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Ecology of Veliidae and Mesoveliidae (Heteroptera: Gerromorpha) in Central Europe

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Ph.D. Thesis

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Annotation

Ecology of Veliidae and Mesoveliidae (Hemiptera: Heteroptera: Gerromorpha) was studied in selected European species. The research of these non-gerrid semiaquatic bugs was especially focused on voltinism, overwintering with physiological consequences and wing polymorphism with dispersal pattern. Hypotheses based on data from field surveys were tested by laboratory, mesocosm and field experiments. New data on life history traits and their ecophysiological consequences are discussed in seven original research papers (four papers published in peer-reviewed journals, one paper accepted to publication, one submitted paper and one communication in a conference proceedings), creating core of this thesis.

Keywords

Insects, semiaquatic bugs, life history, overwintering, voltinism, dispersion, wing polymorphism.

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Declaration

I hereby declare that I worked out this Ph.D. thesis on my own, or in collaboration with the co-author of the presented papers and manuscript, and only using the cited literature. I declare that in accordance with the Czech legal code § 47b law No. 111/1998 in its valid version, I consent to the publication of my Ph.D. thesis (in an edition made by removing marked parts archived by the Faculty of Science) in an electronic way in the public access to the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

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Author contribution statement

Tomáš Ditrich, author of this Ph.D. thesis, is the first author of all papers and manuscripts included in his thesis. All coauthors hereby declare that he carried out all experiments, analyzed most data and significantly worked on text of the papers and manuscripts.

All co-authors hereby consent to the involvement of the papers into the Ph.D. thesis of Tomáš Ditrich and support it by their signatures:

Prof. RNDr. Miroslav Papáček, CSc.

Doc. Ing. Vladimír Košťál, CSc.

Prof. Mikko Heino, PhD.

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List of original papers

Ditrich, T. & Papáček, M. (2009) Effective strategy of the overwintering of semiaquatic bugs: overwintering of *Velia caprai* (Heteroptera: Gerromorpha: Veliidae). *Journal of Natural History* 43, 529 - 543.

Ditrich, T., Papáček, M. & Heino, M. The latitudinal uniformity of the unique life history of *Velia caprai* (Heteroptera: Veliidae) and notes to the pre-overwintering period of selected water striders (Heteroptera: Gerridae). *Entomologica Fennica, accepted.*

Ditrich, T. & Papáček, M. (2009) A question of voltinism of *Microvelia reticulata* (Veliidae) and *Mesovelia furcata* (Mesoveliidae) (Heteroptera: Gerromorpha) in Central Europe. P. 20 – 23. In Soldán, T., Papáček, M. & Boháč, J. (Eds) Communications and Abstracts, SIEEC 21, June 28 – July 3, 2009. University of South Bohemia, České Budějovice, 96 pp.

Ditrich, T. & Košťál, V. Overwintering strategies of semiaquatic bugs: fixed versus flexible. *Submitted to Physiological Entomology*.

Ditrich, T., Papáček, M. & Broum, T. (2008) Spatial distribution of semiaquatic bugs (Heteroptera: Gerromorpha) and their wing morphs in a small scale of the Pohorsky Potok stream spring area (Novohradske Hory Mts.). *Silva Gabreta* **14**, 173-178.

Ditrich, T. & Papáček, M. (2010) Effect of population density on the development of *Mesovelia furcata* (Mesoveliidae), *Microvelia reticulata* and *Velia caprai* (Veliidae) (Heteroptera: Gerromorpha). *European Journal of Entomology* **107**, 579 – 587.

Ditrich, T. & Papáček, M. (2009) Correlated traits for dispersal pattern: Terrestrial movement of the water cricket *Velia caprai* (Heteroptera: Gerromorpha: Veliidae). *European Journal of Entomology* **106**, 551-555.

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I would like to dedicate my special thanks to my whole family for their help, tolerance and support during my whole study. Within my family, I have to highlight role of my parents Zdeňka Ditrichová and Oleg Ditrich, and especially of my brother Vít Ditrich, who were always prepared to satisfy my extraordinary needs and wishes.

My great thanks go to my wife Petra, who supported me every moment of my study and patiently withstood all my extravagancies, and to my son Vojtěch, who, with his recent birth, stimulated me to finish the thesis.

Last but not least I would like to thank to all particular anonymous reviewers whose comments significantly improved quality of the manuscripts.

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General introduction

Semiaquatic bugs (Hemiptera: Heteroptera: Gerromorpha) are insects mostly capable of movement on the water surface. Whereas several species of some insects (e.g. some Diptera, Orthoptera, Coleoptera) and other Arthropods (e.g. some Araneae, Collembola or Crustacea) (e.g. Bush & Hu, 2006, Bush, Hu & Prakashc, 2007, Andersen, 1982) spend various times of their life on the water surface, almost all gerromorphan bugs are obligatorily associated with this unique environment. They move on the surface of the water, feed on arthropods caught in the water surface film and search for a mate through vibratory signals spreading on the water surface. Some gerrids (water striders, Gerridae) spend all their life on the water surface, without even a brief contact with land. As other insect taxon associated with water surface, family Chresmodidae (Insecta: Archaeorthoptera), became extinct during upper Cretaceous (Nel, Azar, Martinez-Delclos *et al.*, 2004, Delclos, Nei, Azar *et al.*, 2008), gerromorphan bugs are the only higher insect taxon largely inhabiting the water surface. Gerromorphan bugs are important for ecological studies because they live on the water as well as in the air and are usually at least partly connected with the shore. Their distribution on the water surface creates an easily determined 2-dimensional area, which allows working with precise population densities. Gerromorphan bugs thus provide a good chance to study many interactions within a single species, as they have to cope with completely different environments and also with both aquatic and terrestrial organisms.

Eight families of Gerromorpha can be currently recognized: Mesoveliidae, Hebridae, Paraphrynoveliidae, Macroveliidae, Hydrometridae, Hermatobatidae, Veliidae and Gerridae (sorted from the most basal clade) (Schuh & Slater, 1995, Andersen, 1982). However, monophyly of some families, especially Veliidae, is not supported by recent research and system of higher taxa within Gerromorpha and the concept of their phylogeny should be revised (Damgaard, 2008).

Most of gerromorphan species and all the families are found in the tropics, while only Mesoveliidae, Hydrometridae, Veliidae and Gerridae are present in Europe (Andersen, 1982). Species richness of the infraorder Gerromorpha (cca 1600 species) is mainly represented by Veliidae (630 spp.) and Gerridae (530 spp.) (Aukema & Rieger, 1995). As data on ecology of non-gerrid families are relatively scarce, most of the ecological work generalized to Gerromorpha deal with water striders (Gerridae), even though generalization within single family showed many difficulties (Vepsäläinen & Spence, 2000).

The aim of this thesis is to examine ecology of selected gerromorphan taxa and species, especially important ecological features traditionally explored in Gerridae. Partial aims include research on life histories, with special attention to overwintering as winter survival is crucial to populations of temperate insects. Another partial aim was to evaluate significance of wing polymorphism in selected taxa. Veliidae is a sister taxon to Gerridae, together forming Gerroidea. Family Mesoveliidae is the most basal within Gerromorpha. Findings on the ecology of these two families thus should significantly contribute to the recent knowledge of gerromorphan ecology. Species from Veliidae and Mesoveliidae are inconspicuous, but common in Central Europe. Their abundance thus allows intensive sampling for experiments needed for purpose of the thesis.

Life histories

Gerromorphan bugs usually have a variable life history, strongly influenced by environmental conditions (Spence & Andersen, 1994). Nevertheless, some generalizations can be made. Smaller species usually produce more generations per season than larger ones, e.g. minute *Microvelia* spp. and *Mesovelia* spp. are usually bivoltine to polyvoltine (Taylor & McPherson, 2000, Taylor & McPherson, 2003, Taylor & McPherson, 1999, Muraji, Miura & Nakasuji, 1989, Zimmermann, 1984), whereas larger species are usually univoltine to bivoltine (Spence, 1989, Andersen, 1982, Pfenning, Gerstner & Poethke, 2008, Vepsäläinen, 1974b, Hauser, 1982, Harada, 1992b, Blanckenhorn & Fairbairn, 1995, Fairbairn, 1985, Wood & Mcpherson, 1995, Hilsenhoff, 1986). Voltinism also vary within species – individuals from populations in warmer environments tend to produce more generations compared to the specimens from colder habitats (Tramontin & Sih, 1995, Blanckenhorn *et al.*, 1995, Vepsäläinen, 1974b).

Whereas some tropical species may reproduce throughout the whole year (Nummelin, 1997, Cheng, Baars & Oosterhuis, 1990, Spence *et al.*, 1994), most species have a dormant period in some developmental stage or generation during adverse environmental conditions. Many species, both tropical and temperate, aestivate during summer. Such aestivation is known for *A. remigis* (Wilcox & Maier, 1991), *G. lacustris* (Hauser, 1982), *Limnogonus fossarum* and *L. nitidus* (Selvanayagam & Rao, 1988) and supposed for *Rheumatobates tenuipes* (Taylor, 2009). However, all temperate species go through dormancy during winter. Overwintering is a crucial phase of life history in most temperate insects, as successful spring colonization of breeding sites is enabled by surviving the adverse winter conditions. Flightless semiaquatic bugs overwinter at the shore near water, usually in the moss or litter (Nummelin & Vepsalainen, 1982, Matthey, 1974, Spence *et al.*, 1994). Winged individuals usually fly to various overwintering sites, sometimes distant from the breeding site (Kaitala & Hulden, 1990, Spence, 1989). According to recent knowledge, all temperate *Gerris* and *Aquarius* spp. overwinter as adults in diapause (Wróblewski, 1980, Andersen, 1982, Vepsäläinen, 1974b, Vepsäläinen, 1971b, Kopfli, Hauser & Zimmermann, 1987, Savage, 1989, Spence, 1989, Blanckenhorn *et al.*, 1995, Harada, Ito, Hodkova *et al.*, 2004), Nearctic gerrids *Neogerris hesione, Metrobates hesperius*, *Rheumatobates palosi, Trepobates* spp. and Japanese *Metrocoris histrio* overwinter in the egg stage (Taylor & McPherson, 1998, Taylor, 2009, Hilsenhoff, 1986, Ban, Shigeaki & Ishikawa, 1988). The overwintering stage can differ even within one genus in some families – *Microvelia reticulata*, *M. douglasi*, *M. horvathi, M. hinei*, *M. americana, M. fontinalis, M. albonotata, M. buenoi* (Veliidae) overwinter as adults (Wróblewski, 1980, Muraji *et al.*, 1989, Taylor *et al.*, 2003, Chen, Yu & Zheng, 1999, Numazawa & Kobayashi, 1985, Hilsenhoff, 1986), whereas *Microvelia pulchella* overwinters as eggs (Taylor *et al.*, 1999, Hilsenhoff, 1986). Concerning other veliids, the data are relatively scarce. Murray and Giller (1991) claimed overwintering of *Velia caprai* as adults in various developmental stages, with the possibility of overwintering of last larval instar. Nearctic *Rhagovelia oriander* and *R. obesa* probably overwinter as eggs (Taylor, 2009, Hilsenhoff, 1986). Looking at temperate Mesoveliidae, European *Mesovelia furcata* overwinters at the egg stage (Zimmermann, 1984), as do Nearctic *M. mulsanti* (Taylor et al., 2000).

Although overwintering stage differs at the species level, it is fixed in all species – all bugs overwinter either in the adult or egg diapause. Different situation seem to arise among the water cricket *Velia caprai* (Veliidae) with overwintering in several developmental stages (see above). One of partial aims of the dissertation was thus a closer examination of flexible overwintering of *V. caprai* (output A). Findings of relatively rare overwintering strategy, as *V. caprai* regularly overwinter both at egg and adult stage, brought numerous new questions. One of these questions was whether this overwintering strategy is unique in Central Europe or shared by populations from Northern regions. Results from Norwegian populations, claiming sharing of this overwintering strategy, are presented by output B. This section on life histories of selected gerromorphan bugs is accompanied by results of a field survey, following phenology of *Mesovelia furcata* and *Microvelia reticulata* (output C), bringing data on voltinism and overwintering of these species.

Output A:

Ditrich, T. & Papáček, M. (2009) Effective strategy of the overwintering of semiaquatic bugs: overwintering of *Velia caprai* (Heteroptera: Gerromorpha: Veliidae). *Journal of Natural History* **43**, 529 - 543.

First author's contribution: 80 %

Effective strategy of the overwintering of semiaquatic bugs: overwintering of *Velia caprai* (Heteroptera: Gerromorpha: Veliidae)

Abstract

Overwintering of *Velia caprai* was studied during the winter months 2006–2007 in the area of South Bohemia (Czech Republic) by (1) field phenological observations and samples, (2) study of artificially established experimental cohorts in an unheated glasshouse, and (3) auxiliary experiments in a laboratory. *Velia caprai* has a unique way of overwintering within the gerromorphan bugs that is rare among insects generally; it can overwinter in both an adult and an egg stage. Most females reach sexual maturity before overwintering, mate with mature males, overwinter actively on the water surface and lay eggs during the winter. The dormant eggs can be induced to hatch by increasing temperatures. Winter oviposition can be interpreted as a sign of a risk-spreading reproductive strategy. The overwintering of both adults and eggs provides a chance to adapt to changes in the local environmental conditions and could be an important determinant in broad variability of life-history traits.

Výstup A:

Ditrich, T. & Papáček, M. (2009) Effective strategy of the overwintering of semiaquatic bugs: overwintering of *Velia caprai* (Heteroptera: Gerromorpha: Veliidae). *Journal of Natural History* **43**, 529 - 543.

Podíl prvního autora: 80 %

Účinná strategie přezimování semiakvatických ploštic: přezimování hladinatky *Velia caprai* (Heteroptera: Gerromorpha: Veliidae)

Shrnutí

Během zimního období 2006-2007 v oblasti Jižních Čech (Česká Republika) bylo studováno přezimování hladinatky *Velia caprai* (1) terénním pozorováním a odběry (2) sledováním uměle založených experimentálních kohort v nevytápěných sklenících a (3) pokusy v laboratoři. Strategii přezimování hladinatka Velia caprai je unikátní mezi semiakvatickými ploštícemi a vzácná u hmyzu obecně: přezimuje zároveň ve stádiu dospělce i vajíčka. Většina samic dosáhne dospělosti před přezimováním, páří se, přezimuje aktivně na vodní hladině a během zimy klade vajíčka. Vývoj dormantních vajíček může být vyvolán zvýšením teploty. Zimní ovipozice může být vysvětlena jako známka reprodukční strategie „rozdělování rizik“. Přezimování dospělců i vajíček poskytuje šanci adaptovat se na změny v podmínkách místního prostředí a může být významný faktor určující širokou variabilitu životní historie.

Output B:

Ditrich, T., Papáček, M. & Heino, M. The latitudinal uniformity of the unique life history of *Velia caprai* (Heteroptera: Veliidae) and notes to the pre-overwintering period of selected water striders (Heteroptera: Gerridae). *Entomologica Fennica, accepted.*

First author's contribution: 75 %

The latitudinal uniformity of the unique life history of *Velia caprai* (Heteroptera: Veliidae) and notes to the pre-overwintering period of selected water striders (Heteroptera: Gerridae)

Abstract

Temperate water striders (Gerridae) overwinter as adults and die after spring reproduction. European water cricket *Velia caprai* (Veliidae) overwinter concurrently in egg and adult stage in Central Europe. This rare overwintering strategy goes with longevity of this species. Adults can survive two winters in Central Europe, unlike other semiaquatic bugs. Scandinavian populations of *V. caprai* and water striders *Gerris lacustris* and *G. lateralis* were examined at the beginning and end of September to determine their life histories. Both gerrids start to overwinter during September, females prior to males and macropterous individuals prior to brachypterous. All females of *G. lacustris* and *G. lateralis* enter reproductive diapause before winter. Water cricket *V. caprai* overwinter in both adult and egg stage in Norway, and can probably survive two winters. Central European and Scandinavian populations of *V. caprai* share the same unique way of overwintering and probably also whole life history.

Výstup B:

Ditrich, T., Papáček, M. & Heino, M. The latitudinal uniformity of the unique life history of *Velia caprai* (Heteroptera: Veliidae) and notes to the pre-overwintering period of selected water striders (Heteroptera: Gerridae). *Entomologica Fennica, přijato k tisku.*

Podíl prvního autora: 75 %

Jednotnost jedinečné životní historie hladinatky *Velia caprai* (Heteroptera: Veliidae) v různých zeměpisných šířkách a poznámky k přípravě na přezimování výbraných bruslařek (Heteroptera: Gerridae)

Shrnutí

Temperátní bruslařky (Gerridae) přezimují ve stádiu dospělce a hynou po jarním rozmnožování. Evropská hladinatka *Velia caprai* přezimuje ve střední Evropě souběžně ve stádiu vajíčka i dospělce. Tato vzácná strategie přezimování je spojena s dlouhověkostí tohoto druhu. Dospělci ve střední Evropě mohou na rozdíl od ostatních semiakvatických ploštic úspěšně přežít dvě zimní období. Na začátku a konci září byly zkoumány skandinávské populace *V. caprai* a bruslařek *Gerris lacustris* a *G. lateralis* za účelem určit hlavní rysy životního cyklu. Oba druhy bruslařek začínají přezimovat v průběhu září, samice dříve než samci a dlouhokřídlí jedinci před krátkokřídlými. Všechny samice *G. lacustris* a *G. lateralis* před zimním obdobím vstupují do diapauzy. Hladinatka *V. caprai* v Norsku přezimuje ve stádiu vajíčka i dospělce a pravděpodobně může přežít dvě zimní období. Středoevropské a skandinávské populace *V. caprai* sdílejí neobvyklý způsob přezimování a pravděpodobně i životní historii.

Output C:

Ditrich, T. & Papáček, M. 2009: A question of voltinism of *Microvelia reticulata* (Veliidae) and *Mesovelia furcata* (Mesoveliidae) (Heteroptera: Gerromorpha) in Central Europe. P. 20 – 23. In Soldán, T., Papáček, M. & Boháč, J. (Eds) Communications and Abstracts, SIEEC 21, June 28 – July 3, 2009. University of South Bohemia, České Budějovice, 96 pp.

First author's contribution: 80 %

A question of voltinism of *Microvelia reticulata* (Veliidae) and *Mesovelia furcata* (Mesoveliidae) (Heteroptera: Gerromorpha) in Central Europe

Abstract

Population dynamics of two common inconspicuous water surface bugs, Microvelia reticulata (Veliidae) and *M. furcata* (Mesoveliidae) (Heteroptera: Gerromorpha), was monitored in two ponds in South Bohemia, Czech Republic during year 2008. *M. reticulata* overwinters in adult stage, whereas *M. furcata* overwinters in the egg stage. Both species are partly trivoltine in South Bohemia. Macropters of *M. reticulata* occur rarely; all specimens of *M. furcata* we found were apterous. Voltinism of *M. reticulata* is probably closely related with temperature and latitude.

Výstup C:

Ditrich, T. & Papáček, M. 2009: A question of voltinism of *Microvelia reticulata* (Veliidae) and *Mesovelia furcata* (Mesoveliidae) (Heteroptera: Gerromorpha) in Central Europe. P. 20 – 23. In Soldán, T., Papáček, M. & Boháč, J. (Eds) Communications and Abstracts, SIEEC 21, June 28 – July 3, 2009. University of South Bohemia, České Budějovice, 96 pp.

First author's contribution: 80 %

Otázka voltinismu ploštic *Microvelia reticulata* (Veliidae) a *Mesovelia furcata* (Mesoveliidae) (Heteroptera: Gerromorpha) ve střední Evropě.

Shrnutí

V r. 2008 byla sledována populační dynamika dvou běžných nenápadných hladinových ploštic, hladinatky *Microvelia reticulata* (Veliidae) a nártnice *Mesovelia furcata* (Mesoveliidae) na dvou rybnících v jižních Čechách. *M. reticulata* přezimuje jako dospělec, zatímco *M. furcata* přezimuje ve stádiu vajíčka. Oba druhy jsou v jižních Čechách částečně trivoltinní. Dlouhokřídlí jedinci *M. reticulata* se vyskytují vzácně, všichni odchycení jedinci *M. furcata* byli bezkřídlí. Voltinismus *M. reticulata* je pravděpodobně úzce spojen s teplotou a zeměpisnou šířkou.

Cold tolerance

Cold hardiness, especially ability to survive subzero temperatures, allows survival through the winter period and it is one of the key temperate insect attributes (Bale, 1989). As origin of insects is supposed to be in tropic area within 10° from equator (see Grimaldi & Engel, 2005, Rasnitsyn & Quicke, 2002), a strategy how to cope with low temperatures had to evolve in the species that dispersed to the temperate zone. Species are adapted to the cold environment morphologically (e.g. by body size and wing reduction, extent of melanism), behaviorally (e.g. by habitat selection, migration) ecologically (e.g. by prolonged lifespan, univoltinism) and physiologically (evolution of various mechanisms avoiding/tolerating freezing of the body fluids) (see Somme, 1989, Block, 1990). Physiological adaptations have deserved the biggest attention (see e.g. Zachariassen, 1985, Clark & Worland, 2008).

Generally, according to survival of freezing body fluids, freeze-tolerant and freeze-avoiding species can be distinguished. Freeze-avoidance is widespread among insects and supposed to be ancestral physiological strategy, whereas freeze-tolerance seems to have evolved at least six times (Sinclair, Addo-Bediako & Chown, 2003). However, this classification was found insufficient and more categories have been established. Additional categories are based on the causes of cold injury (Nedved, 2000), or on the values of the supercooling point (SCP) and lower lethal temperature (LLT) (Sinclair, 1999, Bale, 1996). Supercooling point refers to the temperature at which crystallization of the body fluids starts. Lower lethal temperature is the temperature lethal for an individual. Usually, freeze-tolerant species have SCP higher than LLT, whereas freeze-avoiding have SCP below LLT (Turnock & Fields, 2005). While SCP can be relatively easily determined by cooling down the insect and recording the occurrence of the exotherm (a latent heat released from the insect), LLT has to be estimated, usually by survival tests of a number of specimens exposed to various temperatures and periods (see Nedved, Lavy & Verhoef, 1998). The cold hardiness depends not only on temperature, but also on the time of exposure (Chown & Nicolson, 2004) and, within species, also on the developmental stage (Bowler & Terblanche, 2008). Concerning freeze-avoiding insects, SCP can be used as a lower limit of cold hardiness, whereas LLT50 (refers to the temperature at which 50% of a population die after standard exposure) can be used as upper estimate of short-term cold hardiness (after standardized exposure to the LLT50, half of the population still survives).

Preventing or delaying water crystallization (i.e. lowering SCP) can be generally achieved by removing ice nucleators from haemolymph and gut content, by colligative acting of low molecular weight cryoprotectants such as polyols (e.g. glycerol, sorbitol, mannitol) and sugars (e.g. trehalose, glucose, fructose) and by production of antifreeze proteins (thermal hysteresis factors) (Chown et al., 2004).

Whereas data on life histories of semiaquatic bugs are relatively rich (see above), data on their cold hardiness are scarce. The only exception is a work by Harada (2003) on *Aquarius paludum* (Gerridae), claiming freeze-avoidance in this water strider; and by Duman et al. (2004) finding thermal hysteresis in *Limnoporus dissortis* (Gerridae). Another aim of research within this thesis was to examine cold hardiness in Central European gerromorphan bugs. We determined characterizations of cold hardiness in nine gerromorphan species (*Hydrometra stagnorum* (Hydrometridae), *Aquarius paludum, G. argentatus, G. gibbifer, G. lacustris, G. odontogaster* (Gerridae), *Microvelia reticulata, V. caprai* and *V. saulii* (Veliidae). Obtained data were used for comparison of wider coherency between fixed overwintering strategies (found in most temperate gerromorphan species) *versus* flexible strategy employed by *V. caprai* (manuscript D). This submitted manuscript shows that adults of *Velia* spp. are very low cold tolerant, with low probability to survive extremely cold winters. Concurrent overwintering at the much more cold-tolerant egg stage is a kind of “insurance” in case of the harsh winter, forming risk-spreading overwintering strategy. These findings raised two important questions (still unanswered) about bet-hedging (i.e. risk-spreading) overwintering strategy connected with low cold hardiness appeared:

1) Is the low cold hardiness shared by adults of all species, regularly overwintering at both the egg and adult stage? In such case, low cold hardiness of the overwintering adults should indicate another overlooked overwintering stage and vice versa.

2) What is the cause and what the consequence - bet hedging overwintering strategy (egg-and-adult overwintering) or low cold tolerance? Both scenarios are possible. According to the majority of heteropterans overwintering as adults, we suppose this strategy as plesiomorphic. Genus *Velia* is mainly distributed in Mediterranean region, probable area of origin of this species. Cold tolerance in this area is not crucial for survival. Hence, if low cold tolerance in the genus *Velia* preceded dispersion to the North, only species that were able to adopt some strategy enabling survival in low temperatures (physiologically, behaviorally or ecologically) could establish permanent populations in temperate regions. We can hypothesize that *Velia* spp. lack some exaptation, necessary for physiological cold hardiness. Bet-hedging overwintering strategy is thus another way how to cope

However, opposite progress is also possible. If the egg-and-adult overwintering strategy appeared in the population of cold hardy individuals, these specimens were advantaged: they did not have to maintain costly cold hardiness, because they survived most winters as adults and sporadic extremes as eggs. Natural selective pressure, maintaining high cold tolerance, disappeared. A necessary condition of this second case is an increased fitness of low cold tolerant individuals, compared to the more cold hardy ones.

Output D:

Ditrich, T. & Košťál, V. Overwintering strategies of semiaquatic bugs: fixed versus flexible. *Submitted to Physiological Entomology*.

First author's contribution: 70 %

Overwintering strategies of semiaquatic bugs: fixed versus flexible

Abstract

Insects often overwinter in cryothermic state, *i.e.* at body temperatures below equilibrium freezing point. Insects evolved diverse overwintering strategies including avoidance/tolerance of freezing of body water plus multiple physiological adjustments. Such strategies are either *fixed* (strictly programmed) or more or less *flexible* (plastic). The strategies remain mostly unexplored in semiaquatic bugs (Insecta, Heteroptera, Gerromorpha). Here we present analysis of ecophysiological aspects of overwintering in nine species. Our results show that all studied species avoid formation of ice by more or less extensive supercooling of their body fluids. There was a tight statistical correlation between supercooling capacity and lower lethal temperature. Different species employ different physiological adjustments increasing their chances for survival in supercooled state: the high osmolality of body fluids and partial dehydration; the thermal hysteresis between equilibrium melting and freezing points; the accumulation of low molecular weight sugars and polyols. Most of the species strictly fix their overwintering to adult stage, while *Velia caprai* can overwinter flexibly either in the adult or in the egg stage. The supercooling capacity of *V. caprai* adults is not sufficient to prevent the risk of freezing and thus the adults survive only opportunistically in suitable microhabitats and/or during mild winters. Adult overwintering probably reflects original Mediterranean

life-cycle of *V. caprai* and allows them to maintain reproductive activity until / during winter months. Such strategy may maximize exploitation of seasonal time. The winter survival in a population level population is assured by a risk-spreading between adults and highly cold tolerant overwintering eggs.

Výstup D:

Ditrich, T. & Košťál, V. Overwintering strategies of semiaquatic bugs: fixed versus flexible. *Odesláno do Physiological Entomology.*

Podíl prvního autora: 70 %

Přezimovací strategie semiakvatických ploštic: fixní *versus* flexibilní

Shrnutí

Hmyz často přezimuje v kryotermním stavu, t.j. s tělní teplotou pod rovnovážným bodem mrznutí. U různých druhů hmyzu se vyvinuly rozdílné přezimovací strategie zahrnující vyhýbání se či tolerování zmrznutí tělní vody, společně s nastavením dalších fyziologických mechanismů. Tyto strategie jsou buď *fixní* (přesně řízeny), anebo více či méně *flexibilní* (plastické). Přezimovací strategie semiakvatických ploštic (Insecta, Heteroptera, Gerromorpha) jsou převážně neznámy. V této práci uvádíme výsledky analýz ekofyziologických aspektů přezimování devíti druhů této skupiny ploštic. Podle našich výsledků se všechny studované druhy vyhýbají krystalizaci tělní vody více či méně intenzivním podchlazením tělních tekutin. Kapacita podchlazení je těsně korelována s letální teplotou. Různé druhy vykazují různá fyziologické mechanismy zvyšující šanci přežít v podchlazeném stavu: vysokou osmolalitu tělních tekutin a částečnou dehydrataci; termální hysterezi mezi rovnovážným bodem tání a mrznutí; akumulaci nízkomolekulárních cukrů a polyolů. Většina druhů přezimuje fixně ve stádiu dospělce, zatímco výsledky studií životního cyklu ukazují, že hladinatka *Velia caprai* může přezimovat flexibilně ve stádiu vajíčka i dospělce. Kapacita podchlazení dospělců *V. caprai* však není dostatečná k zabránění zmrznutí a dospělci tak přežívají jen oportunisticky v příznivých mikrohabitatech a/nebo během mírných zim. Přezimování dospělců pravděpodobně odráží původní mediteránní životní cyklus rodu *Velia* a

umožňuje jim reprodukční aktivitu až do počátku i během zimy Tato strategie může maximalizovat exploataci příznivého období sezóny. Zimní přežívání na populační úrovni je zajištěno rozložením rizik mezi dospělce a vysoce chladově odolná přezimující vajíčka.

Wing polymorphism

Wing polymorphism or pterypolymorphism is characteristic for many true bugs, including most Gerromorpha. Wing polymorphic species have various wing lengths even within a population. Lengths of the wings is rather continuous, from complete reduction (aptery) to fully developed wings (macroptery), in many gerromorphan species (Andersen, 1982). However, based on flight capability, usually only long-winged (LW) and short-winged (SW – covering apterous, micropterous and brachypterous individuals) morph is distinguished for ecological purposes. Individuals of different morphs have different migratory capability and wing polymorphism thus forms an important part of dispersal polymorphism (Harrison, 1980). Wing polymorphism is usually considered as a result of fitness trade-off between flight capability and reproduction, as LW individuals have to allocate energy from reproduction to development and maintaining flight organs (Zera & Denno, 1997). Indeed, this trade-off has been confirmed in many wing-polymorphic insects, including grasshoppers, crickets, planthoppers, aphids and many true bugs and beetles (see Zera et al., 1997). This trade-off has also been confirmed in many gerromorphan bugs, including *Microvelia* spp. (Muraji & Nakasuji, 1988) and many gerrids (Kaitala, Kaitala & Getz, 1989, Zera, 1984, Kaitala, 1988, Fairbairn, 1988, Harada, 1992b, Spence, 1989). This trade-off applies even for flight muscle polymorphism, known from many insects including gerromorphan bugs (Kaitala, 1988, Spence *et al.*, 1994, Harrison, 1980). However, investigation of flight muscle polymorphism was not included in the present research.

Whereas SW females have greater fecundity compared to LW ones, winged individuals have the option to disperse from one site to another. Frequency of LW individuals thus should be high in situations where dispersal or migrations is needed; otherwise SW morph (with higher reproductive effort) should be favored. Indeed, macropters dominate in overwintering generation of many gerrids, hibernating far from the breeding site and dispersing in the spring (Vepsäläinen, 1971b, Brinkhurst, 1959, Zera & Tiebel, 1991). Second situation, when LW morph is essential, is incidence of adverse conditions at the habitat. As for all aquatic organisms, drying out of water body represents such adverse conditions. Macropterous individuals thus should be frequently present at temporary water bodies such as pools, puddles or small streams, where drying out is probable. Contrarily, permanent habitats, such as ponds, lakes and rivers, should be predominantly occupied by SW morph to maximize reproductive effort (Brinkhurst, 1959, Vepsäläinen, 1971b). Wing polymorphism is thus an adaptive strategy in gerromorphan bugs, with macroptery as ancestral and wing polymorphism as advanced state (Andersen, 1982). Complete aptery thus should appear in species living at temporary habitat, not dispersing after hibernation or not hibernating at all, e.g. sea-skaters (Gerridae: Halobatinae) (Andersen, 1982, Andersen & Cheng, 2004).

Occurrence of LW individuals at temporary water bodies is not surprising, given the difficult colonization of such habitats by SW morph. However, even permanent habitat can disappear. Nymphs, developing in habitats with a high risk of drought or other hostility, thus should preferably develop wings for the possibility of escaping such a habitat. Similarly, nymphs of polyvoltine species, developing before winter, should switch to LW morph needed for flight to and from overwintering sites. Environmental cues indicating proximity of need for dispersion thus should be observed and recognized. Indeed, nymphs of many gerromorphan bugs react to different environmental factors and proportion of particular wing morph within population is affected by environmental conditions. Proximity of winter, indicated by shortening photoperiod, is perceived by most temperate insects (Danks, 2006). Nymphs of many gerromorphan bugs developing before winter thus switch to appropriate wing morph. Usually, as written above, overwintering generation is predominantly LW, whereas summer generation(s) are SW. Shortening photoperiod thus causes development of LW morph in many species (Vepsäläinen, 1971a, Kopfli *et al.*, 1987, Harada & Numata, 1993, Zera, Innes & Saks, 1983, Zera *et al.*, 1991). Opposite wing morph development as a response to shortening days is also known (e.g. Vepsäläinen, 1974a, Calabrese, 1979, Muraji *et al.*, 1989). Its adaptive significance is usually explained as better survival of SW morph during harsh winters (Vepsäläinen, 1974a, Ahlroth, Alatalo, Hyvarinen *et al.*, 1999).

Temporary water bodies irregularly dry out. However, such incidental events can be predicted according to environmental conditions. High probability of drought comes with high temperatures; such conditions thus should lead to increased number of LW individuals within a population. This predicted pattern is confirmed in many gerromorphan species (Harada, 1992a, Muraji *et al.*, 1989, Pfenning & Poethke, 2006, Pfenning *et al.*, 2008), but does not hold generally (Spence et al., 1994).

Another cue of incoming habitat desiccation is increased population density – as water amount and water level diminishes, area of water surface shrinks and it causes crowding of aquatic organisms. High population density during nymphal development results in high frequency of LW morph in several tested species (Muraji *et al.*, 1988, Muraji *et al.*, 1989, Harada, Tabuchi & Koura, 1997). This phenomenon seems adaptive even at permanent water bodies – although drying out of such habitat is unlikely, crowding implies less food, shelters etc. Leaving crowded site and colonizing new one should be advantageous in any event. However, opposite response (i.e. lower frequency of LW morph at high population density) was observed in *Gerris buenoi* (Harada & Spence, 2000). Authors of this research suggest two possible explanation of this result: 1) Increased population density results in increased cannibalism among conspecifics and brings a great advantage for individuals with fastest development. Because wings development is costly, *G. buenoi* preferably invest the energy into the faster development instead of growth of wings. Second explanation 2) is more speculative – a habitat with low density of bugs is probably inhospitable and adults should leave such habitat. Crowded habitats, indicating favorable conditions, thus result in decreased frequency of LW morph.

There are also other factors affecting wing polymorphism, such as food level. However, the effect of decreased / increased food level is usually minor and unclear (Muraji *et al.*, 1989, Kaitala, 1988, Pfenning, Poethke & Hovestadt, 2007). Much evidence suggests significant importance of hereditability of wing polymorphism in some species, but inheritance of wing morph is rather complex and unresolved in most species (Vepsäläinen, 1978, Spence, 1989, Calabrese, 1979, Zera *et al.*, 1983, Spence *et al.*, 1994).

Papers in this section recount spatial distribution of several semiaquatic bugs and their wing morphs within relatively small area in Novohradské hory Mts. This survey brings, among others, data on mass occurrence of wingless water cricket *Velia caprai* at temporary habitats (output E). Next paper deals with effect of population density on several life history traits in *M. furcata*, *M. reticulata* and *V. caprai*, including wing polymorphism (output F). Results of these experiments prompt surprising situation in *V. caprai*, which occur in temporary habitats, but development of LW morph is very rare. The results lead to hypothesis of terrestrial dispersion of *V. caprai,* with consequential suppression of LW morph development as a response to environmental factors. This hypothesis was confirmed as described in next paper (output G). During field survey with mark-recapture experiments for purpose of determination of dispersal, unusual prolonged lifespan of adults *V. caprai* was recorded. Both males and females can apparently survive at least two succeeding winters, which gives survival of three winters speculating on survival of the first overwintering at the egg stage. Adults thus can be reproductively active during three seasons.

Output E:

Ditrich, T., Papáček, M. & Broum, T. (2008) Spatial distribution of semiaquatic bugs (Heteroptera: Gerromorpha) and their wing morphs in a small scale of the Pohorsky Potok stream spring area (Novohradske Hory Mts.). *Silva Gabreta* **14**, 173-178.

First author's contribution: 70%

Spatial distribution of semiaquatic bugs (Heteroptera: Gerromorpha) and their wing morphs in a small scale of the Pohorsky Potok stream spring area (Novohradske Hory Mts.)

Abstract

A survey of semiaquatic bugs (Heteroptera: Gerromorpha) was managed in a small scale area (72 ha; spring area of Pohorsky Potok stream, Novohradske Hory Mts., Czech Republic, Central Europe). Species composition of assemblages and rates of their pteromorphs were observed in the relation to selected environmental characteristics [long dash] stream velocity, site permanence, water surface coverage and site shading. *Gerris gibbifer* Schummel, 1832, *Gerris lateralis* Schummel, 1832 and *Velia caprai* Tamanini, 1947 are dominant gerromorphan species in the study area. *Gerris* species are univoltine; bivoltinism of Veliidae species cannot be excluded in this area. A redundancy analysis showed significant effect of stream velocity, site shading and site permanence on species and wing morphs composition of assemblages. *Velia caprai* mostly occur in shaded habitats with flowing water, whereas other species prefer still water bodies. *Gerris lateralis* prefers shaded sites as the only gerrid. Occurrence of wing morphs of the only notably wing dimorphic species *G. lateralis* in the study area depends on site permanence. Permanent water bodies are occupied by both macropterous and apterous specimens, temporary sites are almost exclusively colonized by macropterous individuals. Ecological consequences are discussed.

Výstup E:

Ditrich, T., Papáček, M. & Broum, T. (2008) Spatial distribution of semiaquatic bugs (Heteroptera: Gerromorpha) and their wing morphs in a small scale of the Pohorsky Potok stream spring area (Novohradske Hory Mts.). *Silva Gabreta* **14**, 173-178.

Podíl prvního autora: 70%

Prostorová distribuce semiakvatických ploštic (Heteroptera: Gerromorpha) a jejich křídelních morf v malé oblasti Prameniště Pohořského potoka (Novohradské hory).

Shrnutí

V oblasti Prameniště Pohořského potoka (72 ha, Novohradské hory, Česká republika) byla provedena studie semiakvatických ploštic (Heteroptera: Gerromorpha). Sledováno bylo druhové složení a frekvence křídelních morf ve společenstvech v závislosti na vybraných faktorech prostředí (rychlost proudu, trvalost lokality, zárůst vodní hladiny a zastíněnost lokality). *Gerris gibbifer* Schummel, 1832, *Gerris lateralis* Schummel, 1832 a *Velia caprai* Tamanini, 1947 jsou dominantními gerromorfními druhy v této oblasti. Druhy rodu *Gerris* jsou univoltinní; bivoltinismus druhů čeledi Veliidae nemůže být vyloučen. Redudantní analýza ukázala signifikantní vliv rychlosti proudu, zastíněnosti a trvalosti vodního tělesa na druhové složení i výskyt křídelních morf ve společenstvech. *Velia caprai* se nejčastěji vyskytuje v zastíněných habitatech s tekoucí vodou., zatímco ostatní druhy preferují vodu stojatou. *Gerris lateralis* jako jediná bruslařka preferuje zastíněná stanoviště. Výskyt křídelních morf jediného zřetelně dimorfního druhu *G. lateralis* ve sledované oblasti závisí na trvalosti / dočasnosti stanoviště. Trvalá vodní tělesa jsou osídlena dlouhokřídlými i bezkřídlými jedinci, dočasná stanoviště jsou téměř výhradně kolonizována dlouhokřídlými jedinci. V práci jsou diskutovány ekologické souvislosti výsledů.

Output F:

Ditrich, T. & Papáček, M. Effect of population density on the development of *Mesovelia furcata* (Mesoveliidae), *Microvelia reticulata* and *Velia caprai* (Veliidae) (Heteroptera: Gerromorpha). *European Journal of Entomology* **107**, 579 – 587.

First author's contribution: 80%

Effect of population density on the development of *Mesovelia furcata* (Mesoveliidae), *Microvelia reticulata* and *Velia caprai* (Veliidae) (Heteroptera: Gerromorpha)

Abstract

Population density during nymphal development affects body size, developmental rate and wing polymorphism in semiaquatic bugs. Nymphs from crowded habitats grow faster and thus gain an advantage in the later stadia. Rapid development results in smaller body size in several gerrids. Macropterous adults develop more frequently at high population densities in most species, which enables the bugs to leave crowded habitats. Three European widespread species *Mesovelia furcata* Mulsant & Rey, 1852 (Mesoveliidae), *Microvelia reticulata* Burmeister, 1835 and *Velia caprai* Tamanini, 1947 (Veliidae) were reared individually and simultaneously either at a low or high population density. Duration of postembryonic development, wing morph, body size and length of distal oocyte in females were recorded. High population density accelerates development in *Mesovelia furcata* and *Microvelia reticulata*. However, there was no trade-off between developmental rate and body size. Accelerated development without a decrease in body size was probably because maturation was delayed. Individually reared nymphs developed faster than nymphs from communal cohorts. No long-winged *Microvelia reticulata* specimen developed in any treatment. However, more macropterous individuals developed in high-density treatments in *Mesovelia furcata* (significant) and *Velia caprai* (not significant). All the nymphs of the species that were reared individually developed into apterous adults. The results suggest that population density strongly influences the life history of semiaquatic bugs. However, the only commonly shared response seems to be an increase in developmental rate when reared at high population densities. Other traits such as wing dimorphism, body size and rate of oogenesis differ at the species level.

Výstup F:

Ditrich, T. & Papáček, M. Effect of population density on the development of *Mesovelia furcata* (Mesoveliidae), *Microvelia reticulata* and *Velia caprai* (Veliidae) (Heteroptera: Gerromorpha). *European Journal of Entomology* **107**, 579 – 587.

Podíl prvního autora: 80%

Vliv populační hustoty na vývoj ploštic *Mesovelia furcata* (Mesoveliidae), *Microvelia reticulata* a *Velia caprai* (Veliidae) (Heteroptera: Gerromorpha)

Shrnutí

Populační hustota během larválního vývoje semiakvatických ploštic ovlivňuje jejich velikost těla, rychlost vývoje a křídelní polymorfismus. Nymfy z vyšších populačních hustot rostou rychleji a získávají tak výhodu staršího instaru. U několika bruslařek má rychlejší vývoj za následek menší velikost těla. Dlouhokřídlí jedinci se častěji vyvíjejí ve vysokých populačních hustotách, což následně ploštícím umožňuje opustit přeplněná stanoviště. Ploštice tří rozšířených evropských druhů, *Mesovelia furcata* Mulsant & Rey, 1852 (Mesoveliidae), *Microvelia reticulata* Burmeister, 1835 a *Velia caprai* Tamanini, 1947 (Veliidae), byly chovány souběžně individuálně, v nízké a vysoké populační hustotě. Sledována byla rychlost vývoje, křídelní morfa, velikost těla a délka distálního oocytu. Vysoká populační hustota urychlila vývoj ploštic *Mesovelia furcata* a *Microvelia reticulata*, nebyl však zaznamenán trade-off mezi rychlostí vývoje a velikostí těla. Zrychlený vývoj bez zmenšení velikosti těla byl pravděpodobně umožněn zpožděním oogeneze. Individuálně chované nymfy se vyvíjely rychleji než nymfy z hromadných chovů. V žádné populační hustotě se nevyvinul žádný dlouhokřídlý jedinec *Microvelia reticulata,* více dlouhokřídlých ploštic *Mesovelia furcata* (signifikantní rozdíl) a *Velia caprai* (nebyl signifikantní rozdíl) se však vyvinulo ve vysoké populační hustotě. Všichni individuálně chovaní jedinci všech druhů se vyvinuli do bezkřídlého dospělce. Výsledky naznačují, že populační hustota významně ovlivňuje životní historie semiakvatických ploštic. Jediná obecně sdílená reakce je zvýšení rychlosti vývoje ve vysokých populačních hustotách. Ostatní životní rysy, jako křídelní polymorfismus, velikost těla a rychlost oogeneze se liší na druhové úrovni.

Output G:

Ditrich, T. & Papáček, M. (2009) Correlated traits for dispersal pattern: Terrestrial movement of the water cricket *Velia caprai* (Heteroptera: Gerromorpha: Veliidae). *European Journal of Entomology* **106**, 551-555.

First author's contribution: 80%

Correlated traits for dispersal pattern: Terrestrial movement of the water cricket *Velia caprai* (Heteroptera: Gerromorpha: Veliidae).

Abstract

Macropterous individuals of wing polymorphic semiaquatic bugs (Heteroptera: Gerromorpha) usually occur at a high frequency if there is a need to leave an unfavorable habitat or in a generation migrating to/from an overwintering site. Velia caprai (Veliidae) is usually found in unpredictable habitats, but the macropterous morph is rare. Laboratory, mesocosm and field experiments were used to test the hypothesis that individuals of this species migrate by walking rather than by flight. Laboratory experiments that focused on the development of macropterous morph under conditions that usually stimulate the development of this morph in water striders were unsuccessful. A high temperature shortened the duration of nymphal development, but no winged specimens of Velia caprai developed in the laboratory when reared under either high or low temperatures, long or short photoperiods or on the surface of water or wet filter paper. Mesocosm experiments with apterous adults revealed they are able to walk on land. Both the males and females dispersed by walking in semi-natural conditions. Long-term field experiments using mark and recapture confirmed that this species can disperse by walking. Apterous individuals can compensate for downstream drift by upstream terrestrial migration and colonize newly established pools and ditches even several tens of meters from source sites. The development of a macropterous morph in response to environmental factors is replaced by terrestrial dispersal in V. caprai.

Výstup G:

Ditrich, T. & Papáček, M. (2009) Correlated traits for dispersal pattern: Terrestrial movement of the water cricket *Velia caprai* (Heteroptera: Gerromorpha: Veliidae). *European Journal of Entomology* **106**, 551-555.

Podíl prvního autora: 80%

Shrnutí

Dlouhokřídlí jedinci křídelně polymorfních semiakvatických ploštic (Heteroptera: Gerromorpha) se obvykle vyskytují ve zvýšené frekvenci v případě, že je nutné opustit nepříznivé stanoviště, anebo v generaci migrující na a ze zimovišť. Hladinatka *Velia caprai* (Veliidae) se většinou vyskytuje na nepředvídatelných stanovištích, dlouhokřídlá morfa je však vzácná. Laboratorními, mesokosmovými a terénními experimenty byla testována hypotéza o šíření tohoto druhu spíše po zemi chůzí nežli letem. Laboratorní experimenty zaměřené na vývin dlouhokřídlých jedinců, v podmínkách stimulující vývoj této morfy u většiny semiakvatických ploštic, byly neúspěšné. Vysoká teplota zkrátila období larválního vývoje, ale žádný dlouhokřídlý jedinec se nevyvinul v žádné kombinaci vysoké a nízké teploty, dlouhé a krátké fotoperiody či během chovu na vodní hladině a vlhkém filtračním papíře. Mesocosmové experimenty prokázaly schopnost hladinatek pohybu v suchozemském terénu – samci i samice se v semi-přírodních podmínkách šířili chůzí. Bezkřídlí jedinci mohou kompenzovat proudový drift terestrickou migrací proti směru vodního toku a kolonizovat nově vzniklé tůně a kalužiny i několik desítek metrů od zdrojového stanoviště. Vývin dlouhokřídlé morfy jako odpověď na okolní prostředí je u hladinatky *V. caprai* potlačena a nahrazena terestrickým šířením.

General conclusions

Ecology of non-gerrid species deserves special attention when generalizing ecology of semiaquatic bugs. The most notable results of this thesis are these concerning widespread European water cricket *Velia caprai*. It has complex life history, differing from all temperate water striders. Wing dimorphism, characteristic for gerromorphan bugs, has been suppressed in *V caprai* as it disperses terrestrially. Unlike in other aquatic insects, flightless individuals of this species thus occur even at temporary habitats. *V. caprai* also exhibits unusual egg-and-adult overwintering strategy, which can be at least partly explained by physiology of overwintering stages. Whereas overwintering eggs are highly cold tolerant, comparable to the overwintering stages of other species, adults of *V. caprai* have very low cold tolerance. Such strategy can be considered as risk spreading. Two evolutionary scenarios of development of this overwintering strategy are suggested. Increased lifespan of *V. caprai* just complements to exceptionality of this common species.

Microvelia reticulata and *Mesovelia furcata*, other species examined in detail, do not differ from most generalizations based on gerrid surveys. However, they differ in development of nymphs from various population densities. Gerrids from high densities grow faster but are smaller as adults, showing trade-off between developmental rate and body size. However, nymphs from high population densities of both non-gerrid species examined grow faster and adults are larger than siblings from lower densities. This is allowed by another trade-off between increased developmental rate and body size *versus* sexual maturation.

Ecological patterns and models for semiaquatic bugs (Heteroptera: Gerromorpha), based mainly on data from water striders (Gerridae), cannot be applied to other gerromorphan families. Uniqueness of water cricket *Velia caprai* and unpredictability of ecological traits in other examined species shows a necessity of species-level approach for studying ecology of semiaquatic bugs.

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