6067d), podzim 2009, 2 ex.; 74 – Nový Dvůr (6167b), podzim 2009, 3 ex.; 79 – Zvole – sever (6167d), podzim 2009, 1 ex.; 80 – Lukavice (6167d), podzim 2009, 8 ex.; 82 – Mohelnice – sever (6267b), podzim 2009, 2 ex.; 84 – Třeština – severozápad (6167d), podzim 2009, 4 ex.

Rozšíření a ekologie. Palearktický druh, rozšířený od Evropy a severní Afriky až na východní Sibiř a do severozápadní Číny (Růžička & Schneider, 2004). Na našem území velmi hojný hrobařík

(např. Vysoký 2007). Eurytopní druh, který se vyskytuje jak v otevřené krajině, tak i v lesích (Růžička, 1994; Kočárek & Benko, 1997; Vysoký, 2007). Ve studovaných oblastech početný výskyt.

***Nicrophorus investigator* Zetterstedt, 1824**

Studovaný materiál. **Bohemia:** *Louny*: 25 – Pozdeň I. (5749d), podzim 2008, 1 ex.;

Kutná Hora: 9 – Červený domek (6057b), podzim 2008, 1 m*; 10 – Nové Dvory I. (6058a), podzim 2008, 1 f*; **Moravia:** *Židlochovice*: 43 – Rebešovice (6865d), jaro 2009, 1 ex.; 48 – Kupařovice (6965c), jaro 2009, 1 ex.; 53 – Vranovice (7065b), jaro 2009, 1 ex.; 50 – Cvrčovice (6965c), léto 2009, 2 ex.; 55 – Nosislav (6965d), léto 2009, 1 ex.; 60 – Ladná II. (7267a), léto 2009, 1 ex.

Rozšíření a ekologie. Široce rozšířený holarktický druh (Růžička & Schneider, 2004). U nás běžný, ale vyskytuje se prakticky pouze v lesních biotopech (Růžička, 1994; Kočárek & Benko, 1997; Vysoký, 2007). Jeho zálety do otevřené krajiny, jak je vidět i v našem výčtu materiálu, jsou dosti vzácné.

***Nicrophorus sepultor* Charpentier, 1825**

Studovaný materiál. **Bohemia:** *Louny*: 27 – Hořešovice I. (5749b), jaro 2008, 1 ex.; 26 – Pozdeň II. (5749b), léto 2008, 14 ex.; 28 – Hořešovice II. (5749b), léto 2008, 60 ex., podzim 2008, 4 ex.; 30 – Klobuky (5749b), léto 2008, 256 ex.; 25 – Pozdeň I. (5749d), podzim 2008, 2 ex.; 29 – Hořešovice III. (5749b), podzim 2008, 1 ex.; 34 – Postolopry (5648a), jaro 2009, 8 ex., léto 2009, 135 ex., podzim 2009, 10 ex.; 38 – Veltěže (5649c), jaro 2009, 11 ex., léto 2009, 352 ex., podzim 2009, 3 ex.; 40 – Slavětín (5649a), jaro 2009, 1 ex., léto 2009, 295 ex.; 41 – Stradonice (5649b), jaro 2009, 1 ex., podzim 2009, 16 ex.; 31 – Skupice I. (5648c), léto 2009, 6 ex.; 32 – Skupice II.

(5648c), léto 2009, 5 ex.; 35 – Březno (5648a), léto 2009, 2 ex., podzim 2009, 2 ex.; 36 – Louny I. (5648b), léto 2009, 20 ex., podzim 2009, 7 ex.; 39 – Počedělice (5649a), léto 2009, 3 ex.; 42 – Křesín (5650a), léto 2009, 112 ex.; 33 – Malnice (5648c), podzim 2009, 4 ex.; 37 – Louny II. (5648b), podzim 2009, 2 ex.; **Kutná hora:** 2 – Kalabousek (6058c), léto 2008, 5 m*m*, 8 f*f*; 3 – Žleby (6058d), léto 2008, 1 m*, 1 f*; 5 – Horní Bučice (6058d), jaro 2008, 1 f*, léto 2008, 8 m*m*, 2 f*f*; 9 – Červený domek (6057b), jaro 2008, 1 m*; 12 – Skalka (6057a), jaro 2008, 1 m*; 13 – Hluboký důl (5957c), jaro 2009, 1 m*, léto 2009, 2 f*f*, podzim 2009, 1 m*; 14 – Starý Kolín II. (5957b), jaro 2009, 6 m*m*, 1 f*, léto 2009, 1 f*, podzim 2009, 1 m*; 15 – Libenice (6057b), léto 2009, 1 m*, 2 f*f*; 17 – Nové Dvory II. (6057b), léto 2009, 11 m*m*, 7 f*f*, podzim 2009, 2 m*m*, 4 f*f*; 18 – Chotusice – letiště (6058a), jaro 2009, 5 m*m*, 3 f*f*; 19 – Chotusice (6058a), léto 2009, 128 m*m*, 163 f*f*, podzim 2009, 1 m*; 20 – Druhanice (6058d), léto 2009, 3 m*m*, 6 f*f*; 21 – Výčapy (6058d), léto 2009, 3 m*m*, 1 f*, podzim 2009, 1 m*, 3 f*f*; 22 – Vrdy II. (6058d), jaro 2009, 1 f*, léto 2009, 15 m*m*, 31 f*f*; 24 – Malín II. (6057b), podzim 2009, 1 f*; **Moravia: Židlochovice:** 43 – Rebešovice (6865d), jaro 2009, 1 ex., léto 2009, 4 ex., podzim 2009, 1 ex.; 47 – Medlov (6965c), jaro 2009, 22 ex., léto 2009, 26 ex.; 50 – Cvrčovice (6965c), jaro 2009, 38 ex., léto 2009, 2 ex., podzim 2009, 11 ex.; 52 – Přibice (7065a), jaro 2009, 61 ex., léto 2009, 228 ex., podzim 2009, 10 ex.; 53 – Vranovice (7065b), jaro 2009, 37 ex., léto 2009, 2 ex., podzim 2009, 1 ex.; 60 – Ladná II. (7267a), jaro 2009, 12 ex.; 49 – Odrovice (6965c), léto 2009, 5 ex., podzim 2009, 3 ex.; 56 – Velké Němčice I. (7065b), léto 2009, 1 ex.; 44 – Modřice (6865d), podzim 2009, 1 ex.; 51 – Pohořelice (7064a), podzim 2009, 2 ex.; 59 – Ladná I. (7167c), podzim 2009, 14 ex.; **Zábřeh:** 80 – Lukavice (6167d), léto 2009, 1 ex., podzim 2009, 1 ex.

Rozšíření a ekologie. Palearktický druh, rozšířený od Evropy až do Mongolska, východní Sibiře a do severozápadní Číny (Růžička & Schneider, 2004). U nás jednotlivé starší i novější nálezy z Čech i Moravy (Vysoký 2007; J. Růžička, nepubl.). Hojný výskyt u Nákladu (6368), Lhoty nad Moravou (6368) a Drahanovic (6468) a méně hojný u Chválkovic (6369) v okolí Olomouce uvádí z přelomu 50. a 60. let Novák (1961, 1962, 1965). Recentně nalézáno většinou jednotlivě (např. jednotlivé nálezy z Ústeckého kraje shrnuje Vysoký (2007)), ale známe i masový výskyt v Čechách, severně od Žabovřesk nad Ohří (5550) a v okolí Kostelce nad Černými lesy (6055), obojí

v lučních biotopech (J. Růžička, nepubl.). Vzácnější druh hrobaříka, který je v červeném seznamu ČR veden v kategorii téměř ohrožený (Růžička, 2005). Druh otevřené krajiny, včetně chladnějších biotopů (Vysoký 2007; J. Růžička, nepubl.); Novák (1962) popisuje jeho vazbu na lokality se sprašovými půdami. Vysoký (2007) zmiňuje i výskyt na okraji lesních biotopů. Ve třech studovaných oblastech zjištěn poměrně početný výskyt, v okolí Zábřehu jen dva jednotlivé nálezy na jediné lokalitě.

***Nicrophorus vespillo* (Linnaeus, 1758)**

Studovaný materiál. **Bohemia:** **Louny:** 35 – Březno (5648a), jaro 2009, 22 ex., léto 2009, 71 ex., podzim 2009, 14 ex.; 27 – Hořešovice I. (5749b), jaro 2008, 281 ex.; 28 – Hořešovice II. (5749b), jaro 2008, 552 ex., léto 2008, 169 ex., podzim 2008, 151 ex.; 29 – Hořešovice III. (5749b), jaro 2008, 412 ex., podzim 2008, 9 ex.; 30 – Klobuky (5749b), jaro 2008, 213 ex., léto 2008, 183 ex., podzim 2008, 4 ex.; 42 – Křesín (5650a), jaro 2009, 122 ex., léto 2009, 225 ex., podzim 2009, 4 ex.; 36 – Louny I. (5648b), jaro 2009, 128 ex., léto 2009, 36 ex., podzim 2009, 77 ex.; 37 – Louny II. (5648b), jaro 2009, 59 ex., léto 2009, 72 ex., podzim 2009, 33 ex.; 33 – Malnice (5648c), jaro 2009, 2 ex., podzim 2009, 23 ex.; 39 – Počedělice (5649a), jaro 2009, 104 ex., léto 2009, 81 ex., podzim 2009, 8 ex.; 34 – Postoloprty (5648a), jaro 2009, 209 ex., léto 2009, 62 ex., podzim 2009, 61 ex.; 25 – Pozdeň I. (5749d), jaro 2008, 171 ex., podzim 2008, 151 ex.; 26 – Pozdeň II. (5749b), jaro 2008, 292 ex., léto 2008, 75 ex., podzim 2008, 24 ex.; 31 – Skupice I. (5648c), jaro 2009, 31 ex., léto 2009, 16 ex., podzim 2009, 27 ex.; 32 – Skupice II. (5648c), jaro 2009, 71 ex., léto 2009, 32 ex.; 40 – Slavětín (5649a), jaro 2009, 233 ex., léto 2009, 163 ex.; 41 – Stradonice (5649b), jaro 2009, 64 ex., podzim 2009, 88 ex.; 38 – Veltěže (5649c), jaro 2009, 189 ex., léto 2009, 202 ex., podzim 2009, 45 ex.; **Kutná Hora:** 1 – Církvice (6058c), jaro 2008, 12 m*m*, 7 f*f*, léto 2008, 4 m*m*, 4 f*f*, podzim 2008, 23 m*m*, 33 f*f*; 2 – Kalabousek (6058c), jaro 2008, 8 m*m*, 21 f*f*, léto 2008, 24 m*m*, 31 f*f*, podzim 2008, 39 m*m*, 39 f*f*; 3 – Žleby (6058d), jaro 2008, 17 m*m*, 20 f*f*, léto 2008, 10 m*m*, 7 f*f*; 4 – Vrdy I. (6058d), jaro 2008, 8 m*m*, 6 f*f*, léto 2008, 7 m*m*, 5 f*f*, podzim 2008, 33 m*m*, 33 f*f*; 5 – Horní Bučice (6058d), jaro 2008,

5 m*m*, 4 f*f*, léto 2008, 18 m*m*, 18 f*f*, podzim 2008, 51 m*m*, 63 f*f*; 6 – Bojmany (6058d), jaro 2008, 37 m*m*, 30 f*f*, léto 2008, 1 f*, podzim 2008, 62 m*m*, 80 f*f*; 7 – Kolín (5957c), jaro 2008, 8 m*m*, 9 f*f*; 8 – Starý Kolín I. (5957d), jaro 2008, 35 m*m*, 35 f*f*, léto 2008, 9 m*m*, 8 f*f*, podzim 2008, 18 m*m*, 20 f*f*; 9 – Červený domek (6057b), jaro 2008, 46 m*m*, 73 f*f*, léto 2008, 8 m*m*, 9 f*f*, podzim 2008, 122 m*m*, 120 f*f*; 10 – Nové Dvory I. (6058a), jaro 2008, 8 m*m*, 2 f*f*, léto 2008, 32 m*m*, 46 f*f*, podzim 2008, 151 m*m*, 119 f*f*; 11 – Malín I. (6057a), jaro 2008, 48 m*m*, 83 f*f*, léto 2008, 35 m*m*, 70 f*f*, podzim 2008, 198 m*m*, 226 f*f*; 12 – Skalka (6057a), jaro 2008, 23 m*m*, 13 f*f*, léto 2008, 4 m*m*, 10 f*f*, podzim 2008, 126 m*m*, 115 f*f*; 13 – Hluboký důl (5957c), jaro 2009, 54 m*m*, 58 f*f*, léto 2009, 32 m*m*, 25 f*f*, podzim 2009, 42 m*m*, 43 f*f*; 14 – Starý Kolín II. (5957b), jaro 2009, 11 m*m*, 23 f*f*, léto 2009, 8 m*m*, 12 f*f*, podzim 2009, 81 m*m*, 83 f*f*; 15 – Libenice (6057b), jaro 2009, 11 m*m*, 17 f*f*, léto 2009, 30 m*m*, 17 f*f*; 16 – Hlízov (6057b), jaro 2009, 92 m*m*, 95 f*f*, podzim 2009, 81 m*m*, 70 f*f*; 17 – Nové Dvory II. (6057b), jaro 2009, 10 m*m*, 16 f*f*, léto 2009, 60 m*m*, 64 f*f*, podzim 2009, 36 m*m*, 58 f*f*; 18 – Chotusice – letiště (6058a), jaro 2009, 90 m*m*, 116 f*f*, léto 2009, 17 m*m*, 22 f*f*, podzim 2009, 306 m*m*, 304 f*f*; 19 – Chotusice (6058a), jaro 2009, 73 m*m*, 88 f*f*, léto 2009, 61 m*m*, 71 f*f*, podzim 2009, 105 m*m*, 124 f*f*; 20 – Druhanice (6058d), jaro 2009, 17 m*m*, 25 f*f*, léto 2009, 29 m*m*, 28 f*f*; 21 – Výčapy (6058d), jaro 2009, 65 m*m*, 99 f*f*, léto 2009, 17 m*m*, 17 f*f*, podzim 2009, 73 m*m*, 70 f*f*; 22 – Vrdy II. (6058d), jaro 2009, 177 m*m*, 176 f*f*, léto 2009, 84 m*m*, 112 f*f*; 23 – Vinice (6058d), jaro 2009, 142 m*m*, 133 f*f*; 24 – Malín II. (6057b), jaro 2009, 59 m*m*, 64 f*f*, podzim 2009, 45 m*m*, 39 f*f*; **Moravia: Židlochovice:** 50 – Cvrčovice (6965c), jaro 2009, 51 ex., léto 2009, 9 ex., podzim 2009, 150 ex.; 45 – Holasice (6965b), jaro 2009, 3 ex., léto 2009, 31 ex.; 48 – Kupařovice (6965c), jaro 2009, 2 ex., léto 2009, 3 ex., podzim 2009, 36 ex.; 59 – Ladná I. (7167c), jaro 2009, 3 ex., léto 2009, 41 ex., podzim 2009, 17 ex.; 60 – Ladná II. (7267a), jaro 2009, 16 ex., léto 2009, 71 ex.; 47 – Medlov (6965c), jaro 2009, 4 ex., léto 2009, 64 ex., podzim 2009, 7 ex.; 44 – Modřice (6865d), jaro 2009, 27 ex., léto 2009, 35 ex., podzim 2009, 23 ex.; 55 – Nosislav (6965d), jaro 2009, 2 ex., léto 2009, 4 ex., podzim 2009, 1 ex.; 49 – Odrovice (6965c), jaro 2009, 9 ex., léto 2009, 67 ex., podzim 2009, 36 ex.; 51 – Pohořelice (7064a), jaro 2009, 4 ex.,

léto 2009, 26 ex., podzim 2009, 12 ex.; 52 – Přibice (7065a), jaro 2009, 27 ex., léto 2009, 87 ex., podzim 2009, 42 ex.; 54 – Přísnice (7065b), podzim 2009, 1 ex.; 43 – Rebešovice (6865d), jaro 2009, 5 ex., léto 2009, 4 ex., podzim 2009, 14 ex.; 58 – Uherčice (7065b), jaro 2009, 5 ex., léto 2009, 11 ex., podzim 2009, 4 ex.; 56 – Velké Němčice I. (7065b), jaro 2009, 16 ex., léto 2009, 75 ex., podzim 2009, 59 ex.; Velké Němčice, jaro 2009, 1 ex., léto 2009, 8 ex., podzim 2009, 11 ex.; 46 – Vojkovice (6965b), jaro 2009, 8 ex., léto 2009, 11 ex.; 53 – Vranovice (7065b), jaro 2009, 23 ex., léto 2009, 1 ex., podzim 2009, 18 ex.; **Zábřeh:** 72 – Dubicko (6167d), jaro 2009, 19 ex., léto 2009, 29 ex., podzim 2009, 16 ex.; 62 – Kolšov (6067d), jaro 2009, 41 ex., léto 2009, 1 ex.; 75 – Leština (6167b), jaro 2009, 33 ex., léto 2009, 14 ex.; 76 – Leština – západ (6167a), jaro 2009, 15 ex., léto 2009, 14 ex., podzim 2009, 2 ex.; 69 – Libivá (6267a), jaro 2009, 50 ex.; 81 – Libivá – východ (6167d), jaro 2009, 16 ex.; 80 – Lukavice (6167d), léto 2009, 50 ex., podzim 2009, 26 ex.; 70 – Mohelnice (6267b), jaro 2009, 10 ex.; 82 – Mohelnice – sever (6267b), jaro 2009, 5 ex.; 83 – Mohelnice – východ (6267b), léto 2009, 1 ex., podzim 2009, 1 ex.; 74 – Nový Dvůr (6167b), jaro 2009, 19 ex.; 66 – Rájec (6167a), jaro 2009, 89 ex., léto 2009, 1 ex.; 61 – Sudkov (6067d), jaro 2009, 2 ex.; 73 – Sudkov – jih (6067d), jaro 2009, 7 ex., podzim 2009, 51 ex.; 71 – Třeština (6267b), jaro 2009, 29 ex., léto 2009, 1 ex.; 84 – Třeština – severozápad (6167d), jaro 2009, 10 ex., podzim 2009, 3 ex.; 68 – Vlachov (6167c), jaro 2009, 19 ex.; 78 – Zábřeh (6167a), jaro 2009, 54 ex.; 64 – Zábřeh – sever (6167a), jaro 2009, 73 ex.; 67 – Zvole (6167c), jaro 2009, 20 ex., léto 2009, 1 ex.; 79 – Zvole – sever (6167d), podzim 2009, 4 ex.

Rozšíření a ekologie. Palearktický druh, rozšířený od Evropy až na východní Sibiř, do Mongolska a severozápadní Číny (Růžička & Schneider, 2004). U nás běžný druh hrobaříka (např. Vysoký 2007). Druh otevřené krajiny, který však může zaletovat i do lesů (Růžička, 1994). Vyskytoval se prakticky na všech námi prozkoumaných lokalitách, často ve velkém množství.

***Nicrophorus vespilloides* Herbst, 1784**

Studovaný materiál. Bohemia: **Louny:** 27 – Hořešovice I. (5749b), jaro 2008, 1 ex.; 28 – Hořešovice II. (5749b), jaro 2008, 1 ex.; 26 – Pozdeň II. (5749b), léto 2008, 1 ex.; 33 – Malnice

(5648c), jaro 2009, 1 ex.; 39 – Počedělice (5649a), jaro 2009, 1 ex.; **Kutná Hora:** 3 – Žleby (6058d), jaro 2008, 1 m*; 8 – Starý Kolín I. (5957d), jaro 2008, 1 m*, léto 2008, 2 m*m*, 1 f*, podzim, 2008, 1 m*; 9 – Červený domek (6057b), jaro 2008, 48 m*m*, 90 f*f*; 10 – Nové Dvory I. (6058a), léto 2008, 1 m*, 1 f*; podzim 2008, 2 m*m*, 1 f*; 13 – Hluboký důl (5957c), léto 2009, 1 m*; 16 – Hlízov (6057b), jaro 2009, 1 f*, podzim 2009, 1 m*; 24 – Malín II. (6057b), podzim 2009, 1 m*; **Moravia: Zábřeh:** 62 – Kolšov (6067d), jaro 2009, 1 ex.

Rozšíření a ekologie. Široce rozšířený holarktický druh (Růžička & Schneider, 2004). U nás velmi hojný hrobařík (např. Vysoký 2007). Vyskytuje se především v lesích a mimo ně zalétá pouze zřídka (např. Růžička 1994, Kočárek & Benko 1997). Ve studovaných oblastech z polí jen jednotlivé nálezy. Pouze na lokalitě Červený Domek u Kutné Hory, která je v blízkosti lesa, byl zaznamenán masový výskyt.

podčeled' Silphinae

***Oiceoptoma thoracicum* (Linnaeus, 1758)**

Studovaný materiál. **Bohemia: Louň:** 26 – Pozdeň II. (5749b), jaro 2008, 3 ex.; 28 – Hořešovice II. (5749b), jaro 2008, 1 ex., léto 2008, 1 ex.; 38 – Veltěže (5649c), jaro 2009, 1 ex.; 35 – Březno (5648a), léto 2009, 1 ex.; 42 – Křesín (5650a), léto 2009, 1 ex.; **Kutná Hora:** 2 – Kalabousek (6058c), jaro 2008, 1 m*; 3 – Žleby (6058d), jaro 2008, 2 m*m*, 4 f*f*; 7 – Kolín (5957c), jaro 2008, 2 m*m*, 1 f*; 8 – Starý Kolín I. (5957d), jaro 2008, 1 m*; 9 – Červený domek (6057b), jaro 2008, 11 m*m*, 23 f*f*; 12 – Skalka (6057a), jaro 2008, 1 f*; 24 – Malín II. (6057b), jaro 2009, 1 m*; **Moravia: Židlochovice:** 56 – Velké Němčice I. (7065b), jaro 2009, 1 ex.; 59 – Ladná I. (7167c), léto 2009, 1 ex.; **Zábřeh:** 67 – Zvole (6167c), jaro 2009, 1 ex., léto 2009, 2 ex.; 62 – Kolšov (6067d), léto 2009, 1 ex.; 72 – Dubicko (6167d), léto 2009, 1 ex.

Rozšíření a ekologie. Transpalearktický druh, rozšířený od Evropy po Japonsko (Růžička & Schneider, 2004; Růžička et al., 2004). U nás velmi hojný druh (např. Vysoký 2007, mapka),

vázán především na lesní biotopy (Růžička 1994, Kočárek & Benko 1997). Ve studovaných oblastech v polích jen jednotlivé nálezy.

***Phosphuga atrata atrata* (Linnaeus, 1758)**

Studovaný materiál. **Bohemia:** *Kutná Hora*: 12 – Skalka (6057a), jaro 2008, 2 m*m*; **Moravia:** *Židlochovice*: 58 – Uherčice (7065b), podzim 2009, 1 ex.

Rozšíření a ekologie. Transpalearktický druh, od Evropy až do Japonska (Růžička & Schneider, 2004). Jedná se o predátora specializovaného na lov ulitnatých plžů (Šustek 1981). U nás hojný druh, ale do pastí padá pouze jednotlivě (Růžička, 1994; Kočárek & Benko, 1997). Ve dvou studovaných oblastech zachycen jen jednotlivými nálezy.

***Silpha carinata* Herbst, 1783**

Studovaný materiál. **Bohemia:** *Louny*: 26 – Pozdeň II. (5749b), jaro 2008, 1 ex.; 28 – Hořešovice II. (5749b), léto 2008, 1 ex.; 30 – Klobuky (5749b), léto 2008, 9 ex.; 31 – Skupice I. (5648c), jaro 2009, 2 ex., léto 2009, 6 ex., podzim 2009, 2 ex.; 32 – Skupice II. (5648c), jaro 2009, 2 ex., léto 2009, 4 ex.; 34 – Postolopry (5648a), jaro 2009, 6 ex., léto 2009, 14 ex., podzim 2009, 2 ex.; 41 – Stradonice (5649b), jaro 2009, 2 ex., podzim 2009, 8 ex.; 35 – Březno (5648a), léto 2009, 4 ex.; 36 – Louny I. (5648b), léto 2009, 4 ex., podzim 2009, 2 ex.; 38 – Veltěže (5649c), podzim 2009, 2 ex.; **Moravia:** *Židlochovice*: 56 – Velké Němčice I. (7065b), jaro 2009, 3 ex., léto 2009, 18 ex., podzim 2009, 1 ex.; 58 – Uherčice (7065b), jaro 2009, 1 ex., léto 2009, 2 ex.; 47 – Medlov (6965c), léto 2009, 1 ex., podzim 2009, 3 ex.; 48 – Kupařovice (6965c), léto 2009, 2 ex., podzim 2009, 10 ex.; 52 – Přibice (7065a), léto 2009, 2 ex.; 54 – Přísnotice (7065b), podzim 2009, 1 ex.; **Zábřeh:** 82 – Mohelnice – sever (6267b), léto 2009, 2 ex.

Rozšíření a ekologie. Palearktický druh, od Evropy (kde chybí pouze ve Španělsku a Irsku) na východní Sibiř, do Mongolska a severozápadní Číny (Růžička & Schneider, 2004). U nás hojný druh, výskyt od nížin do hor, v otevřené krajině i v lesních ekosystémech (Vysoký 2007). Ve dvou studovaných oblastech vzácně, v okolí Zábřehu zachycen jen na jedné lokalitě.

***Silpha obscura obscura* Linnaeus, 1758**

Studovaný materiál. **Bohemia:** Louny: 35 – Březno (5648a), jaro 2009, 31 ex., léto 2009, 19 ex., podzim 2009, 1 ex.; 42 – Křesín (5650a), jaro 2009, 2 ex.; 36 – Louny I. (5648b), jaro 2009, 12 ex., léto 2009, 3 ex., podzim 2009, 2 ex.; 33 – Malnice (5648c), podzim 2009, 13 ex.; 34 – Postolopry (5648a), jaro 2009, 2286 ex., léto 2009, 1553 ex., podzim 2009, 28 ex.; 31 – Skupice I. (5648c), jaro 2009, 38 ex., léto 2009, 351 ex., podzim 2009, 1 ex.; 32 – Skupice II. (5648c), jaro 2009, 3 ex., léto 2009, 3 ex.; 40 – Slavětín (5649a), jaro 2009, 1 ex., léto 2009, 1 ex.; 38 – Veltěže (5649c), jaro 2009, 103 ex., léto 2009, 7 ex., podzim 2009, 2 ex.; **Kutná Hora:** 2 – Kalabousek (6058c), jaro 2008, 1 m*, 1 f*; 5 – Horní Bučice (6058d), jaro 2008, 4 m*m*, léto 2008, 3 m*m*, 1 f*; 6 – Bojmany (6058d), jaro 2008, 3 m*m*, 6 f*f*; **Moravia:** **Židlochovice:** 50 – Cvrčovice (6965c), jaro 2009, 17 ex., léto 2009, 14 ex., podzim 2009, 13 ex.; 48 – Kupařovice (6965c), jaro 2009, 1 ex., léto 2009, 8 ex.; 59 – Ladná I. (7167c), podzim 2009, 15 ex.; 60 – Ladná II. (7267a), jaro 2009, 308 ex., léto 2009, 208 ex.; 51 – Pohořelice (7064a), jaro 2009, 1 ex.; 52 – Přibice (7065a), jaro 2009, 4 ex., léto 2009, 32 ex., podzim 2009, 3 ex.; 58 – Uherčice (7065b), jaro 2009, 1 ex.; 56 – Velké Němčice I. (7065b), jaro 2009, 13 ex., léto 2009, 2 ex.; 46 – Vojkovice (6965b), jaro 2009, 31 ex., léto 2009, 45 ex.; 53 – Vranovice (7065b), jaro 2009, 11 ex.; **Zábřeh:** 72 – Dubicko (6167d), jaro 2009, 1 ex.; 62 – Kolšov (6067d), jaro 2009, 1 ex., léto 2009, 1 ex.; 75 – Leština (6167b), jaro 2009, 1 ex.; 66 – Rájec (6167a), jaro 2009, 1 ex.; 68 – Vlachov (6167c), jaro 2009, 1 ex.; 64 – Zábřeh – sever (6167a), jaro 2009, 64 ex.

Rozšíření a ekologie. Palearktický druh se třemi poddruhy, od Evropy (kromě Irska) až na východní Sibiř, do Mongolska a severozápadní Číny, jihovýchodně až na severozápad Indie

(Růžička & Schneider, 2004). U nás hojně, především v otevřených biotopech (např. Vysoký 2007). Ve studovaných oblastech početně, v okolí Postoloprt masový výskyt.

***Silpha tristis* Illiger, 1798**

Studovaný materiál. **Bohemia:** *Louny*: 35 – Březno (5648a), jaro 2009, 6 ex., léto 2009, 10 ex., podzim 2009, 5 ex.; 29 – Hořešovice III. (5749b), jaro 2008, 1 ex.; 30 – Klobuky (5749b), jaro 2008, 2 ex.; 42 – Křesín (5650a), jaro 2009, 3 ex., léto 2009, 2 ex.; 36 – Louny I. (5648b), podzim 2009, 2 ex.; 37 – Louny II. (5648b), jaro 2009, 7 ex.; 33 – Malnice (5648c), podzim 2009, 7 ex.; 34 – Postolopry (5648a), podzim 2009, 2 ex.; 31 – Skupice I. (5648c), léto 2009, 2 ex.; 32 – Skupice II. (5648c), jaro 2009, 6 ex., léto 2009, 9 ex.; 40 – Slavětín (5649a), jaro 2009, 3 ex., léto 2009, 1 ex.; 41 – Stradonice (5649b), jaro 2009, 3 ex., podzim 2009, 2 ex.; 38 – Veltěže (5649c), jaro 2009, 3 ex., podzim 2009, 2 ex.; **Kutná Hora:** 1 – Církvice (6058c), jaro 2008, 1 f*; 2 – Kalabousek (6058c), jaro 2008, 2 m*m*, 1 f*, léto 2008, 1 m*, 1 f*; 3 – Žleby (6058d), jaro 2008, 2 m*m*, 6 f*f*; 5 – Horní Bučice (6058d), jaro 2008, 7 m*m*, 8 f*f*; 6 – Bojmany (6058d), jaro 2008, 15 m*m*, 24 f*f*; 8 – Starý Kolín I. (5957d), jaro 2008, 1 m*; 9 – Červený domek (6057b), jaro 2008, 2 f*f*; 11 – Malín I. (6057a), jaro 2008, 2 m*m*; 13 – Hluboký důl (5957c), jaro 2009, 1 m*; 16 – Hlízov (6057b), jaro 2009, 4 f*f*, podzim 2009, 2 m*m*; 19 – Chotusice (6058a), jaro 2009, 2 f*f*; 21 – Výčapy (6058d), léto 2009, 1 m*, 1 f*; 22 – Vrdy II. (6058d), jaro 2009, 3 m*m*, 2 f*f*; 23 – Vinice (6058d), jaro 2009, 1 f*; **Moravia:** *Židlochovice*: 50 – Cvrčovice (6965c), podzim 2009, 1 ex.; 45 – Holasice (6965b), podzim 2009, 5 ex.; 48 – Kupařovice (6965c), podzim 2009, 1 ex.; 59 – Ladná I. (7167c), podzim 2009, 1 ex.; 60 – Ladná II. (7267a), jaro 2009, 27 ex., léto 2009, 14 ex.; **Zábřeh:** 72 – Dubicko (6167d), léto 2009, 22 ex., podzim 2009, 3 ex.; 62 – Kolšov (6067d), jaro 2009, 6 ex., léto 2009, 5 ex.; 76 – Leština – západ (6167a), jaro 2009, 2 ex., léto 2009, 7 ex., podzim 2009, 1 ex.; 80 – Lukavice (6167d), léto 2009, 1 ex.; 83 – Mohelnice – východ (6267b), podzim 2009, 7 ex.; 74 – Nový Dvůr (6167b), podzim 2009, 2 ex.; 66 – Rájec (6167a), jaro 2009, 1 ex.; 73 – Sudkov – jih (6067d), jaro 2009, 5 ex.; 84 – Třeština – severozápad (6167d), podzim 2009, 1 ex.

Rozšíření a ekologie. Západopalearktický druh, většina Evropy, Turecko a Írán (Růžička & Schneider, 2004). U nás hojně, preferuje spíše vlhké otevřené biotopy (např. Vysoký 2007; J. Strejček (Praha), nepubl.). Ve studovaných oblastech rozšířený, ale většinou zachycen jen jednotlivými nálezy.

***Thanatophilus rugosus* (Linnaeus, 1758)**

Studovaný materiál. **Bohemia:** *Louny*: 35 – Březno (5648a), jaro 2009, 3 ex., léto 2009, 7 ex., podzim 2009, 10 ex.; 27 – Hořešovice I. (5749b), jaro 2008, 92 ex.; 28 – Hořešovice II. (5749b), jaro 2008, 1 ex., léto 2008, 12 ex., podzim 2008, 7 ex.; 29 – Hořešovice III. (5749b), jaro 2008, 28 ex., podzim 2008, 2 ex.; 30 – Klobuky (5749b), jaro 2008, 3 ex., léto 2008, 12 ex.; 42 – Křesín (5650a), jaro 2009, 32 ex., léto 2009, 58 ex., podzim 2009, 3 ex.; 36 – Louny I. (5648b), jaro 2009, 9 ex., léto 2009, 3 ex., podzim 2009, 16 ex.; 37 – Louny II. (5648b), jaro 2009, 6 ex., léto 2009, 3 ex., podzim 2009, 6 ex.; 33 – Malnice (5648c), jaro 2009, 4 ex.; 39 – Počedělice (5649a), jaro 2009, 6 ex., léto 2009, 14 ex., podzim 2009, 2 ex.; 34 – Postoloprty (5648a), jaro 2009, 11 ex., léto 2009, 70 ex., podzim 2009, 56 ex.; 25 – Pozdeň I. (5749d), jaro 2008, 3 ex., podzim 2008, 35 ex.; 26 – Pozdeň II. (5749b), jaro 2008, 11 ex., léto 2008, 27 ex., podzim 2008, 9 ex.; 31 – Skupice I. (5648c), jaro 2009, 16 ex., léto 2009, 15 ex.; 32 – Skupice II. (5648c), jaro 2009, 8 ex., léto 2009, 24 ex.; 40 – Slavětín (5649a), jaro 2009, 2 ex., léto 2009, 32 ex.; 41 – Stradonice (5649b), jaro 2009, 23 ex., podzim 2009, 127 ex.; 38 – Veltěže (5649c), jaro 2009, 11 ex., léto 2009, 42 ex., podzim 2009, 18 ex.; **Kutná Hora:** 1 – Církvice (6058c), jaro 2008, 3 m*m*, 1 f*, podzim 2008, 2 f*f*; 2 – Kalabousek (6058c), jaro 2008, 13 m*m*, 6 f*f*, léto 2008, 1 m*, podzim 2008, 4 m*m*, 3 f*f*; 3 – Žleby (6058d), jaro 2008, 2 m*m*, 4 f*f*; 4 – Vrdy I. (6058d), léto 2008, 2 f*f*, podzim 2008, 4 m*m*, 3 f*f*; 5 – Horní Bučice (6058d), jaro 2008, 1 m*, léto 2008, 2 m*m*, 3 f*f*, podzim 2008, 1 m*, 1 f*; 6 – Bojmany (6058d), podzim 2008, 4 m*m*, 1 f*; 8 – Starý Kolín I. (5957d), jaro 2008, 5 m*m*, 5 f*f*, léto 2008, 2 m*m*, 2 f*f*; 9 – Červený domek (6057b), jaro 2008, 26 m*m*, 17 f*f*, podzim 2008, 4 m*m*, 3 f*f*; 10 – Nové Dvory I. (6058a), jaro 2008, 8 m*m*, 3f*f*, léto 2008, 1 f*, podzim 2008, 4 m*m*, 7 f*f*; 11 – Malín I.

(6057a), jaro 2008, 1 m*, 1 f*; léto 2008, 3 m*m*, 1 f*, podzim 2008, 1 m*, 3 f*f*; 12 – Skalka (6057a), jaro 2008, 9 m*m*, 5 f*f*.; 13 – Hluboký důl (5957c), jaro 2009, 1 m*, 4 f*f*, podzim 2009, 4 m*m*, 5 f*f*; 14 – Starý Kolín II. (5957b), jaro 2009, 2 m*m*, 5 f*f*, léto 2009, 1 f*, podzim 2009, 16 m*m*, 8 f*f*; 15 – Libenice (6057b), jaro 2009, 5 m*m*, 5 f*f*; 16 – Hlízov (6057b), jaro 2009, 8 m*m*, 7 f*f*, podzim 2009, 21 m*m*, 17 f*f*; 17 – Nové Dvory II. (6057b), jaro 2009, 6 m*m*, 9 f*f*, léto 2009, 12 m*m*, 11 f*f*, podzim 2009, 2 m*m*, 2 f*f*; 18 – Chotusice – letiště (6058a), jaro 2009, 9 m*m*, 8 f*f*, léto 2009, 1 f*, podzim 2009, 4 m*m*, 4 f*f*; 19 – Chotusice (6058a), jaro 2009, 17 m*m*, 7 f*f*, léto 2009, 2 m*m*, 1 f*, podzim 2009, 13 m*m*, 14 f*f*; 20 – Druhanice (6058d), jaro 2009, 2 m*m*; 21 – Výčapy (6058d), jaro 2009, 4 m*m*, 4 f*f*, podzim 2009, 2 m*m*; 22 – Vrdy II. (6058d), jaro 2009, 4 m*m*, 3 f*f*, léto 2009, 1 m*; 23 – Vinice (6058d), jaro 2009, 1 f*; 24 – Malín II. (6057b), jaro 2009, 1 m*, 2 f*f*, podzim 2009, 10 m*m*, 8 f*f*; **Moravia: Židlochovice:** 50 – Cvrčovice (6965c), jaro 2009, 13 ex., podzim 2009, 28 ex.; 45 – Holasice (6965b), jaro 2009, 4 ex., léto 2009, 2 ex.; 48 – Kupařovice (6965c), jaro 2009, 4 ex.; 59 – Ladná I. (7167c), podzim 2009, 3 ex.; 60 – Ladná II. (7267a), jaro 2009, 13 ex.; 47 – Medlov (6965c), jaro 2009, 4 ex., léto 2009, 1 ex., podzim 2009, 1 ex.; 44 – Modřice (6865d), jaro 2009, 3 ex., podzim 2009, 1 ex.; 55 – Nosislav (6965d), jaro 2009, 1 ex.; 49 – Odrovice (6965c), jaro 2009, 10 ex.; 51 – Pohořelice (7064a), jaro 2009, 12 ex.; 52 – Přibice (7065a), jaro 2009, 29 ex., léto 2009, 5 ex., podzim 2009, 2 ex.; 54 – Přísnice (7065b), jaro 2009, 12 ex., podzim 2009, 4 ex.; 43 – Rebešovice (6865d), jaro 2009, 3 ex., podzim 2009, 1 ex.; 58 – Uherčice (7065b), jaro 2009, 38 ex.; 56 – Velké Němčice I. (7065b), jaro 2009, 38 ex., léto 2009, 3 ex., podzim 2009, 45 ex.; 57 – Velké Němčice II. (7066a), jaro 2009, 4 ex., léto 2009, 1 ex., podzim 2009, 22 ex.; 46 – Vojkovice (6965b), jaro 2009, 7 ex.; 53 – Vranovice (7065b), jaro 2009, 57 ex., podzim 2009, 21 ex.; **Zábřeh:** 72 – Dubicko (6167d), jaro 2009, 1 ex.; 75 – Leština (6167b), jaro 2009, 1 ex.; 81 – Libivá – východ (6167d), jaro 2009, 2 ex.; 80 – Lukavice (6167d), podzim 2009, 4 ex.; 82 – Mohelnice – sever (6267b), jaro 2009, 1 ex.; 83 – Mohelnice – východ (6267b), jaro 2009, 4 ex.; 66 – Rájec (6167a), jaro 2009, 3 ex.; 71 – Třeština (6267b), jaro 2009, 2 ex.; 68 – Vlachov (6167c), jaro 2009, 2 ex.; 78 – Zábřeh (6167a), jaro 2009, 1 ex.; 64 – Zábřeh – sever (6167a), jaro 2009, 1 ex.

Rozšíření a ekologie. Transpalearktický druh, rozšířený od Evropy do Japonska, včetně velké části Číny (Růžička & Schneider, 2004). U nás hojný druh (např. Vysoký 2007, mapka), preferující otevřené biotopy (Růžička, 1994; Kočárek & Benko, 1997). Ve studovaných oblastech rozšířený druh, často početné nálezy.

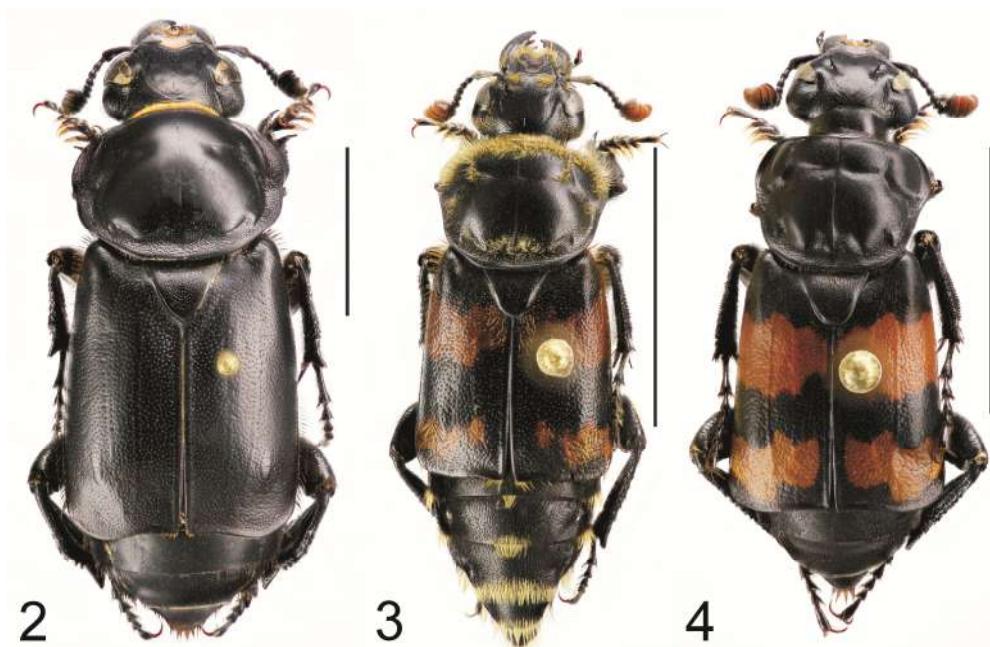
***Thanatophilus sinuatus* (Fabricius, 1775)**

Studovaný materiál. **Bohemia:** **Louny:** 35 – Březno (5648a), jaro 2009, 301 ex., léto 2009, 78 ex., podzim 2009, 39 ex.; 27 – Hořešovice I. (5749b), jaro 2008, 1983 ex.; 28 – Hořešovice II. (5749b), jaro 2008, 504 ex., léto 2008, 582 ex., podzim 2008, 5 ex.; 29 – Hořešovice III. (5749b), jaro 2008, 1084 ex.; 30 – Klobuky (5749b), jaro 2008, 342 ex., léto 2008, 537 ex., podzim 2008, 1 ex.; 42 – Křesín (5650a), jaro 2009, 1112 ex., léto 2009, 943 ex., podzim 2009, 3 ex.; 36 – Louny I. (5648b), jaro 2009, 743 ex., léto 2009, 174 ex., podzim 2009, 39 ex.; 37 – Louny II. (5648b), jaro 2009, 267 ex., léto 2009, 54 ex., podzim 2009, 36 ex.; 33 – Malnice (5648c), jaro 2009, 208 ex., podzim 2009, 5 ex.; 39 – Počedělice (5649a), jaro 2009, 372 ex., léto 2009, 479 ex., podzim 2009, 3 ex.; 34 – Postolopry (5648a), jaro 2009, 1081 ex., léto 2009, 538 ex., podzim 2009, 31 ex.; 25 – Pozdeň I. (5749d), jaro 2008, 601 ex., podzim 2008, 25 ex.; 26 – Pozdeň II. (5749b), jaro 2008, 1074 ex., léto 2008, 799 ex., podzim 2008, 6 ex., 31 – Skupice I. (5648c), jaro 2009, 408 ex., léto 2009, 169 ex.; 32 – Skupice II. (5648c), jaro 2009, 340 ex., léto 2009, 411 ex.; 40 – Slavětín (5649a), jaro 2009, 327 ex., léto 2009, 497 ex.; 41 – Stradonice (5649b), jaro 2009, 632 ex., podzim 2009, 62 ex.; 38 – Veltěže (5649c), jaro 2009, 940 ex., léto 2009, 742 ex., podzim 2009, 36 ex.; **Kutná Hora:** 1 – Církvice (6058c), jaro 2008, 50 m*m*, 49 f*f*, podzim 2008, 1 f*; 2 – Kalabousek (6058c), jaro 2008, 140 m*m*, 186 f*f*, léto 2008, 451 m*m*, 338 f*f*, podzim 2008, 6 m*m*, 1 f*; 3 – Žleby (6058d), jaro 2008, 268 m*m*, 462 f*f*, léto 2008, 108 m*m*, 87 f*f*; 4 – Vrdy I. (6058d), jaro 2008, 17 m*m*, 12 f*f*, léto 2008, 2 m*m*, podzim 2008, 6 m*m*, 1 f*; 5 – Horní Bučice (6058d), jaro 2008, 38 m*m*, 41 f*f*, léto 2008, 161 m*m*, 157 f*f*, podzim 2008, 2 m*m*, 4 f*f*; 6 – Bojmany (6058d), jaro 2008, 43 m*m*, 19 f*f*, podzim 2008, 5 m*m*, 7 f*f*; 7 – Kolín (5957c), jaro 2008, 3 m*m*, 1 f*; 8 – Starý Kolín I. (5957d), jaro

2008, 208 m*m*, 244 f*f*, léto 2008, 212 m*m*, 218 f*f*, podzim 2008, 1 m*, 2 f*f*; 9 – Červený domek (6057b), jaro 2008, 85 m*m*, 107 f*f*, léto 2008, 9 m*m*, 6 f*f*, podzim 2008, 2 m*m*, 8 f*f*; 10 – Nové Dvory I. (6058a), jaro 2008, 173 m*m*, 248 f*f*, léto 2008, 23 m*m*, 32 f*f*, podzim 2008, 1 m*, 2 f*f*; 11 – Malín I. (6057a), jaro 2008, 133 m*m*, 87 f*f*, léto 2008, 114 m*m*, 72 f*f*, podzim 2008, 4 m*m*, 7 f*f*; 12 – Skalka (6057a), jaro 2008, 66 m*m*, 81 f*f*, léto 2008, 2 m*m*, podzim 2008, 2 m*m*, 3 f*f*; 13 – Hluboký důl (5957c), jaro 2009, 178 m*m*, 274 f*f*, léto 2009, 106 m*m*, 97 f*f*, podzim 2009, 1 f*; 14 – Starý Kolín II. (5957b), jaro 2009, 294 m*m*, 309 f*f*, léto 2009, 16 m*m*, 5 f*f*, podzim 2009, 4 m*m*, 5 f*f*; 15 – Libenice (6057b), jaro 2009, 137 m*m*, 147 f*f*, léto 2009, 2 m*m*, 6 f*f*; 16 – Hlízov (6057b), jaro 2009, 376 m*m*, 486 f*f*, podzim 2009, 12 m*m*, 5 f*f*; 17 – Nové Dvory II. (6057b), jaro 2009, 275 m*m*, 251 f*f*, léto 2009, 1337 m*m*, 1081 f*f*, podzim 2009, 1 f*, 1 m*; 18 – Chotusice – letiště (6058a), jaro 2009, 694 m*m*, 949 f*f*, léto 2009, 2 m*m*, 5 f*f*, podzim 2009, 4 m*m*, 5 f*f*; 19 – Chotusice (6058a), jaro 2009, 747 m*m*, 923 f*f*, léto 2009, 471 m*m*, 388 f*f*, podzim 2009, 10 m*m*, 7 f*f*; 20 – Druhanice (6058d), jaro 2009, 103 m*m*, 151 f*f*, léto 2009, 69 m*m*, 52 f*f*; 21 – Výčapy (6058d), jaro 2009, 400 m*m*, 457 f*f*, léto 2009, 5 m*m*, 4 f*f*, podzim 2009, 12 m*m*, 10 f*f*; 22 – Vrdy II. (6058d), jaro 2009, 357 m*m*, 432 f*f*, léto 2009, 297 m*m*, 253 f*f*; 23 – Vinice (6058d), jaro 2009, 405 m*m*, 576 f*f*; 24 – Malín II. (6057b), jaro 2009, 308 m*m*, 286 f*f*, podzim 2009, 9 m*m*, 8 f*f*; **Moravia:** **Židlochovice:** 50 – Cvrčovice (6965c), jaro 2009, 558 ex., léto 2009, 40 ex., podzim 2009, 12 ex.; 45 – Holasice (6965b), jaro 2009, 193 ex., léto 2009, 86 ex.; 48 – Kupařovice (6965c), jaro 2009, 118 ex. léto 2009, 11 ex., podzim 2009, 1 ex.; 59 – Ladná I. (7167c), jaro 2009, 3 ex., léto 2009, 7 ex., podzim 2009, 1 ex.; 60 – Ladná II. (7267a), jaro 2009, 169 ex., léto 2009, 68 ex.; 47 – Medlov (6965c), jaro 2009, 130 ex., léto 2009, 30 ex.; 44 – Modřice (6865d), jaro 2009, 331 ex., léto 2009, 6 ex., podzim 2009, 1 ex.; 55 – Nosislav (6965d), jaro 2009, 10 ex., léto 2009, 4 ex.; 49 – Odrovice (6965c), jaro 2009, 11 ex., léto 2009, 17 ex., podzim 2009, 2 ex.; 51 – Pohořelice (7064a), jaro 2009, 60 ex., léto 2009, 5 ex.; 52 – Přibice (7065a), jaro 2009, 439 ex., léto 2009, 1036 ex., podzim 2009, 1 ex.; 54 – Přísnotice (7065b), jaro 2009, 230 ex., léto 2009, 2 ex., podzim 2009, 3 ex.; 43 – Rebešovice (6865d), jaro 2009, 528 ex., léto 2009, 289 ex., podzim 2009, 2 ex.; 58 – Uherčice (7065b), jaro 2009, 340 ex.; 56 – Velké

Němčice I. (7065b), jaro 2009, 194 ex., léto 2009, 121 ex., podzim 2009, 1 ex.; 57 – Velké Němčice II. (7066a), jaro 2009, 83 ex., léto 2009, 8 ex., podzim 2009, 5 ex.; 46 – Vojkovice (6965b), jaro 2009, 229 ex., léto 2009, 204 ex.; 53 – Vranovice (7065b), jaro 2009, 304 ex., léto 2009, 6 ex., podzim 2009, 7 ex.; **Zábřeh:** 72 – Dubicko (6167d), jaro 2009, 360 ex., léto 2009, 1 ex., podzim 2009, 2 ex.; 62 – Kolšov (6067d), jaro 2009, 60 ex.; 75 – Leština (6167b), jaro 2009, 114 ex., léto 2009, 77 ex.; 76 – Leština – západ (6167a), jaro 2009, 3 ex.; léto 2009, 10 ex.; 69 – Libivá (6267a), jaro 2009, 44 ex.; 81 – Libivá – východ (6167d), jaro 2009, 244 ex.; 80 – Lukavice (6167d), léto 2009, 34 ex., podzim 2009, 30 ex.; 70 – Mohelnice (6267b), jaro 2009, 38 ex.; 82 – Mohelnice – sever (6267b), jaro 2009, 152 ex.; 83 – Mohelnice – východ (6267b), jaro 2009, 114 ex., léto 2009, 1 ex.; 74 – Nový Dvůr (6167b), jaro 2009, 7 ex.; 66 – Rájec (6167a), jaro 2009, 455 ex., léto 2009, 2 ex.; 73 – Sudkov – jih (6067d), jaro 2009, 15 ex., podzim 2009, 3 ex.; 71 – Třeština (6267b), jaro 2009, 212 ex.; 84 – Třeština – severozápad (6167d), jaro 2009, 2 ex., podzim 2009, 11 ex.; 68 – Vlachov (6167c), jaro 2009, 413 ex.; 78 – Zábřeh (6167a), jaro 2009, 241 ex.; 64 – Zábřeh – sever (6167a), jaro 2009, 93 ex.; 67 – Zvole (6167c), jaro 2009, 29 ex.

Rozšíření a ekologie. Transpalearktický druh, od Evropy a severu Afriky do Japonska, včetně velké části Číny (Růžička & Schneider, 2004). U nás velmi hojný druh (např. Vysoký 2007, mapka), preferující otevřené biotopy (Růžička 1994, Kočárek & Benko 1997). Ve studovaných oblastech většinou velmi početné nálezy.



Obr. 2–4. Habitus vzácnějších druhů hrobaříků, dorzálně: 2 – *Nicrophorus germanicus* (Linnaeus, 1758), 3 – *N. antennatus* (Reitter, 1884), 4 – *N. sepultor* Charpentier 1825.

Figs 2–4. Habitus of rare burying beetle species, dorsal view: 2 – *Nicrophorus germanicus* (Linnaeus, 1758), 3 – *N. antennatus* (Reitter, 1884), 4 – *N. sepultor* Charpentier 1825.

C.4 Diskuse

Tři zjištěné vzácnější druhy hrobaříků (*Nicrophorus antennatus*, *N. germanicus* a *N. sepultor*) mají společné to, že se jedná o druhy preferující otevřenou krajину. Zřejmě se primárně jedná o druhy stepní či obecně xerofilní, početnější na jihu Ruska (např. Pushkin 2002, Pushkin & Shapovalov 2011). V podmírkách střední Evropy pro ně kulturní stepi polních ekosystémů mohou představovat náhradní biotopy.

Další dva druhy otevřené krajiny, které jsou vzácné ve střední Evropě, nebyly v naší studii zachyceny. Jedná se o druh *Thanatophilus dispar* (Herbst, 1793), palearktický druh mrchožrouta preferujícího biom tundry, který se ve střední Evropě recentně vyskytuje v Německu (shrnuje Köhler & Klausnitzer 1998) a v Polsku (např. Aleksandrowicz & Komosiński 2005). Tento druh byl historicky hlášen v ČR z Moravy – konkrétní nálezy byly publikovány např. z okolí Nákla (6368)

(Novák 1966) a Litovle (6268–6368) (Kočárek 1997). V Čechách známe pouze jednotlivé starší nálezy (J. Růžička, nepubl.). Recentně nebyl na území ČR nalezen.

Druhým druhem, který se nám nepodařilo zachytit, je *Nicrophorus vestigator* Herschel, 1807. Tento hrobařík je morfologicky velmi podobný druhu *N. antennatus* (Šustek 1981). Celkově je u nás hodnocen jako řídce se vyskytující (Šustek 1981). Hojně nálezy (za dva roky více než 200 ex.) z Chválkovic (6369) uvádí z přelomu 50. a 60. let Novák (1962). Jednotlivé nálezy z okolí Nákla (6368) a Drahanovic (6468) v Olomouckém okrese z téže doby zmiňuje Novák (1961, 1965). Novák (1962: 289) diskutuje také možnou vazbu tohoto druhu na lehké, písčité a propustnější půdy.

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C.5 Použitá literatura

ALEKSANDROWICZ O. & KOMOSIŃSKI K. 2005: On the fauna of carrion beetles (Coleoptera, Silphidae) of Mazurian lakeland (north-eastern Poland). Pp. 147–153. In: SKŁODOWSKI J., HURUK S., BARŠEVSKIS A. & TARASIUK S. (eds): *Protection of Coleoptera in the Baltic Sea Region*. Warsaw Agricultural University Press, Warszawa, 239 pp.

ANDERSON R.S. 1982: Resource partitioning in the carrion beetle (Coleoptera: Silphidae) fauna of southern Ontario: ecological and evolutionary considerations. *Canadian Journal of Zoology* **60**: 1314–1325.

BOCÁKOVÁ M. 2003: Fauna brouků nadčeledi Staphylinoidea přírodní rezervace Království v Grygově u Olomouce. (Fauna of the superfamily Staphylinoidea of the Království Nature Reserve in Central Moravia). *Zprávy Vlastivědného Muzea v Olomouci* **279**: 56–67 (in Czech, English summary).

BOHÁČ J. & MATĚJÍČEK J. 2009: Společenstva brouků (Insecta, Coleoptera) v lesích u obce Luštěnice u Mladé Boleslavi a jejich antropogenní ovlivnění. (Communities of beetles

- (Insecta, Coleoptera) in forests in the vicinity of Luštěnice near Mladá Boleslav and its anthropogenic interference). *Bohemia Centralis* **29**: 111–126 (in Czech, English abstract).
- GREBENNIKOV V. V. & NEWTON A.F. 2012: Detecting the basal dichotomies in the monophylum of carrion and rove beetles (Insecta: Coleoptera: Silphidae and Staphylinidae) with emphasis on the Oxyteline group of subfamilies. *Arthropod Systematics & Phylogeny* **70**: 133–165.
- HAMET A., HAMETOVÁ VAŠÍČKOVÁ K. & MLEJNEK R. 2012: Faunistický průzkum brouků (Coleoptera) Národní přírodní rezervace Vývěry Punkvy v letech 1991–2010. (Faunistic survey of beetles (Coleoptera) in the Vývěry Punkvy National Nature Reserve in 1991–2010). *Klapalekiana* **48**: 29–73 (in Czech, English abstract).
- HAMET A. & VANCL Z. (eds) 2005: *Katalog brouků (Coleoptera) CHKO Broumovsko. (Catalogue of beetles (Coleoptera) of the Broumovsko Protected Landscape Area)*. O. Čermáková, Hradec Králové, 126 pp. (in Czech, English summary).
- HÁVA J. 2009: Výsledky faunistického průzkumu brouků čeledí Dermestidae a Silphidae (Coleoptera) v přírodní rezervaci Údolí Únětického potoka. (Results of faunistic research of the beetle families Dermestidae and Silphidae (Coleoptera) in Údolí Únětického potoka Nature Reserve (Prague, Czech Republic)). *Bohemia Centralis* **29**: 101–110 (in Czech, English summary).
- KOČÁREK P. 1997: Výskyt brouků ze skupin Silphidae a Leiodidae: Cholevinae (Coleoptera) na území CHKO Litovelské Pomoraví. (The occurrence [sic] of Silphidae and Leiodidae: Cholevinae (Coleoptera) in the Litovelské Pomoraví Protected Landscape Area). *Zprávy Vlastivědného Muzea v Olomouci* **275**: 17–29 (in Czech, English summary).
- KOČÁREK P. 2001: Diurnal activity rhythms and niche differentiation in a carrion beetle assemblage (Coleoptera: Silphidae) in Opava, the Czech Republic. *Biological Rhythm Research* **32**: 431–438.
- KOČÁREK P. 2002a: Decomposition and Coleoptera succession on exposed carrion of small mammal in Opava, the Czech Republic. *European Journal of Soil Biology* **39**: 31–45.
- KOČÁREK P. 2002b: Diel activity patterns of carrion-visiting Coleoptera studied by timesorting pitfall traps. *Biologia (Bratislava)* **57**: 199–211.
- KOČÁREK P. & BENKO K. 1997: Výskyt a sezónní aktivita brouků čeledi Silphidae na Hlučínsku (Slezsko, Česká republika). (The occurrence and seasonal activity of Silphidae in the Hlučín region (Silesia, Czech Republic). *Časopis Slezského Zemského Muzea, Série A – Vědy Přírodní* (Opava) **46**: 173–179 (in Czech, English summary).
- KOČÁREK P. & ROHÁČOVÁ M. 1997: Mrchožroutovití brouci (Coleoptera: Silphidae) v ekosystému horského lesa (Moravskoslezské Beskydy, Česká republika). (Carrion beetles

- (Coleoptera: Silphidae) in the mountain forest ecosystem (Moravskoslezské Beskydy Mts., Czech Republic). *Práce a Studie Muzea Beskyd* **11**: 67–74 (in Czech, English summary).
- KÖHLER F. & KLAUSNITZER B. (eds) 1998: Verzeichnis der Käfer Deutschlands. *Entomologische Nachrichten und Berichte* (Dresden) **Supplement 4**: 1–185.
- NAKLÁDAL O. 2008: Results of a faunistic survey of beetles (Coleoptera) in floodplain forests of the Litovelské Pomoraví Protected Landscape Area (Czech Republic, Northern Moravia) in 2006. *Klapalekiana* **44**: 237–269.
- NAKLÁDAL O. 2011a: Results of beetles (Coleoptera) survey of Zástudánčí National Nature Reserve (Central Moravia) 2008 – part 1. *Časopis Slezského Zemského Muzea, Serie A – Vědy Přírodní* (Opava) **60**: 63–78.
- NAKLÁDAL O. 2011b: Results of a faunistic survey of beetles (Coleoptera) in Vrapač National Nature Reserve (Czech Republic, Northern Moravia, Litovelské Pomoraví Protected Landscape Area) in 2009. *Klapalekiana* **47**: 213–236.
- NOVÁK B. 1961: Sezónní výskyt hrobaříků v polních entomocenózách (Col. Silphidae). (Saisonmässiges Vorkommen von Totengräbern in Feldbiozönosen (Col. Silphidae)). *Acta Universitatis Palackiana Olomucensis, Facultas Rerum Naturalium* **6**: 45–114 (in Czech, English, German and Russian summaries).
- NOVÁK B. 1962: Příspěvek k faunistice a ekologii hrobaříků (Col. Silphidae). (Ein Beitrag zur Faunistik und Ökologie der Totengräber (Col. Silphidae)). *Acta Universitatis Palackiana Olomucensis, Facultas Rerum Naturalium* **11**: 263–300 (in Czech, German and Russian summaries).
- NOVÁK B. 1965: Faunisticko-ekologická studie o hrobařících z polních biotopů Hané (Col. Silphidae). (Zur Faunistik und Ökologie der Totengräber in den Feldbiotopen von Haná (Col. Silphidae)). *Acta Universitatis Palackiana Olomucensis, Facultas Rerum Naturalium* **19**: 121–151 (in Czech, German summary).
- NOVÁK B. 1966: Dynamika populací brouků ze skupiny Silphini (Coleoptera). (Populationsdynamik der Silphini (Coleoptera)). *Acta Universitatis Palackiana Olomucensis, Facultas Rerum Naturalium* **22**: 129–151 (in Czech, German summary).
- PETRUŠKA F. 1964: Příspěvek k poznání pohyblivosti několika druhů brouků nalézávajících na mršiny (Col. Silphidae et Histeridae). (Beitrag zur Bewegungsaktivität einiger Aaskäfer-Arten (Col. Silphidae et Histeridae)). *Acta Universitatis Palackiana Olomucensis, Facultas Rerum Naturalium* **16**: 159–187 (in Czech, German summary).
- PUSHKIN S. V. 2002: Landshaftno-biotopicheskoe rasprostranenie zhukov-mertvoedov (Coleoptera: Silphidae) v Predkavkaz'ye. (Landscape-biotopical distribution of carrion beetles

- (Coleoptera, Silphidae) in Ciscaucasia). P. 299. In: *Abstracts of XII Congress of Russian Entomological Society, St-Petersburg, August, 19-24, 2002*. Russkoe entomologicheskoe obshchestvo, St. Peterburg, 394 pp. (in Russian, English title).
- PUSHKIN S. V. & SHAPOVALOV M. I. 2011: Ekologo-faunisticheskiy analiz zhukov-mertvoedov (Coleoptera, Silphidae) Respubliki Adygeya. (Fauna and ecology analysis of the burying beetles (Coleoptera, Silphidae) in the Adyghe Republic). *Bulletin of Adyghe State University: Internet Scientific Journal* (Maikop) **2**: 66–76 (in Russian, English abstract).
- RÉBL K. 2010: Výsledky faunistického průzkumu brouků (Coleoptera) na území Chráněné krajinné oblasti a Biosferické rezervace Křivoklátsko (Česká republika). (Results of faunistic survey of beetles (Coleoptera) in the territory of Protected Landscape Area and Biospheric Reservation Křivoklátsko (Czech Republic)). *Elateridarium 4 (Supplementum)*: 1–253 (in Czech, English abstract).
- RŮŽIČKA J. 1994: Seasonal activity and habitat associations of Silphidae and Leiodidae: Cholevinae (Coleoptera) in central Bohemia. *Acta Societatis Zoologicae Bohemicae* **58**: 67–78.
- RŮŽIČKA J. 1999: Beetle communities (Insecta: Coleoptera) of rock debris on the Boreč hill (Czech Republic: České středohoří mts). *Acta Societatis Zoologicae Bohemicae* **63**: 315–330.
- RŮŽIČKA J. 2000: Beetle communities (Insecta: Coleoptera) of rock debris on the Kamennec hill (Czech Republic: České středohoří mts). *Acta Universitatis Purkynianae, Studia Biologica* **4**: 175–182.
- RŮŽIČKA J., HÁVA J. & SCHNEIDER J. 2004: Revision of Palaearctic and Oriental Oiceoptoma (Coleoptera: Silphidae). *Acta Societatis Zoologicae Bohemicae* **68**: 30–51.
- RŮŽIČKA J. 2005a: Icones Insectorum Europae Centralis. Coleoptera: Agrytidae, Silphidae. *Folia Heyrovskyana, Series B* **3**: 1–9 (in English and Czech).
- RŮŽIČKA J. 2005b: Silphidae. Pp. 429–430. In: FARKAČ J., KRÁL D. & ŠKORPÍK M. (eds): *Červený seznam ohrožených druhů České republiky. Bezobratlí. Red list of threatened species in the Czech Republic. Invertebrates*. Agentura ochrany přírody a krajiny ČR, Praha, 760 pp. (in English and Czech).
- RŮŽIČKA J. 2007: Brouci (Coleoptera) v sutích Komářího vrchu v katastrálním území Nová Ves u Kraslic. [Beetles (Coleoptera) in rock debris of Komáří vrch hill, catastrophe of Nová Ves near Kraslice]. Pp. 83–102. In: HEJKAL J., HAVALOVÁ A. & MICHÁLEK J. (eds): *Příroda Kraslicka 1. [Nature of Kraslice region 1.]*. Nakladatelství Jan Farkač, Praha, 134 pp. (in Czech).
- RŮŽIČKA J. & SCHNEIDER J. 2004: Silphidae. Pp. 229–237. In: LÖBL I. & SMETANA A. (eds): *Catalogue of Palaearctic Coleoptera, Volume 2: Hydrophiloidea – Histeroidea – Staphylinoidea*. Apollo books, Stenstrup, 942 pp.

SIKES D. 2005: Silphidae Latreille, 1807. Pp. 288–296. In: BEUTEL R. G. & LESCHEN R. A. B. (eds): *Handbook of Zoology, Volume IV: Arthropoda: Insecta, Part 38: Coleoptera, Beetles. Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim)*. Walter de Gruyter, Berlin, 632 pp.

SIKES D. 2008: Carrion beetles (Coleoptera: Silphidae). Pp. 749–758. In: CAPINERA J. L. (ed.): *Encyclopedia of Entomology*. Springer, Berlin, 4346 pp.

ŠUSTEK Z. 1981: Mrchožroutovití Československa (Coleoptera, Silphidae). [Key to identification of insects: Carrion beetles of Czechoslovakia (Coleoptera, Silphidae)]. *Zprávy Československé Společnosti Entomologické při ČSAV, Klíče k určování hmyzu* 2: 1–47 (in Czech).

VYSOKÝ V. 2007: Zástupci čeledí Agyrtidae, Silphidae a Leiodidae vyskytující se na území Ústeckého kraje (Coleoptera). [Representatives of the families Agyrtidae, Silphidae and Leiodidae occurring on the territory of Ústí nad Labem region (Coleoptera)]. *Fauna Bohemiae Septentrionalis 2007 (Suplementum)*: 1–254 (in Czech).

C.6 English summary

This study presents distribution data for beetles of the family Silphidae, collected during ecological studies in the vicinities of Louny, Kutná Hora, Zábřeh and Židlochovice (Fig. 1). These areas are warm lowlands with two different soil-types (loess and fluvisols).

Beetles were collected using 420 pitfall traps with a 1:1 water: ethylene glycol solution, and baited with ripe cheese and fish.

Traps were placed in lines of five on fields at least 50 m from the ecotone and 20 m from each other. Traps were left for two weeks, and only in spring 2008 was this extended to three weeks because of cold weather. Traps were placed in 84 localities. In total, 71 234 individuals of 15 species were collected and determined.

Specimens were determined using keys by Šustek (1981). Doubtful specimens were examined and confirmed by Jan Růžička. All material is housed in the collection of Jan Růžička, except samples from Kutná Hora, which are in the collection of Pavel Jakubec.

The list of localities is divided by place and year of collection. It includes serial number, name of closest habitation, faunistic map code, GPS coordinates of the centre of the trap line and scientific name of the crop-plant surrounding the trap.

Detailed comments are given below on three endangered species, listed in the local Red List of Invertebrates (Růžička 2005b):

(1) *Nicrophorus antennatus* (Reitter, 1884) is a Palaearctic species, widely distributed throughout Europe (except Scandinavia and Great Britain), in Asia it is known from Turkey up to Kashmir and north-western China (Růžička & Schneider 2004). In the Czech Republic, the species is known only from several older records from Bohemia and Moravia (J. Růžička, unpubl.). Novák (1961, 1965) reported abundance of this species in the 1950/60s in northern Moravia near Náklo (6368) and Drahonovice (6468), but only rarely near Chválkovice (6369), all in the vicinity of Olomouc. Recently, abundant occurrence was registered in Bohemia, near Žabovřesky nad Ohří (5550) (J. Růžička, unpubl.). In the Czech Republic, *N. antennatus* is evaluated as vulnerable (VU) in the local Red list (Růžička 2005b). Novák (1962) reported abundant occurrence of *N. antennatus* in open landscape, linked with loess soils. We only recorded it in two of the studied regions (Louny and Židlochovice) (Table 1).

(2) *Nicrophorus germanicus* (Linnaeus, 1758) is a western Palaearctic species, distributed from Europe through Turkey, southern Russia and Iran up to Turkmenistan (Růžička & Schneider 2004). In the Czech Republic, abundant older records are known from Bohemia and Moravia (J. Růžička, unpubl.). Novák (1961, 1962, 1965) reported this species as abundant in 1950/60s in northern Moravia near Náklo (6368), Chválkovice (6369) and Drahonovice (6468), and less abundant near Lhota nad Moravou (6368), all in the vicinity of Olomouc. Recently it has only been rarely reported, but we are aware of at least two additional localities with recent abundant occurrence – Žabovřesky nad Ohří (5550) in Bohemia and near Kyjov (7068) in Moravia. In both cases, the habitats consist mostly of meadows (J. Růžička, unpubl.). In the Czech Republic, like the previous species, *N. germanicus* is listed as vulnerable (VU) in the local Red list (Růžička 2005b). Novák (1962) reported *N. germanicus* as abundant in open landscape,

on warmer localities with loessy soils. Here, we recorded the species as abundant in two regions (Louny, Židlochovice), with only a single record around Zábřeh (Table 1).

(3) *Nicrophorus sepultor* Charpentier, 1825 is a Palaearctic species, widely distributed from Europe to Mongolia, eastern Siberia and north-western China (Růžička & Schneider 2004). In the Czech Republic, individual older and/or recent records are known from Bohemia and Moravia (Vysoký 2007; J. Růžička, unpubl.). Novák (1961, 1962, 1965) reported this species as abundant in 1950/60s in northern Moravia near Náklo (6368), Lhota nad Moravou (6368) and Drahanovice (6468), and less abundant near Chválkovice (6369), all in the vicinity of Olomouc. Recently, only isolated records from the Czech Republic are known (e.g., records from Ústí nad Labem region are summarized by Vysoký (2007)). We know of two localities with recent abundant occurrence of *N. sepultor* in Bohemia – around Žabovřesky nad Ohří (5550) and Kostelec nad Černými lesy (6055); both habitats consist mostly of meadows (J. Růžička, unpubl.). In the Czech Republic, *N. sepultor* is evaluated as near threatened (NT) in the local Red list (Růžička 2005b). Records are mostly from open landscapes, including colder habitats (Vysoký 2007; J. Růžička, unpubl.). Novák (1962) linked its occurrence to habitats with loessy soils. Vysoký (2007) also mentioned records on the margins of forested habitats. Here, we recorded the species relatively abundantly in three regions (Louny, Kutná hora, Židlochovice); two specimens were found at a single locality around Zábřeh (Table 1).

A further two species of carrion beetles, found rarely in open landscapes in central Europe, were not recorded in our study. The first such species is *Thanatophilus dispar* (Herbst, 1793), with a Palaearctic distribution and a preference for tundra biome, with recent occurrence in central Europe in Germany (distribution reviewed by Köhler & Klausnitzer 1998) and Poland (e.g., Aleksandrowicz & Komosiński 2005). This species was historically reported in the Czech Republic from Moravia – with confirmed records near Náklo (6368) (Novák 1966) and Litovel (6268–6368) (Kočárek 1997). In Bohemia, only several old records are known (J. Růžička, unpubl.). There are no recent records of *T. dispar* from the Czech Republic.

The other species not recorded in our study, is *Nicrophorus vestigator* Herschel, 1807. This burying beetle is morphologically very similar to *N. antennatus* (Šustek 1981). Generally, it is

regarded as rare in the Czech Republic (Šustek 1981). Novák (1962) reported it as abundant (more than 200 specimens over a two year period of pitfall trapping) in 1950/1960s in northern Moravia near Chválkovice (6369). Single records from Náklo (6368) and Drahanovice (6468) (all in surrounding of Olomouc) from the same period were recorded by Novák (1961, 1965). Novák (1962: 289) discussed a possible preference of *N. vestigator* for habitats with light, sandy and more permeable soil.

In central Europe, field ecosystems can regarded as substitute habitats for species of open landscape carrion beetles. Most of them are primarily steppe or more generally, xerophilous species, more abundant in southern Russia (e.g., Pushkin 2002, Pushkin & Shapovalov 2011).

4. Principal conclusions of the thesis

European necrophagous species are overlooked, but they deserve much more attention, because they play major role in nutrient cycling and information about their ecology and evolution can have great impact on applied fields of science like forensic entomology and nature protection (Lomolino *et al.*, 1995; Lomolino & Creighton, 1996; Ratcliffe, 1996; Begon *et al.*, 2006; Looney *et al.*, 2009; Crawford & Hoagland, 2010; Midgley *et al.*, 2010; Jurzenski *et al.*, 2014; Houston *et al.*, 2015).

During the field work on article **A** and **C** we captured and identified 15 species of Central European carrion beetles. Three of which are currently considered as rare and are on the Czech Red List of Invertebrates as Endangered (*Nicrophorus antennatus* and *N. germanicus*) or Nearly Endangered (*N. sepultor*) (Růžička, 2005). The last ecological studies of these species in Europe were done almost 50 years ago when they were probably much more common (Novák, 1966; Petruška, 1968).

The most frequently observed species was *Thanatophilus sinuatus*, whose dominance was overshadowed by *N. vespillo* and *T. rugosus*, but only in autumn. All these species seem to be very common in open landscape habitats and our findings confirm the earlier observations of Novák, (1962, 1965, 1966) and Petruška (1964). Both species of genus *Thanatophilus* are therefore fairly common in the Czech Republic and they visit regularly the carcasses of large animals.

T. sinuatus and *T. rugosus* are considered to be co-occurring species without spatially or temporally differentiated niches (Novák, 1966). The higher abundance of *T. rugosus* in autumn samples could indicate a temporal niche differentiation.

All these traits could be used in forensic entomology, but larval identification, instar determination and thermal summation models are not established for them yet. In contrast, successful case report of estimation of PMI based on closely related African species of genus *Thanatophilus* (*T. mutilatus* and *T. micans*) was published last year (Ridgeway *et al.*, 2014). These species were only recently studied and proposed thermal summation models made them

available for use in forensic entomology (Midgley & Villet, 2009a; Ridgeway *et al.*, 2014). *T. sinuatus* and *T. rugosus* are showing similar qualities and options for future research looks very promising.

We were able to show in the article **A** that the abundance of seven of the carrion beetles (*N. antennatus*, *N. germanicus*, *N. humator*, *N. interruptus*, *N. sepultor*, *Silpha obscura obscura* and *T. sinuatus*) differed significantly in areas with chernozem and fluvisol soils, and therefore soil type is an important factor in determining the occurrence of these carrion beetles. Our findings are supported by the results of the CCA analysis and Wilcoxon rank-sum tests (article **A**).

CCA analysis in article **A** also revealed that the factors that are significantly associated with the species composition are both soil types (chernozem and fluvisol) and also three crops (*Zea mays*, *Hordeum vulgare* and *Helianthus annus*). The association between the abundance of the carrion beetles and these crops is very interesting and we did not expect such a relationship. We think that it could be due to the microclimatic conditions in fields with these crops. Based on our experience, *Z. mays* provides a much more humid and cooler environment than *H. vulgare* and *H. annus*. Further study is needed to reveal causality.

Association between abundance of Nicrophorinae and soil characteristics was assumed by many authors (Pukowski, 1933; Paulian, 1946; Theodorides & Heerdt, 1952; Novák, 1961, 1962). Heretofore, this phenomenon was empirically proven only for North American species (Muths, 1991; Bishop *et al.*, 2002; Looney *et al.*, 2009), where the association of beetles of the subfamily Silphinae with a particular soil was previously reported by Bishop *et al.* (2002).

However, burying beetles are good fliers and can cover long distances they mostly choose to stay close to their original locations (e.g., *Nicrophorus americanus*, which is a relatively large and robust beetle, is capable of flying as far as 7.41 km in a single night, but more typically travels less than 1.6 km/night) (Jurzenksi *et al.*, 2011). Limited mobility coupled with adaptation to local conditions could cause the observed spatial structure rather than individual habitat choice (preferential colonization). This is also in line with general local adaptation hypotheses (Alstad, 1998). It is also possible that the abundances of those species are different throughout their distribution area, as pointed out by Scott (1998).

Among other species, which were more abundant on cernozem, we also identified three endangered species (*N. antennatus*, *N. germanicus* and *N. sepultor*). Our finding can help in actions towards the conservation of these species, which is currently not a topical issue in the Czech Republic and Europe generally, but these beetles are charismatic and could become a widely accepted flagship species for stakeholders and policymakers, as indicated by the public interest in and the vast number of studies on the American burying beetle (*N. americanus*) (e.g., Anderson, 1982b; Lomolino *et al.*, 1995, 1999; Lomolino & Creighton, 1996; Bedick *et al.*, 1999, 2004; Szalanski *et al.*, 2000; Sikes & Raithel, 2002; Bishop *et al.*, 2002; Walker & Hoback, 2007; Crawford & Hoagland, 2010; Jurzenski *et al.*, 2011, 2014; Black, 2012; Hall *et al.*, 2015; Houston *et al.*, 2015).

The article **B** provides parameter estimates of thermal summation model of *Sciodrepoides watsoni* together with new character for instar determination. *S. watsoni* is very common necrophagous beetle (Růžička, 1994, 2000; GBIF, 2015), which occurs across Holarctic region (Peck & Cook, 2002; Perreau, 2004). This species was offered as with some utility for forensic entomology by Schilthuizen *et al.* (2011). This view was recently challenged by Kilian & Mądra (2015), but unfortunately they did not show any evidence to support their claim that this species is irrelevant for forensic entomology.

The mean development time decreased with increasing temperature (article **B**, Fig. 6), except for L2 and L3 instars in the 25°C treatment. This might indicate that between 21°C and 25°C should be an optimal temperature for the development of these two stages. Optimal temperatures for lower stages are probably even higher. This agrees with findings of Engler (1981), who reported *S. watsoni* as warm season species in contrast to some species of *Choleva* and *Catops* that prefers to breed during the winter season and their optimal temperatures for development were below 16°C.

During the breeding we observed very high levels of mortality in later stages of development (third larval instar and pupae). It is more likely that separation from other larvae and adults was the reason for this phenomenon. Peck (1975) mentioned that *Ptomaphagus hirtus* (Tellkampf, 1844) (Leiodidae: Cholevinae: Ptomaphagini) needed soil from the cave of its origin to

successfully complete the development. Soil bacteria probably played some part in this process, because specimens did not develop on autoclaved soil (Peck, 1975). It is possible that adults feeding along with larvae could provide such bacteria in our case. Another explanation could be that feeding of multiple individuals is much more effective or improves the quality of the food source.

Methodology of measuring the size of the instars of *S. watsoni* was based on continual observation of individuals from egg until pupation. This approach differs from other studies with similar goals (see Velásquez & Viloria, 2010; Fratczak & Matuszewski, 2014), where authors tried to estimate the stage of development based on the size of selected characters without prior knowledge of the true stage of the specimen. This approach is from my point of view a little bit problematic, because those measured characters are correlated, therefore bigger larvae could be misidentified as higher instar than they really are. This bias would probably not affect the obtained mean values, but it would give distorted picture about variation.

I found an overlap in the head width between of all instars. This is especially true for the first and second instar, but measuring more, probably correlated, characters would not solve the problem. The first instar larva has only primary setae on its body, but after molt to the second instar a secondary set of setae will emerge and they are present unchanged also in the third instar. Thus chaetotaxy can be used for the discrimination of the first and second instar larvae. For additional differential diagnosis of those morphological characters, see Kilian & Mądra (2015).

The article **B** established developmental parameters for *Sciodrepoides watsoni* together with the new and reliable character for instar determination. This species is so far the smallest necrophagous beetle with known thermal summation model. The developmental characteristics provided in this study will help to estimate the PMI_{min} in cases where it was not possible before. The instar determination is the integral part of the PMI_{min} estimation, because without accurate determination it we could not reach the right conclusion. We strongly encourage other authors to adopt our methodology for establishing the size-based instar characteristics, because it provides correct picture about its variability.

Principal conclusions of the thesis

Altogether, these tree articles aim to contribute to growth of our knowledge about ecological and evolutional strategies of necrophagous beetles and I hope that I bring some of them to attention of profesional public.

5. References

- ABELL, D.H., WASTI, S.S. & HARTMANN, G.C. 1982: Saprophagous Arthropod Fauna Associated with Turtle Carrion. *Applied Entomology and Zoology*, **17**, 301–307.
- ALSTAD, D. 1998: Population Structure and Conundrum of Local Adaptation. In *Genetic Structure and Local Adaptation in Natural Insect Populations: Effects of Ecology, Life History and Behavior* (ed. by Mopper, S. & Strauss, S.Y.). Springer-Science+Business Media, Florence, pp. 3–21.
- AMAT-GARCÍA, G. & VALCÁRCEL, J.P. 2014: Una nueva especie de sílfido (Coleoptera: Silphidae) de la región del Piedemonte Orinocense de Columbia (América del Sur). *Arquivos Entomológicos*, **12**, 165–71.
- AMENDT, J., CAMPOBASSO, C.P., GAUDRY, E., REITER, C., LEBLANC, H.N. & J. R. HALL, M. 2007: Best practice in forensic entomology - Standards and guidelines. *International Journal of Legal Medicine*, **121**, 90–104.
- AMENDT, J., RICHARDS, C.S., CAMPOBASSO, C.P., ZEHNER, R. & HALL, M.J.R. 2011: Forensic entomology: Applications and limitations. *Forensic Science, Medicine, and Pathology*, **7**, 379–392.
- AMOS, T.G. 1968: Some laboratory observations on the rates of development, mortality and oviposition of *Dermestes frischii* (Kug.) (Col., Dermestidae). *Journal of Stored Products Research*, **4**, 103–117.
- ANDERSON, R.S. 1982a: Resource partitioning in the carrion beetle (Coleoptera: Silphidae) fauna of southern Ontario: ecological and evolutionary considerations. *Canadian Journal of Zoology*, **60**, 1314–1325.
- ANDERSON, R.S. 1982b: On the decreasing abundance of *Nicrophorus americanus* Olivier (Coleoptera: Silphidae) in eastern North America. *The Coleopterists' Bulletin*, **36**, 362–365.
- ARCHER, M.S. & ELGAR, M. A. 2003a: Yearly activity patterns in southern Victoria (Australia) of seasonally active carrion insects. *Forensic Science International*, **132**, 173–176.
- ARCHER, M.S., ELGAR, M. A., BRIGGS, C. A. & RANSON, D.L. 2006: Fly pupae and puparia as potential contaminants of forensic entomology samples from sites of body discovery. *International Journal of Legal Medicine*, **120**, 364–368.
- ARCHER, M.S. & ELGAR, M.A. 2003b: Effects of decomposition on carcass attendance in a guild of carrion-breeding flies. *Medical and Veterinary Entomology*, **17**, 263–271.

References

- BAQUÉ, M., AMENDT, J., VERHOFF, M.A. & ZEHNER, R. 2015a: Descriptive analyses of differentially expressed genes during larval development of *Calliphora vicina* (Diptera: Calliphoridae). *International Journal of Legal Medicine*, **129**, 891–902.
- BAQUÉ, M., FILMANN, N., VERHOFF, M.A. & AMENDT, J. 2015b: Establishment of developmental charts for the larvae of the blow fly *Calliphora vicina* using quantile regression. *Forensic Science International*, **248**, 1–9.
- BEDICK, J.C., RATCLIFFE, B.C. & HIGLEY, L.G. 2004: A new sampling protocol for the endangered American burying beetle, *Nicrophorus americanus* Olivier (Coleoptera: Silphidae). *Coleopterists Bulletin*, **58**, 57–70.
- BEDICK, J.C., RATCLIFFE, B.C., WYATT HOBACK, W. & HIGLEY, L.G. 1999: Distribution, ecology, and population dynamics of the American burying beetle [*Nicrophorus americanus* Olivier (coleoptera, silphidae)] in south-central Nebraska, USA. *Journal of Insect Conservation*, **3**, 171–181.
- BEGON, M., HARPER, J.L. & TOWNSEND, C.R. 2006: *Ecology: Individuals, Populations and Communities*. Blackwell science.
- BETZ, O., THAYER, M.K. & NEWTON, A.F. 2003: Comparative morphology and evolutionary pathways of the mouthparts in spore-feeding Staphylinidae (Coleoptera). *Acta Zoologica*, **84**, 179–238.
- BISHOP, A.A., HOBACK, W.W., ALBRECHT, M. & SKINNER, K.M. 2002: A comparison of an ecological model and GIS spatial analysis to describe niche partitioning amongst carrion beetles in Nebraska. *Transactions in GIS*, **6**, 457–470.
- BLACK, S.H. 2012: *Insect Conservation: Past, Present and Prospects*. *Insect Conservation: Past, Present and Prospects*. Springer Netherlands, Dordrecht.
- BREWER, M. & HOFF, K. 2002: Degree-day accumulation to time initiation of sampling for alfalfa weevil using on-site, near-site, and regional temperature data, **19**, 141–149.
- BRIERE, J., PRACROS, P., ROUX, A. LE & PIERRE, J. 1999: A novel rate model of temperature-dependent development for arthropods. *Environmental Entomology*, **28**, 22–29.
- CAI, C.-Y., THAYER, M.K., ENGEL, M.S., NEWTON, A.F., ORTEGA-BLANCO, J., WANG, B., ET AL. 2014: Early origin of parental care in Mesozoic carrion beetles. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 14170–4.
- COOMBS, C.W. 1978: The effect of temperature and relative humidity upon the development and fecundity of *Dermestes lardarius* L. (Coleoptera, Dermestidae). *Journal of Stored Products Research*, **14**, 111–119.

References

- COOMBS, C.W. 1979: The effect of temperature and humidity upon the development and fecundity of *Dermestes haemorrhoidalis* Küster and *Dermestes peruvianus* Laporte de Castelnau (Coleoptera: Dermestidae). *Journal of Stored Products Research*, **15**, 43–52.
- CRAWFORD, P.H.C. & HOAGLAND, B.W. 2010: Using species distribution models to guide conservation at the state level: the endangered American burying beetle (*Nicrophorus americanus*) in Oklahoma. *Journal of Insect Conservation*, **14**, 511–521.
- DEKEIRSSCHIETER, J., FREDERICK, C., VERHEGGEN, F.J., DRUGMAND, D. & HAUBRUGE, E. 2013: Diversity of forensic rove beetles (Coleoptera, Staphylinidae) associated with decaying pig carcass in a forest biotope. *Journal of forensic sciences*, **58**, 1032–40.
- DEKEIRSSCHIETER, J., VERHEGGEN, F., LOGNAY, G. & HAUBRUGE, E. 2011: Large carrion beetles (Coleoptera, Silphidae) in Western Europe: a review. *Biotechnologie Agronomie Societe et Environnement*, **15**, 435–447.
- DENLINGER, D.L. & LEE, R.E. Eds. 2010: *Low Temperature Biology of Insects*. Cambridge University Press, New York.
- DOBBLER, S. & MÜLLER, J.K. 2000: Resolving phylogeny at the family level by mitochondrial cytochrome oxidase sequences: phylogeny of carrion beetles (Coleoptera, Silphidae). *Molecular phylogenetics and evolution*, **15**, 390–402.
- EGGERT, A.-K. 1992: Alternative male mate-finding tactics in burying beetles. *Behavioral Ecology*, **3**, 243–254.
- EGGERT, A.-K. & MÜLLER, J.K. 1992: Joint breeding in female burying beetles. *Behavioral Ecology and Sociobiology*, **31**, 237–242.
- EGGERT, A.-K. & MÜLLER, J.K. 2011: Timing of oviposition enables dominant female burying beetles to destroy brood-parasitic young. *Animal Behaviour*, **82**, 1227–1233.
- ENGEL, K.C., HOERMANN, C. von, EGGERT, A.-K., MÜLLER, J.K. & STEIGER, S. 2014: When males stop having sex: adaptive insect mating tactics during parental care. *Animal Behaviour*, **90**, 245–253.
- ENGLER, I. 1981: Vergleichende Untersuchungen zur jahreszeitlichen Einpassung von Catopiden (Col.) in ihren Lebensraum. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere*, **109**, 399–432.
- FRATCZAK, K. & MATUSZEWSKI, S. 2014: Instar determination in forensically useful beetles *Necrodes littoralis* (Silphidae) and *Creophilus maxillosus* (Staphylinidae). *Forensic Science International*, **241**, 20–26.

References

- FULLER, M.E. 1934: The insect habitants of carrion: a study in animal ecology. *Australian Council for Scientific Industrial Research Bulletin*, **82**, 1–62.
- GALANTE, E. & ANGELES, M.G. 2008: Decomposer Insects. In *Encyclopedia of Entomology* (ed. by Capinera, J.L.). Springer, pp. 1158–1169.
- GBIF. 2015: Sciodrepoides watsoni [WWW Document]. URL <http://www.gbif.org/species/4445042> [accessed on 2015].
- GIACHINO, P.M., VAILATI, D. & CASALE, A. 1998: Major questions in the phylogeny and biogeography of Cholevidae (Coleoptera), with emphasis on the subfamily Leptodirinae. In *Phylogeny and Evolution of Subterranean and Endogeal Cholevidae (=Leiodidae Cholevinae)* (ed. by Giachino, P.M. & Peck, S.B.). Museo Regionale di Scienze Naturali, Torino, pp. 179–209.
- GOFF, M.L. 2009: Forensic Entomology. In *Encyclopedia of Insects* (ed. by Resh, V.H. & Cardé, R.T.). Elsevier, London, pp. 381–386.
- GREBENNIKOV, V. V. & NEWTON, A.F. 2012: Detecting the basal dichotomies in the monophylum of carrion and rove beetles (Insecta: Coleoptera: Silphidae and Staphylinidae) with emphasis on the Oxyteline group of subfamilies. *Arthropod Systematics & Phylogeny*, **70**, 133–165.
- HALL, C.L., HOWARD, D.R., SMITH, R.J. & MASON, A.C. 2015: Marking by elytral clip changes stridulatory characteristics and reduces reproduction in the American burying beetle, *Nicrophorus americanus*. *Journal of Insect Conservation*, **19**, 155–162.
- HÁVA, J. & RŮŽIČKA, J. 1997: Faunistic records from the Czech Republic - 58. Coleoptera: Silphidae. *Klapalekiana*, **33**, 6.
- HÁVA, J., SCHNEIDER, J. & RŮŽIČKA, J. 1999: Four new species of Carrion beetles from China (Coleoptera: Silphidae). *Entomological problems*, **30**, 67–82.
- HIGLEY, L.G., PEDIGO, L.P. & OSTLIE, K.R. 1986: Degday: A Program for Calculating Degree-days, and Assumptions Behind the Degree-day Approach. *Environmental Entomology*, **15**, 999–1016.
- HOERMANN, C. VON, RUTHER, J., REIBE, S., MADEA, B. & AYASSE, M. 2011: The importance of carcass volatiles as attractants for the hide beetle *Dermestes maculatus* (De Geer). *Forensic science international*, **212**, 173–9.
- HOUSTON, D.D., MITCHELL, K.S., CLOUSE, J.W., MAUGHAN, P.J., CURTIS CREIGHTON, J., SMITH, A.N., ET AL. 2015: SNP development in North American burying beetles (Coleoptera: Silphidae): a tool to inform conservation decisions. *Conservation Genetics Resources*, **7**, 349–352.
- CHAPMAN, R.F. 2012: *The Insects - Structure and Function*. Cambridge University Press, Cambridge.

References

- CHO, Y.B. & KWON, Y.J. 1999: New silphids (Coleoptera: Silphidae) from Korea. *Korean Journal of Entomology*, **29**, 221–223.
- CHONG, J.-H. & OETTING, R.D. 2006: Influence of temperature and mating status on the development and fecundity of the mealybug parasitoid, Anagyrus sp nov nr. sinope Noyes and Menezes (Hymenoptera : Encyrtidae). *Environmental Entomology*, **35**, 1188–1197.
- IKEDA, H., KAGAYA, T., KUBOTA, K. & ABE, T. 2013: Evolutionary Relationships among Food Habit, Loss of Flight , and Reproductive Traits: Life- History Evolution in the Silphinae (Coleoptera : Silphidae). *Evolution*, **62**, 2065–2079.
- IKEDA, H., KUBOTA, K., KAGAYA, T. & ABE, T. 2007: Flight capabilities and feeding habits of silphine beetles: Are flightless species really “carrion beetles”? *Ecological Research*, **22**, 237–241.
- IKEMOTO, T. & EGAMI, C. 2013: Mathematical elucidation of the Kaufmann effect based on the thermodynamic SSI model. *Applied Entomology and Zoology*, **48**, 313–323.
- IKEMOTO, T. & TAKAI, K. 2000: A New Linearized Formula for the Law of Total Effective Temperature and the Evaluation of Line-Fitting Methods with Both Variables Subject to Error. *Environmental Entomology*, **29**, 671–682.
- JACOB, T.A. & FLEMING, D.A. 1980: Some observations of the fertility of eggs of *Dermestes lardarius* L. and their development periods (Coleoptera: Dermetidae) at various combinations of temperature and relative humidity. *Journal of Stored Products Research*, **16**, 43–44.
- JAROŠÍK, V., HONĚK, A. & DIXON, A.F.G. 2002: Developmental rate isomorphy in insects and mites. *The American naturalist*, **160**, 497–510.
- JEANNEL, R. 1936: Monographie des Catopidae. *Mémoires du Muséum national d'Histoire naturelle*, **1**, 1–438.
- JURZENSKI, J., SNETHEN, D.G., BRUST, M.L. & HOBACK, W.W. 2011: New records of carrion beetles in Nebraska reveal increased presence of the American burying beetle, *Nicrophorus americanus* Olivier (Coleoptera: Silphidae). *Great Plains Research*, **21**, 131–43.
- JURZENSKI, J.D., JORGENSEN, C.F., BISHOP, A., GROSSE, R., RIENS, J. & HOBACK, W.W. 2014: Identifying priority conservation areas for the American burying beetle, *Nicrophorus americanus* (Coleoptera: Silphidae), a habitat generalist. *Systematics and Biodiversity*, **12**, 149–162.
- KAHLE, D. & WICKHAM, H. 2013: ggmap : Spatial Visualization with. *The R Journal*, **5**, 144–161.

References

- KALINOVÁ, B., PODSKALSKÁ, H., RŮZICKA, J. & HOSKOVEC, M. 2009: Irresistible bouquet of death--how are burying beetles (Coleoptera: Silphidae: Nicrophorus) attracted by carcasses. *Die Naturwissenschaften*, **96**, 889–99.
- KAY, I.R. 2010: Effect of constant temperature on the development of *Sceliodes cordalis* (Doubleday) (Lepidoptera: Crambidae) on eggplant. *Australian Journal of Entomology*, **49**, 359–362.
- KHACHIKOV, E.A. 2011: A new species of the genus *Phosphuga* Leach, 1817 (Coleoptera: Silphidae) from the North-Western Caucasus. *Kavkazskii Entomologicheskii Byulleten*, **7**, 39–40.
- KILIAN, A. & MĄDRA, A. 2015: Comments on the biology of *Sciodrepoides watsoni watsoni* (Spence, 1813) with descriptions of larvae and pupa (Coleoptera: Leiodidae: Cholevinae). *Zootaxa*, **3955**, 45–61.
- KIPYATKOV, V.E. & LOPATINA, E.B. 2002: Reaction norm in response to temperature may change to adapt rapid brood development to boreal and subarctic climates in *Myrmica* ants (Hymenoptera: Formicidae). *European Journal of Entomology*, **99**, 197–208.
- KIPYATKOV, V.E. & LOPATINA, E.B. 2010: Intraspecific variation of thermal reaction norms for development in insects: New approaches and prospects. *Entomological Review*, **90**, 163–184.
- Kočárek, P. 2001: Diurnal activity rhythms and niche differentiation in a carrion beetle assemblage (Coleoptera: Silphidae) in Opava, the Czech Republic. *Biological Rhythm Research*, **32**, 431–438.
- Kočárek, P. 2002: Diel activity patterns of carrion-visiting Coleoptera studied by time-sorting pitfall traps. *Biologia*, **57**, 199–211.
- Kočárek, P. 2003: Decomposition and Coleoptera succession on exposed carrion of small mammal in Opava, the Czech Republic. *European Journal of Soil Biology*, **39**, 31–45.
- Koz'MINYKH, V.O. 1995: A new species of carrion beetles of the genus *Thanatophilus* (Coleoptera, Silphidae) from the southern Urals. *Entomologicheskoye Obozreniye*, **74**, 133–137.
- LARDEUX, F.J., TEJERINA, R.H., QUISPE, V. & CHAVEZ, T.K. 2008: A physiological time analysis of the duration of the gonotrophic cycle of *Anopheles pseudopunctipennis* and its implications for malaria transmission in Bolivia. *Malaria journal*, **7**, 141.
- LEWIS, T. & TAYLOR, L.R. 1965: Diurnal periodicity of flight by insects. *Transactions of the Entomological Society of London*, **116**, 393–479.

References

- LOMOLINO, M. V. & CREIGHTON, J.C. 1996: Habitat selection, breeding success and conservation of the endangered American burying beetle *Nicrophorus americanus*. *Biological Conservation*, **77**, 235–241.
- LOMOLINO, M. V., CREIGHTON, J.C., SCHNELL, G.D. & CERTAIN, D.L. 1995: Ecology and Conservation of the Endangered American Burying Beetle (*Nicrophorus americanus*). *Conservation Biology*, **9**, 605–614.
- LOMOLINO, M. V., CREIGHTON, J.C., SCHNELL, G.D. & CERTAIN, D.L. 1999: Ecology and conservation of the endangered American burying beetle (*Nicrophorus americanus*). *NCASI Technical Bulletin*, 316–317.
- LOONEY, C., CALDWELL, B.T., HATTEN, T., LORION, C. & EIGENBRODE, S.D. 2004: Potential habitat factors influencing carrion beetle communities of Palouse prairie remnants. In *Proceedings of the 19th North American Prairie Conference: The Conservation Legacy Lives On...* (ed. by Egan, D. & Harrington, J.A.). University of Wisconsin-Madison, Madison.
- LOONEY, C., CALDWELL, T.B. & EIGENBRODE, D.S. 2009: When the prairie varies: The importance of site characteristics for strategising insect conservation. *Insect Conservation and Diversity*, **2**, 243–250.
- MATUSZEWSKI, S. 2011: Estimating the pre-appearance interval from temperature in *Necrodes littoralis* L. (Coleoptera: Silphidae). *Forensic Science International*, **212**, 180–188.
- MATUSZEWSKI, S., BAJERLEIN, D., KONWERSKI, S. & SZPILA, K. 2010: Insect succession and carrion decomposition in selected forests of Central Europe. Part 1: Pattern and rate of decomposition. *Forensic Science International*, **194**, 85–93.
- MATUSZEWSKI, S., BAJERLEIN, D., KONWERSKI, S. & SZPILA, K. 2011: Insect succession and carrion decomposition in selected forests of Central Europe. Part 3: Succession of carrion fauna. *Forensic Science International*, **207**, 150–163.
- MATUSZEWSKI, S. & SZAFALOWICZ, M. 2013: Temperature-dependent appearance of forensically useful beetles on carcasses. *Forensic Science International*, **229**, 92–99.
- McKENNA, D.D., FARRELL, B.D., CATERINO, M.S., FARNUM, C.W., HAWKS, D.C., MADDISON, D.R., ET AL. 2015: Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. *Systematic Entomology*, **40**, 35–60.
- MÉGNIN, P. 1894: *La faune de cadavres. Application de l'entomologie à la médecine légale*. Encyclopédie scientifique des Aides-Mémoire, Paris.

References

- McHUGH, J. V. & LIEBHERR, J.K. 2009: Coleoptera: (Beetles, Weevils, Fireflies). In *Encyclopedia of Insects* (ed. by Resh, V.H. & Cardé, R.T.). Elsevier, London, pp. 183–201.
- MIDGLEY, J.M., RICHARDS, C.S. & VILLET, M.H. 2010: The Utility of Coleoptera in Forensic Investigations. In *Current Concepts in Forensic Entomology* (ed. by Amendt, J., Goff, M.L., Campobasso, C.P. & Grassberger, M.). Springer Netherlands, Dordrecht, pp. 57–68.
- MIDGLEY, J.M. & VILLET, M.H. 2009a: Development of *Thanatophilus micans* (Fabricius 1794) (Coleoptera: Silphidae) at constant temperatures. *International Journal of Legal Medicine*, **123**, 285–292.
- MIDGLEY, J.M. & VILLET, M.H. 2009b: Effect of the killing method on post-mortem change in length of larvae of *Thanatophilus micans* (Fabricius 1794) (Coleoptera: Silphidae) stored in 70% ethanol. *International Journal of Legal Medicine*, **123**, 103–8.
- MÜLLER, J.K., EGGERT, A.-K. & DRESSEL, J. 1990: Intraspecific brood parasitism in the burying beetle, *Necrophorus vespilloides* (Coleoptera: Silphidae). *Animal Behaviour*, **40**, 491–499.
- MUTHS, E.L. 1991: Substrate Discrimination in Burying Beetles, *Nicrophorus orbicollis* (Coleoptera: Silphidae). *Journal of the Kansas Entomological Society*, **64**, 447–450.
- NABILITY, P.D., HIGLEY, L.G. & HENG-MOSS, T.M. 2006: Effects of temperature on development of *Phormia regina* (Diptera: Calliphoridae) and use of developmental data in determining time intervals in forensic entomology. *Journal of Medical Entomology*, **43**, 1276–86.
- NASSU, M.P., THYSSEN, P.J. & LINHARES, A.X. 2014: Developmental rate of immatures of two fly species of forensic importance: *Sarcophaga* (*Liopygia*) *ruficornis* and *Microcerella halli* (Diptera: Sarcophagidae). *Parasitology Research*, **113**, 217–22.
- NEWTON, A.F. 1998: Phylogenetic problems, current classification and generic catalog of world Leiodidae (including Cholevidae). In *Phylogeny and Evolution of Subterranean and Endogeal Cholevidae (=Leiodidae Cholevinae)* (ed. by Giachino, P.M. & Peck, S.B.). Museo Regionale di Scienze Naturali, Torino, pp. 41–177.
- NEWTON, A.F. 2005: Leiodidae Fleming, 1821. In *Handbuch der Zoologie, Band IV Arthropoda: Insecta. Part 38 Coleoptera, Beetles. Vol. 1: Morphology and Systematics*. (ed. by Bautel, R.G. & Leschen, R.A.B.). Walter de Gruyter, Berlin, pp. 269–280.
- NOVÁK, B. 1961: Sezónní výskyt hrobaříků v polních entomocenózách (Col. Silphidae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **6**, 45–114.
- NOVÁK, B. 1962: Příspěvek k faunistice a ekologii hrobaříků (Col. Silphidae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **11**, 263–296.

References

- NOVÁK, B. 1965: Faunisticko-ekologická studie o hrobařících z polních biotopů Hané (Col. Silphidae) (Zur Faunistik und Ökologie der Totengräber in den Feldbiotopen von Haná (Col. Silphidae)). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **19**, 121–151.
- NOVÁK, B. 1966: Dynamika populací brouků ze skupiny Silphini (Coleoptera). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **22**, 129–151.
- OHKAWARA, K., SUZUKI, S. & KATAKURA, H. 1998: Competitive interaction and niche differentiation among burying beetles (Silphidae, Nicrophorus) in northern Japan. *Entomological Society*, **1**, 551–559.
- OLIVA, A. 2012: A new species of Oxelytrum Gistel (Coleoptera, Silphidae) from southern Argentina, with a key to the species of the genus. *ZooKeys*, **203**, 1–14.
- PAULIAN, R. 1946: Essai de bionomie quantitative sur les nécrophores. *Revue Francoise d'entomologie*, **13**, 93–98.
- PAYNE, J.A. 1965: A Summer Carrion Study of the Baby Pig Sus Scrofa Linnaeus. *Ecology*, **46**, 592–602.
- PECK, S. 1975: The life cycle of a Kentucky cave beetle, Ptomaphagus hirtus, (Coleoptera; Leiodidae; Catopinae). *International Journal of Speleology*, **7**, 7–17.
- PECK, S. & ANDERSON, R. 1985a: Taxonomy, phylogeny and biogeography of the carrion beetles of Latin America (Coleoptera: Silphidae). *Quaestiones Entomologicae*, **21**, 247–317.
- PECK, S.B. 1990: Insecta: Coleoptera Silphidae and the associated families Agyrtidae and Leiodidae. In *Soil Biology Guide*. (ed. by Dinda, D.L.). John Wiley & Sons, New York, pp. 1113–1136.
- PECK, S.B. 1998: Phylogeny and evolution of subterranean and endogean Cholevidae (=Leiodidae, Cholevinae): an introduction. In *Phylogeny and Evolution of Subterranean and Endogean Cholevidae (=Leiodidae, Cholevinae)* (ed. by Giachino, P.M. & Peck, S.B.). Museo Regionale di Scienze Naturali, Torino, pp. 11–40.
- PECK, S.B. 2001: Review of the carrion beetles of Australia and New Guinea (Coleoptera: Silphidae). *Australian Journal of Entomology*, **40**, 93–101.
- PECK, S.B. & ANDERSON, R.S. 1985b: Seasonal activity and habitat associations of adult small carrion beetles in southern Ontario (Coleoptera: Leiodidae: Cholevinae). *The Coleopterists Bulletin*, **39**, 347–353.

- PECK, S.B. & COOK, J. 2002: Systematics, distributions, and bionomics of the small carrion beetles (Coleoptera: Leiodidae: Cholevinae: Cholevini) of North America. *The Canadian Entomologist*, **134**, 723–787.
- PECK, S.B. & COOK, J. 2007: Systematics, distributions, and bionomics of the Neoeocatops gen. nov. and Nemadus of North America (Coleoptera: Leiodidae: Cholevinae: Anemadini). *The Canadian Entomologist*, **139**, 87–117.
- PERREAU, M. 2004: Family Leiodidae Fleming, 1821. In *Catalogue of Palaearctic Coleoptera Hydrophiloidea Histeroidea Staphylinoidea* (ed. by Löbl, I. & Smetana, A.). Apollo Books, Steensrup, pp. 133–203.
- PETRUŠKA, F. 1964: Příspěvek k poznání pohyblivosti několika druhů brouků naléztavajících na mršiny (Col. Silphidae et Histeridae) (Beitrag zur Bewegungsaktivität einiger Aaskräfer-Arten (Col. Silphidae et Histeridae)). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **16**, 159–187.
- PETRUŠKA, F. 1968: Příspěvek k poznání pohyblivosti několika druhů brouků naléztavajících na mršiny (Col. Silphidae et Histeridae) (Beitrag zur Bewegungsaktivität einiger Aaskäfer-Arten (Col. Silphidae et Histeridae)). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **16**, 159–187.
- PODKALSKÁ, H., RŮŽIČKA, J., HOSKOVEC, M. & ŠÁLEK, M. 2009: Use of infochemicals to attract carrion beetles into pitfall traps. *Entomologia Experimentalis et Applicata*, **132**, 59–64.
- PUKOWSKI, E. 1933: Oekologische Untersuchungen an Necrophorus F. *Zeitschrift für Morphologie und Oekologie der Tiere*, **27**, 518–586.
- QUBAIOVÁ, J., RŮŽIČKA, J. & ŠÍPKOVÁ, H. 2015: Taxonomic revision of genus Ablattaria Reitter (Coleoptera, Silphidae) using geometric morphometrics. *ZooKeys*, 79–142.
- R CORE TEAM. 2015: R: A Language and Environment for Statistical Computing.
- RATCLIFFE, B.C. 1996: The carrion beetles (Coleoptera: Silphidae) of Nebraska. *Bulletin of the University of Nebraska State Museum*, **13**, 1–100.
- REED JR., H.B. 1958: A Study of Dog Carcass Communities in Tennessee, with Special Reference to the Insects. *American Midland Naturalist*, **59**, 213–245.
- RÉGNIÈRE, J., POWELL, J., BENTZ, B. & NEALIS, V. 2012: Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *Journal of insect physiology*, **58**, 634–47.

References

- REITER, C. 1984: Zum Wachstumsverhalten der Maden der blauen Schmeißfliege *Calliphora vicina*. *Z. Rechtsmed.*, **91**, 295–308.
- RIDGEWAY, J. A., MIDGLEY, J.M., COLLETT, I.J. & VILLET, M.H. 2014: Advantages of using development models of the carrion beetles *Thanatophilus micans* (Fabricius) and *T. mutilatus* (Castelnau) (Coleoptera: Silphidae) for estimating minimum post mortem intervals, verified with case data. *International Journal of Legal Medicine*, **128**, 207–220.
- RICHARDS, C.S., CROUS, K.L. & VILLET, M.H. 2009: Models of development for blowfly sister species *Chrysomya chloropyga* and *Chrysomya putoria*. *Medical and Veterinary Entomology*, **23**, 56–61.
- RICHARDS, C.S. & VILLET, M.H. 2008: Factors affecting accuracy and precision of thermal summation models of insect development used to estimate post-mortem intervals. *International journal of legal medicine*, **122**, 401–408.
- RICHARDSON, M.S. & GOFF, M.L. 2001: Effects of temperature and intraspecific interaction on the development of *Dermestes maculatus* (Coleoptera: Dermestidae). *Journal of Medical Entomology*, **38**, 347–351.
- ROCHE, C.D. & SMITH, L.W. 1974: Note on the rearing of *Dermestes maculatus* DeGeer (Coleoptera: Dermestidae). *Entomological News*, **85**, 85–87.
- RUZICKA, J. & SCHNEIDER, J. 2011: Revision of Palaearctic and Oriental *Necrophila* Kirby & Spence, part 1: subgenus *Deutosilpha* Portevin (Coleoptera: Silphidae). *Zootaxa*, 1–12.
- RŮŽIČKA, J. 1993: Silphidae, pp. 33–34. In: Jelínek J. (ed.): Checklist of Czechoslovak Insects IV (Coleoptera). *Folia Heyrovskiana, Suppl. 1*, **1**, 33–34.
- RŮŽIČKA, J. 1994: Seasonal activity and habitat associations of Silphidae and Leiodidae: Cholevinae (Coleoptera) in central Bohemia. *Acta Societatis Zoologicae Bohemoslovicae*, **58**, 67–78.
- RŮŽIČKA, J. 2000: Beetle communities (Insecta: Coleoptera) of rock debris on the Kamennec hill (Czech Republic: České středohoří mts). *Acta Universitatis Purkynianae, Studia Biologica*, **4**, 175–182.
- RŮŽIČKA, J. 2005: Silphidae (mrchožroutovití). In *Red list of threatened species in the Czech Republic. Invertebrates* (ed. by Farkač, J., Král, D. & Škorpík, M.). Agentura ochrany a přírody a krajiny ČR, Prague, pp. 429–430.
- RŮŽIČKA, J., HÁVA, J. & SCHNEIDER, J. 2000: Taxonomical and distributional notes on Oriental Silphidae, with description of *Nicrophorus sausai* sp. n. (Insecta: Coleoptera). *Reichenbachia*, **33**, 377–384.

References

- RŮŽIČKA, J. & SCHNEIDER, J. 2004: Family Silphidae Latreille, 1807. In *Catalogue of Palaearctic Coleoptera, Vol. 2: Hydrophiloidea - Histeroidea - Staphylinoidea* (ed. by Löbl, I. & Smetana, A.). Apollo Books, Steensrup, pp. 229–237.
- RŮŽIČKA, J. & VÁVRA, J. 1993: Rozšíření a ekologie brouků rodu Choleva (Coleoptera: Leiodidae: Cholevinae) na území Čech, Moravy a Slovenska (The distribution and ecology of the genus Choleva (Coleoptera: Leiodidae: Cholevinae) throughout Bohemia, Moravia and Slovakia). *Klapalekiana*, **29**, 103–130.
- RYABUCHIN, A.S. 1990: A new species of carrion beetles (Coleoptera, Silphidae) from the north-east of the USSR. *Zoologicheskiy Zhurnal*, **69**, 140–142.
- SAFRYN, S. A. & SCOTT, M.P. 2000: Sizing up the competition: Do burying beetles weigh or measure their opponents? *Journal of Insect Behavior*, **13**, 291–297.
- SANDERS, D.S., STEEL, C.G.H., VAFOUPOULOU, X. & LEWIS, R.D. 2002: *Insect Clocks*. Elsevier, Amsterdam.
- SCOTT, M.P. 1998: The Ecology and Behavior of Burying Beetles. *Annual Review of Entomology*, **43**, 595–618.
- SCOTT, M.P., LEE, W.J. & REIJDEN, E.D. VAN DER. 2007: The frequency and fitness consequences of communal breeding in a natural population of burying beetles: A test of reproductive skew. *Ecological Entomology*, **32**, 651–661.
- SHARPE, P.J.H. & DEMICHELE, D.W. 1977: Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology*, **64**, 649–670.
- SCHAWALLER, W. 1981: Taxonomie und Faunistik der Gattung Thanatophilus (Coleoptera: Silphidae). *Stuttgarter Beiträge zur Naturkunde, Serie A (Biologie)*, **351**, 1–21.
- SCHAWALLER, W. 1987: Faunistische und systematische Daten zur Silphidae-Fauna Südafrikas (Coleoptera: Silphidae). *Entomofauna*, **8**, 277–285.
- SCHILTHUIZEN, M., SCHOLTE, C., WIJK, R.E.J. VAN, DOMMERSHUIZEN, J., HORST, D. VAN DER, ZU SCHLOCHTERN, M.M., ET AL. 2011: Using DNA-barcoding to make the necrobiont beetle family Cholevidae accessible for forensic entomology. *Forensic Science International*, **210**, 91–95.
- SCHWARTZ, M. 1998: Green-wave phenology. *Nature*, **394**, 839–840.
- SIKES, D.S. 2003: *A revision of the subfamily Nicrophorinae Kirby (Insecta: Coleoptera: Silphidae)*.
- SIKES, D.S. 2005: Silphidae. In *Handbook of Zoology, Volume IV: Arthropoda: Insecta, Part 38: Coleoptera, Beetles. Volume 1: Morphology and Systematics (Archostemata, Adephaga,*

References

- Myxophaga, Polyphaga partim)* (ed. by Beutel, R.G. & Leschen, R.A.B.). De Gruyter, Berlin, pp. 288–296.
- SIKES, D.S. 2008: Carrion beetles (Coleoptera: Silphidae). In *Encyclopedia of entomology* (ed. by Capinera, J.L.). Springer Netherlands, pp. 749–758.
- SIKES, D.S., MADGE, R.B. & TRUMBO, S.T. 2006: Revision of *Nicrophorus* in part: New species and inferred phylogeny of the nepalensis-group based on evidence from morphology and mitochondrial DNA (Coleoptera : Silphidae : Nicrophorinae). *Invertebrate Systematics*, **20**, 305–365.
- SIKES, D.S. & MOUSSEAU, T. 2013: Description of *Nicrophorus efferens*, new species, from Bougainville Island (Coleoptera, Silphidae, Nicrophorinae). *ZooKeys*, **311**, 83–93.
- SIKES, D.S. & PECK, S.B. 2000: Description of *Nicrophorus hispaniola*, New Species, from Hispaniola (Coleoptera: Silphidae) and a Key to the Species of *Nicrophorus* of the New World. *Annals of the Entomological Society of America*, **93**, 391–397.
- SIKES, D.S. & RAITHEL, C.J. 2002: A review of hypotheses of decline of the endangered American burying beetle (Silphidae: *Nicrophorus americanus* Olivier). *Journal of Insect Conservation*, **6**, 103–113.
- SIKES, D.S. & VENABLES, C. 2013: Molecular phylogeny of the burying beetles (Coleoptera: Silphidae: Nicrophorinae). *Molecular Phylogenetics and Evolution*, **69**, 552–565.
- SPRINGETT, B.P. 1968: Aspects of the relationship between burying beetles, *NEcrophorus* spp., and the mite, *Poecilochirus necrophori* Vitz. *Journal of Animal Ecology*, **37**, 417–424.
- STEIGER, S., GERSHMAN, S.N., PETTINGER, A.M., EGGERT, A.-K. & SAKALUK, S.K. 2012: Dominance status and sex influence nutritional state and immunity in burying beetles *Nicrophorus orbicollis*. *Behavioral Ecology*, **23**, 1126–1132.
- STORK, N.E. 2009: Biodiversity. In *Encyclopedia of Insects* (ed. by Resh, V. & Cardé, R.). Elsevier, London, pp. 75–80.
- SZALANSKI, A.L., SIKES, D.S., BISCHOF, R. & FRITZ, M. 2000: Population genetics and phylogenetics of the endangered American Burying Beetle, *Nicrophorus Americans* (Coleoptera: Silphidae). *Annals of the Entomological Society of America*, **93**, 589–594.
- SZYMCZAKOWSKI, W. 1961: *Klucze do oznaczania owadów Polski, Część XIX Chrząszcze - Coleoptera, Zeszyt 13 Catopidae. [Keys to identification of Poland insects, Part XIX Beetles - Coleoptera, Issue 13 Small carrion beetles - Catopidae]]*. Państwowe wydawnictwo naukowe, Warszawa.

References

- ŠPICAROVÁ, N. 1972: The Emergence of Burying Beetles from the Soil after their Metamorphosis and its Dependence on Day Light (Col. Silphidae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **39**, 141–155.
- ŠPICAROVÁ, N. 1974: Diurnal activity of young individuals of the species *Necrophorus germanicus* (Col. Silphidae). *Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium*, **47**, 179–188.
- ŠPICAROVÁ, N. 1982: K ekologii druhů čeledí Silphidae a Staphylinidae. [To ecology of the species of the families Silphidae and Staphylinidae]. Autoreferát kandidátské disertace. *Olomouc: Ediční středisko University Palackého*, 27.
- ŠUSTEK, Z. 1981: Keys to identification of insects 2: Carrion beetles of Czechoslovakia (Coleoptera: Silphidae). *Zprávy Československé Společnosti Entomologické při ČSAV*, **2**, 1–47.
- TARONE, A.M. & FORAN, D.R. 2011: Gene expression during blow fly development: improving the precision of age estimates in forensic entomology. *Journal of Forensic Sciences*, **56**, S112–22.
- TARONE, A.M., PICARD, C.J., SPIEGELMAN, C. & FORAN, D.R. 2011: Population and Temperature Effects on *Lucilia sericata* (Diptera: Calliphoridae) Body Size and Minimum Development Time. *Journal of Medical Entomology*, **48**, 1062–1068.
- THEODORIDES, J. & HEERDT, P.F. 1952: Nouvelles recherches écologiques sur les nécrophores (Coleoptera Silphidae); comparison des résultats du terrain avec ceux du laboratoire (thermopreferendum at hygropreferendum). *Physiologia Comparata et Oecologia*, **2**, 297–309.
- TOPP, W. 1990: Selection for an optimal monovoltine life cycle in an unpredictable environment. Studies on the beetle *Catops nigricans* Spence (Col., Catopidae). *Oecologia*, **84**, 134–141.
- TOPP, W. 1994: Seasonal Time Partitioning And Polymorphism In The Developmental Cycles Of Sympatric Staphylinoidae (Coleoptera) Living In An Unstable Environment. *Insect Life-Cycle Polymorphism: Theory, Evolution And Ecological Consequences For Seasonality And Diapause Control*, **52**, 277–312.
- TOPP, W. 2003: Phenotypic plasticity and development of cold-season insects (Coleoptera: Leiodidae) and their response to climatic change. *European Journal of Entomology*, **100**, 233–243.
- TRUMBO, S.T. 1995: Nesting failure in burying beetles and the origin of communal associations. *Evolutionary Ecology*, **9**, 125–130.

References

- TRUMBO, S.T. & FERNANDEZ, A. G. 1995: Regulation of brood size by male parents and cues employed to assess resource size by burying beetles. *Ethology Ecology & Evolution*, **7**, 313–322.
- TRUMBO, S.T. & FIORE, A.J. 1994: Interspecific Competition and the Evolution of Communal Breeding in Burying Beetles. *American Midland Naturalist*, **131**, 169–174.
- VÁVRA, J. & RŮŽIČKA, J. 1993: Faunistic records from the Czech Republic - 4. Coleoptera: Leiodidae: Cholevinae. *Klapalekiana*, **29**, 56.
- VELÁSQUEZ, Y. & VILORIA, A.L. 2009: Effects of temperature on the development of the Neotropical carrion beetle *Oxelytrum discicolle* (Brullé, 1840) (Coleoptera: Silphidae). *Forensic Science International*, **185**, 107–109.
- VELÁSQUEZ, Y. & VILORIA, A.L. 2010: Instar determination of the neotropical beetle *Oxelytrum discicolle* (Coleoptera: Silphidae). *Journal of Medical Entomology*, **47**, 723–726.
- VILLET, M. 2011: African carrion ecosystems and their insect communities in relation to forensic entomology. *Pest Technol*, **5**, 1–15.
- VILLET, M.H., MACKENZIE, B. & MULLER, W.J. 2006: Larval development of the carrion-breeding flesh fly, *Sarcophaga* (*Liosarcophaga*) *tibialis* Macquart (Diptera : Sarcophagidae), at constant temperatures. *African Entomology*, **14**, 357–366.
- VOSS, S.C., COOK, D.F., HUNG, W.-F. & DADOUR, I.R. 2014: Survival and development of the forensically important blow fly, *Calliphora varifrons* (Diptera: Calliphoridae) at constant temperatures. *Forensic Science, Medicine, and Pathology*, **10**, 314–21.
- VOSS, S.C., SPAFFORD, H. & DADOUR, I.R. 2010a: Temperature-dependent development of the parasitoid *Tachinaephagus zealandicus* on five forensically important carrion fly species. *Medical and Veterinary Entomology*, **24**, 189–98.
- VOSS, S.C., SPAFFORD, H. & DADOUR, I.R. 2010b: Temperature-dependant development of *Nasonia vitripennis* on five forensically important carrion fly species. *Entomologia Experimentalis et Applicata*, **135**, 37–47.
- WALKER, T.L. & HOBACK, W.W. 2007: Effects of Invasive Eastern Redcedar on Capture Rates of *Nicrophorus americanus* and Other Silphidae. *Environmental Entomology*, **36**, 297–307.
- WICKHAM, H. 2009: ggplot2: elegant graphics for data analysis.
- WOODCOCK, L., GENNARD, D. & EADY, P. 2013: Egg laying preferences and larval performance in *Dermestes maculatus*. *Entomologia Experimentalis et Applicata*, **148**, 188–195.

References

- ZANETTI, N.I., VISCIARELLI, E.C. & CENTENO, N.D. 2015: Trophic roles of scavenger beetles in relation to decomposition stages and seasons. *Revista Brasileira de Entomologia*, **59**, 132–137.
- ZIMMER, M. 2008: Detritus. In *Encyclopedia of Ecology* (ed. by Jorgensen, S.E.). Elsevier, Amsterdam, p. 3839.
- ZOIA, S. 1998: Considerations of present knowledge of the Italian Cholevidae and their distribution, with particular reference to the hypogean species (Coleoptera). In *Phylogeny and Evolution of Subterranean and Endogeal Cholevidae (=Leiodidae Cholevinae)* (ed. by Giachino, P.M. & Peck, S.B.). Museo Regionale di Scienze Naturali, Torino, pp. 211–226.
- ZUHA, R.M. & OMAR, B. 2014: Developmental rate, size, and sexual dimorphism of *Megaselia scalaris* (Loew) (Diptera: Phoridae): its possible implications in forensic entomology. *Parasitology Research*, **113**, 2285–94.