

WING DIMORPHISM/POLYMORPHISM IN TRUE BUGS (HEMIPTERA, HETEROPTERA) FROM A FUNCTIONAL VIEWPOINT - A REVIEW - PART II: PHYTOPHAGOUS SPECIES

A SZÁRNY DIMORFIZMUS/POLIMORFIZMUS A POLOSKÁKNÁL (HEMIPTERA, HETEROPTERA): ÁTTEKINTÉS FUNKCIONÁLIS NÉZŐPONTBÓL - II. RÉSZ: FITOFÁG FAJOK

ZSOLT GIDÓ
Gido.Zsolt@uni-mate.hu

Abstract

*This is the second part of the article where the available information from the published literature on the wing dimorphism/polymorphism occurring among true bugs (Heteroptera) is reviewed from a functional viewpoint. This paper covers the case studies on phytophagous species and draws some general conclusions. Wing dimorphism/polymorphism has been studied in detail at the red firebug: *Pyrrhocoris apterus* (Linnaeus, 1758), at some blissid species - mainly at the Oriental chinch bug: *Cavelerius saccharivorus* (Okajima, 1922) - at some lygaeid species and at the red-shouldered soapberry bug *Jadera haematoloma* (Herrich-Schäffer, 1847) (Rhopalidae). In general, the macropterous form has a delayed sexual maturation, which further enhances its dispersal ability but represents an obvious reproductive disadvantage. In most known cases of the hemipteran wing dimorphism/polymorphism the wing form is affected by environmental factors (polyphenism), but examples of genetically determined wing dimorphism also have been documented among Lygaeinae. Seasonal wing dimorphism/polymorphism is very common among the well-studied northern temperate species. Wing dimorphic/polymorphic phytophagous “outbreak” species (Blissidae, *Leptoterna dolobrata*) react with mass production of the otherwise rare macropters to high population density and altered food quality. An underlying wing muscle dimorphism/polymorphism frequently co-exists with the externally visible wing dimorphism/polymorphism. Known cases of full or partial de-alation are also mentioned and briefly discussed.*

Keywords: wing dimorphism/polymorphism, Heteroptera, *Pyrrhocoris apterus*, Blissidae, *Jadera haematoloma*

Összefoglalás

*Ez a közlemény a második része a poloskák (Hemiptera:Heteroptera) szárny dimorfizmusát/polimorfizmusát funkcionális nézőpontból tárgyaló szakirodalmi áttekintésnek. Ezen rész a fitofág fajokra vonatkozó esettanulmányokat mutatja be, néhány általános következtetés levonásával. Részletesebben ismert a verőköltő poloska: *Pyrrhocoris apterus* (Linnaeus, 1758), néhány karcsúbodobácsfaj: Blissidae: főleg a *Cavelerius saccharivorus* (Okajima, 1922) néhány bodobácsfaj (Lygaeidae) és a *Jadera haematoloma* (Herrich-Schäffer, 1847) (Rhopalidae) szárny dimorfizmusát/polimorfizmusát. Általában a makropter forma később válik szaporodóképessé, ami hozzájárul a nagyobb terjedőképességéhez, de nyilvánvaló*

reproduktív hátrányt is jelent. A szárny dimorfizmus/polimorfizmus legtöbb ismert esetében a szárnyforma kialakulását erősen befolyásolják a környezeti tényezők (polifenizmus), de a Lygaeinae alcsaládban több ismert példája van a genetikailag determinált szárnydimorfizmusnak. Az évszakos szárnydimorfizmus/polimorfizmus nagyon gyakori a részletesebben tanulmányozott északi mérsékelt övi fajok között. A dimorph/polimorf szárnyú, fitofág “gradációs” fajok (karcsúbodobácsok, *Leptoterna dolobrata*) az egyébként ritka makropterek tömegtermelésével reagálnak a nagy populációsűrűségre és a táplálék minőségi változására. A külsőleg látható szárnydimorfizmust/polimorfizmust gyakran a szárnyizmok dimorfizmusa/polimorfizmusa egészíti ki. A részleges és teljes szárnyvesztés ismert esetei szintén említésre kerülnek.

Kulcsszavak: szárny dimorfizmus/polimorfizmus, Heteroptera, *Pyrrhocoris apterus*, Blissidae, *Jadera haematoloma*

Introduction

This paper is the second part of the review discussing the wing dimorphism/polymorphism in true bugs (Heteroptera) from a functional viewpoint. The first part discussed the wing dimorphism/polymorphism of non-phytophagous heteropterans (GIDÓ, 2023). This second part discusses the wing dimorphism/polymorphism of phytophagous heteropterans and draws some general conclusions.

The term “phytophagous” is used here in a broad sense, for practical reasons. Omnivores which occasionally and facultatively also consume some animal food but depend heavily on their plant diet -like *Pyrrhocoris apterus* - are treated here as phytophagous insects. *P. apterus* even has a clear host plant preference, as it prefers the members of Tiliaceae and Malvaceae families. In Central Europe this species mainly relays on the seeds of linden trees (*Tilia* spp.).

Some well known and species rich heteropteran families which give the majority of the phytophagous true bug species like Tingidae, Scutelleridae, Coreidae, Pentatomidae and Miridae) are not mentioned or seriously underrepresented in this paper. Wing dimorphism-polymorphism and even the monomorphic wing reduction is either very rare or absent in some of these lineages (Tingidae, Scutelleridae, Pentatomidae) or it is not so rare, but has been rarely studied in detail (Miridae).

Terminological issues

Some authors use the term „wing polymorphism” only in those cases when the wing form is rigidly genetically determined. When the environmental factors have a substantial role in determining the wing form, they use the term „polyphenism”. In this paper the term „wing polymorphism” is used for both genetically determined and/or environmentally induced differences in wing form within the species. „Polyphenism” is treated here as a valid sub-category of polymorphism.

Non-macropterous heteropterans show different degrees of wing reduction, depending on the species. SCHUCH and SLATER (1995) distinguishes sub-macroptery, coleoptery, brachytery, staphylinoidy, microptery and aptery based on the external morphology. This descriptive categorisation is recognised here as practically valid and biologically relevant (as the different wing forms probably have different genetic and/or ontogenetic background). In this review sometimes a simplified functional, terminology is used, where all forms with serious, functional wing reduction (from coleopterous to apterous) are referred as “non-macropters” while macropters and sub-macropters are referred as “macropters”.

From functional point of view seasonal wing polymorphism and concurrent wing polymorphism can be distinguished. Concurrent wing polymorphism has been called “genetic polymorphism” (VEPSÄLÄINEN, 1978), later “permanent polymorphism” (ANDERSEN, 2000). Both terms – especially the former – can be misleading, so the term “concurrent wing polymorphism” is proposed here for the wing polymorphism present among the members of the same cohort. Seasonal wing polymorphism and concurrent wing polymorphism often co-occur and overlap in the same population, resulting a rather complex spatial and temporal pattern of macropter/non-macropter ratios.

Case studies of wing dimorphism/polymorphism of phytophagous Heteroptera

Firebugs: Pyrrhocoris apterus and P. sibiricus (Pyrrhocoridae)

The single wing-dimorphic heteropteran species which has been most intensively studied is the familiar red firebug, *Pyrrhocoris apterus* (Linnaeus, 1758). A series of papers describe the various aspects of the wing dimorphism of *P. apterus*: HODKOVÁ and SOCHA (2006); HONĚK (1974; 1976 a, b; 1979; 1981; 1985; 1986 a, b; 1987; 1995), KODRIK and SOCHA (1999); SOCHA (1993; 2004; 2006; 2007; 2008; 2013 a, b); SOCHA and KODRIK (1999); SOCHA and ŠULA (1996; 2006; 2008); SOCHA and ZEMEK (2000 a, b; 2003; 2004 a, b); SOCHA et al. (1997;1998; 2001; 2004); ŠULA et al. (1995; 1998). There is some additional information on wing dimorphism of the closely related *P. sibiricus* Kuschakewitsch, 1886 (SAKASHITA et al.; 1995; 1996; 1997; 1998 a, b). The latter is externally rather wing polymorphic than dimorphic, as multiple wing lengths occur in the population: however, there is some discontinuity, so *P. sibiricus* individuals – somewhat artificially – can be also classified as brachypters or macropters (SAKASHITA et al., 1996). This may indicate that the genetic and/or epigenetic background of the wing polymorphism of *P. sibiricus* is probably somewhat different from that of its close relative, *P. apterus*.

Three distinct wing forms of *P. apterus* are known: macropterous, brachypterous, and micropterous (SOCHA, 1993). The latter is very rare, so natural populations are practically dimorphic. Macropters have fully developed hind wings and apparently well-developed wing muscles as young adults, however they are unable to fly (SOCHA and ZEMEK, 2000a). Brachypters have reduced membrane, rudimental hind wings, and seriously underdeveloped flight muscles (SOCHA and ŠULA, 2006). In most Central European populations, the percentage of macropters is usually under 10%; populations containing up to 36% macropters have been reported in the Mediterranean region (SOCHA and ŠULA, 1996; SOCHA, 2001).

HONĚK (1979) concluded from selection experiments (see also below), that macroptery of *P. apterus* is caused by recessive allele, while the dominant allele causes brachyptery. Firebugs containing the dominant allele always become brachypters, while the recessive homozygotes can develop either to macropters or brachypters depending on the environmental cues acting on the nymphs during the sensitive period. The environmental factors act on metabolic processes coded by different modifier genes. This schematic model has been not cancelled nor further elaborated until the present day, rather is generally accepted (SOCHA, 1993).

Seasonal wing polymorphism is well documented both in *P. apterus* and *sibiricus*: not surprisingly the photoperiod and the temperature are the main determining factors (SOCHA, 1993; SAKASHITA et al, 1998b). Central European *P. apterus* populations are bivoltine; mid-summer generation is wing dimorphic, while the late summer-early autumn generation (which overwinters) is exclusively brachypterous (SOCHA, 2013). Latitudinal differences with clear

adaptive role have been documented between the critical photoperiod lengths of the Central European and Mediterranean populations (SOCHA, 2001).

Contrary, almost nothing has been published on the environmental factors possibly inducing concurrent polymorphism in *P. apterus*. SAKASHITA et al. (1995) noted, that under experimental conditions, moderate nymphal crowding induced an increase in the average wing length of *P. sibiricus*. It might be, that the concurrent wing dimorphism of the summer generation of *P. apterus* is fully explained by the genetic factors, however there are no sufficient data to exclude the possible effects of some, in part density dependent environmental factors (nymphal density in itself, food quantity and quality etc.). *P. apterus* nymphs (like the adults) tend to form dense aggregations, so this species might not be stressed by the direct body contact with the conspecifics, however it cannot be categorically excluded that the quantity and quality of available food for the nymphs might affect the wing morph, as it is known in other phytophagous hemipterans. A strong argument against the significant effect of density-dependent factors on the wing form of *P. apterus* is - that unlike in many wing dimorphic phytophagous hemipterans and orthopterans – no “outbursts of macroptery” (populations where the macropters are in majority) have been reported in this very common and apparent species.

Both macropterous and brachypterous individuals of *P. apterus* are flightless (“non-functional macroptery”), however, the trade-off between reproductive and dispersal abilities (“oogenesis-walking syndrome”, SOCHA) is exceptionally well documented in this species. Macropters belonging to both sexes show much larger walking activity than brachypters (SOCHA and ZEMEK, 2000b; 2003), so they still represent the dispersal form of *P. apterus*. Both sexes of the macropters undergo a period of fasting after they develop to adults; during this time their gonads stay underdeveloped and they show a vigorous walking activity (dispersal phase, “macropterous morph related reproduction arrest”, SOCHA and ŠULA, 1996). Non-diapusing brachypters start feeding shortly after they emerge as adults, and brachypterous females start ovipositing much earlier than macropterous females (HONĚK, 1985; SOCHA and ŠULA, 1996). Brachypterous females are also more receptive, and copulate more than macropters do (SOCHA, 2004b), but this not necessarily means greater reproductive output for females. Reproductive advantage of the male brachypters is manifold: young macropterous males are more often rejected both by brachypterous and macropterous females (SOCHA and ZEMEK, 2004a); so young brachypterous males copulate more often than the young macropterous males (SOCHA and ZEMEK, 2004b). Moreover, the greater fertility of the young brachypterous males has also been documented (SOCHA and ZEMEK, 2008). Male fertility (and perhaps attractiveness ???) is probably related to the size of their male accessory glands, with mature earlier in brachypterous males (SOCHA and ZEMEK, 2008). There is also some compensation, as older macropterous males are more successful both in terms of copulation activity and fertility than brachypters of the same age group (SOCHA and ZEMEK, 2004b; 2008). Earlier reproduction onset of the brachypterous form of both sexes is even more emphasized by the shorter nymphal development of the brachypters. Some documented physiological differences between macropters and brachypters related with the above-mentioned functional differences are: the amount of hexameric storage protein in the haemolymph (ŠULA et al., 1995; SOCHA and ŠULA, 1996), feeding and digestive enzyme activities, the level of glycogen and lipids in the fat body (SOCHA et al., 1997, 1998) and the response to the adipokinetic hormone (SOCHA and KODRÍK, 1999).

An interesting fact is that the diurnal walking and sexual activity peak period for *P. apterus* macropters precedes with approximately 2 hours that of the brachypters (SOCHA and ZEMEK, 2000b; 2004).

HONĚK (1979, 1986b, 1987) and SAKASHITA et al. (1998a) selected *Pyrrhocoris apterus* and *P. sibiricus* both for macroptery and brachyptery. No 100% macropterous populations have

been obtained by selection at neither species, as an equilibrium state with 70-90% of macropters emerged after several generations. In contrast fully brachypterous populations can be rapidly obtained by directional selection.

Selection of *Pyrrhocoris apterus* for macroptery decreases the sensitivity to the photoperiod, but the length of the critical photoperiod does not change (HONĚK, 1979).

Seed bugs: Lygaeidae

KLAUSNER et al. (1981) report the spontaneous appearance of brachypters in the laboratory cultures of the large milkweed bug, *Oncopeltus fasciatus* (Dallas, 1852). No brachypterous or dimorphic populations of this widespread and apparent species are known in the wild; not even on the Guadeloupe Island, from where the mentioned laboratory cultures originated. The authors demonstrated with crossing experiment that this brachyptery is inherited by the simple, Mendelian way, so the recessive allele causes brachyptery. The presence of a wing length variance among the brachypters however signals the effects of modifying factors.

SOLBRECK and ANDERSON (1989) report a remarkable similar case at *Spilostethus pandurus* (Scopoli, 1763). This is also a widespread, apparent and well-known species, with no cases of brachyptery known from any natural population. However, in a laboratory culture, which originated from Crete (Greece) some brachypters appeared in the second laboratory generation. This case of brachyptery is also linked to a single, recessive gene according to the crossing experiments of the authors, although epistatic effects probably occur. In this case the fecundity, longevity, and other life history components of the brachypters were compared with those of the normal winged individuals, and no significant differences have been found. The authors also emphasize, that *S. pandurus* brachypters have fully developed flight muscles, which they do not histolyse.

These simple and rigid, “primitive” cases of wing dimorphism caused by a single mutation are very different from the sophisticated cases of the environmentally sensitive wing polyphenism seen at water striders (Gerridae), at *P. apterus*, at different blissid species, at *Jadera* spp. and in general, at most wing polymorphic hemimetabolous insect species. However, there is at least one known case, where a simple, genetically rigidly determined wing polymorphism exists in wild populations of a heteropteran species.

Horvathiolus gibbicollis (Costa, 1882) belongs to the same subfamily (Lygaeinae) as *O. fasciatus* and *S. pandurus*. *H. gibbicollis* has a brachypterous and a macropterous form. SOLBRECK (1986) demonstrated with crossing and rearing experiments, that this wing dimorphism has also a simple, Mendelian inheritance, unaffected by environmental factors (effects of food, temperature and nymphal density have been tested). In this case, the dominant allele causes brachyptery. However, in sharp contrast with the *S. pandurus*, *H. gibbicollis* brachypters show the usual pattern of quicker nymphal development, and shorter adult pre-oviposition period related to that of the macropters. The author emphasises, that there is an underlying, environmentally flexible flight muscle polymorphism which completes the rigid wing polymorphism. Unlike brachypters, most of young macropters of *H. gibbicollis* have well developed flight muscles, and most of the males retain them during their life. Most of the females, however histolyse their flight muscles if they are well fed and mated when they start ovipositing. Starved and/or virgin females retain their flight muscles.

WEI (2011, 2014) describes the wing polymorphism of *Nysius huttoni* White, 1878, a lygaeid belonging to the Orsilinae subfamily. *N. huttoni* has three wing forms, termed macropterous, sub-brachypterous and brachypterous by the author. According to him, the brachypter is flightless, the other two forms can fly. The ratio of the wing morph can be influenced by temperature and photoperiod, however, in any case, flightless brachypters form only a minority of the natural populations.

Chinch bugs: Blissidae

Wing polymorphism is markedly prevalent in this bug family. However only a few species have been studied in detail.

The oriental chinch bug - *Cavelerius saccharivorus* (Okajima, 1922) is a wing polymorphic pest of the sugar cane in East Asia. Aspects of wing polymorphism of *C. saccharivorus* have been systematically studied in Japan (FUJISAKI, 1985; 1986; 1989 a,b; 1992; 1993).

C. saccharivorus has both macropterous and brachypterous individuals, but these two forms are not discrete as there is a considerable variation in wing length and a low number of individuals with intermediate wing lengths exist (FUJISAKI, 1989a).

The wing polymorphism of *C. saccharivorus* is polyphenism, as temperature, photoperiod and crowding experienced in the sensitive periods of nymphal development have strong effect on the frequency of macropters (FUJISAKI, 1989b). However, there is also a significant genetic background, revealed by breeding experiments (FUJISAKI, 1986a), because under the same environmental conditions macropterous parents produce more macropterous offspring than brachypterous parents. It is straightforward to attribute adaptive significance of the environmental cues determining the wing form. A clearly recognizable seasonal polymorphism and a very apparent concurrent polymorphism can be distinguished. *C. saccharivorus* is trivoltine in Japan. The second, summer generation is the most dispersing, and contains many macropters, induced by high temperature and long daylengths. Weather conditions in the spring and in the autumn are less favourable for dispersal by flight, so the spring and the autumn generations are mostly consisted of brachypters. Large densities of *C. saccharivorus* can turn the local conditions very unfavourable, by seriously damaging or even killing the host plant. So, macroptery induced by high nymphal density helps the individuals to leave the overexploited habitat patches and colonize new ones.

A special feature described only at *C. saccharivorus* is, that high nymphal densities cause not only a high number of macropters, but also several „extreme” brachypters, which have shorter wings than the usual brachypters produced at low nymphal densities (FUJISAKI, 1989b).

Both female and male brachypters start reproducing earlier than the macropters (FUJISAKI, 1986b; 1992). However, the supposed reproductive advantage of the brachypterous females is not unequivocal in *C. saccharivorus*. Under low population densities the population is consisted mainly of brachypters, and these brachypters indeed produce more eggs than the macropters, which appear in large numbers only at high population density. However, if the three morphs present in the populations produced by nymphal density stress are compared, then macropterous females (which are also larger) produce more eggs than normal brachypters, although less than the „extreme” brachypters (FUJISAKI, 1986).

Brachypterous males also mature sexually earlier than macropterous males (FUJISAKI, 1992).

In the breeding experiments the female offspring contained more macropters than the male offspring (FUJISAKI, 1993).

Laboratory experiments and field observations revealed a similar pattern at *Dimorphopterus japonicus* (Hidaka, 1959), a wing dimorphic Oriental blissid bug living on the chinese silver grass (*Miscanthus sinensis* Andersson). *D. japonicus* is univoltine in Japan, and long photoperiod, warm temperature and high nymphal density raise the proportion of macropters (SASAKI et. al, 2002, 2003).

The biology of the European wing-dimorphic blissid, *Ischnodemus sabuleti* Fallén, 1826 was studied in detail by TISCHLER (1960, 1963) in Germany. Derived from field observations TISCHLER concludes, that high population density probably causes a high percentage of macropters in this species too. It is highly probable, that a multi-factorial wing form determination, alike in the case of *C. saccharivorus* operates at *I. sabuleti*, with crowding effect

being one of the determining factors. Field observations of the author (GIDÓ, unpublished) in Hungary corroborate this statement. *I. sabuleti* is mainly univoltine in Central Europe (Germany, Hungary), although this may alter soon due to the climate change. However, the oviposition period is rather long, so the appearance of the new adults starts in early autumn and – as a considerable portion of nymphs overwinter – ends in the spring of the next year. Nymphs hatching in early summer are exposed to quite different temperature and photoperiod effect compared to those hatching in mid-autumn during to their supposed sensitive period. So, the existence of a seasonal wing polymorphism at *I. sabuleti* is quite possible despite its univoltine life cycle. TISCHLER (1963) also mentions that he found eggs in young brachypterous females when at the same time the ovaries of the macropters were immature. So, it is highly probable, that the reproductive superiority of the brachypterous females is also present in *I. sabuleti*.

Seasonal changes in wing dimorphism of the American Southern chinch bug *Blissus insularis* Barber, 1918 were also reported (CHERRY, 2001). CHERRY and WILSON (2003) found a positive correlation among the population density and the ratio of macropters and observed the reduced fertility of macropterous females in *B. insularis*.

Soapberry bugs (Jadera spp., Rhopalidae)

The red-shouldered soapberry bug: *Jadera haematoloma* is increasingly becoming a widely investigated model species for the rapid evolution of different genetic, physiological, morphological and life history traits caused by recent host plant change. *J. haematoloma* originally occurred from the Southern United States, throughout Central America to Columbia and Venezuela. Native populations in Florida have been most intensively studied. Today the *Koelreuteria* adapted ecotype of *J. haematoloma* successfully colonised most parts the USA with temperate climate.

Jadera spp. are oligophagous seed predators of the soapberry family (Sapindaceae). In Florida, the native host plant of *J. haematoloma* is the balloon vine – *Cardiospermum corindum* (L.) In the 1950s soapberry bugs in the USA started to exploit the seeds of the introduced East-Asian goldenrain tree species: *Koelreuteria elegans* Seem. and *K. paniculata* Laxm. Nowadays there are morphologically more or less distinguishable *J. haematoloma* ecotypes feeding on *Cardiospermum* and *Koelreuteria*, as outstanding models for microevolutionary change and speciation. The two forms still hybridise, but the nymphs of *Koelreuteria* ecotype show poor survival if they feed on *Cardiospermum* seeds. The effects of the host plant speciation to the wing dimorphism of the *J. haematoloma* are described and discussed by DINGLE and WINCHELL, (1997); WINCHELL et al. (2000), CAROLL et al. (2003) and FAWCETT et al. (2018).

J. haematoloma displays an apparent wing dimorphism, with well distinguishable brachypterous and macropterous morph. However, there is also an underlying wing muscle dimorphism with three dispersal types of macropters. Some macropters – like all the brachypters – never develop functional flight muscles. Others have functional flight muscles (and are capable to fly) during the young adult age, but histolyse their flight muscles and become flightless when they start to reproduce. The third type of macropters retains its flight muscles and flying ability during their whole adult life.

The mild climate of Florida allows year-round reproduction of *J. haematoloma* if food source is available. *Cardiospermum* plants breed asynchronously, providing a year-round availability of seeds. However, the quantity of the seeds produced by a single plant is not very large. In contrast, the large *Koelreuteria* trees produce a huge number of seeds, but only between December and March in Florida, forcing a long reproductive diapause to the bugs.

The quicker maturation of the brachypterous females has been shown also in *J. haematoloma* (DINGLE and WINCHELL, 1997), although FAWCETT et al. (2018) found a statistically significant difference only in the *Koelreuteria* ecotype.

Theoretically *Cardiospermum* favours a higher percentage of macropters than *Koelreuteria*. After the depletion of the seeds of an individual *Cardiospermum* vine, flying bugs have a reasonable chance to find a new host plant with mature seeds, however, flying is useless against the seasonal, predictable depletion of available *Koelreuteria* seeds. So, the quicker reproduction characteristic to the brachypters looks a better strategy to exploit the seasonal, predictable food bounty provided by the *Koelreuteria* trees. However, in contrast with the pre-maturely published results based on limited amount of data (DINGLE and WINCHELL, 1997) in general there is no apparent difference between the macropter/brachypter ratios of the *Cardiospermum/Koelreuteria elegans* ecotypes in the wild populations (CAROLL et al. 2003; FAWCETT et al., 2018). Individual wild populations show a very high variance in macropter/brachypter ratio, even monomorphic short winged and long winged populations do occur. Contrary to all expectations there is a statistically significant difference between the populations living on the two introduced *Koelreuteria* species (*K. elegans* and *K. paniculata*). As populations living on *K. paniculata* contain significantly more brachypters than either of the populations living on *K. elegans* or on *Cardiospermum*, the combined data of the populations living on two *Koelreuteria* species significantly differs from that of the population living on the *Cardiospermum* in macropter/brachypter ratio. The latter fact seemingly supports the hypothesis that the macroptery is more frequent in the *Cardiospermum* ecotype (FAWCETT et al. 2018). However, this is a rather weak support, maybe an artefact, and the considerable difference among the two *Koelreuteria* species remains unexplained. The geographic location of the examined populations was not a significant explaining factor in explaining variation of the morph frequencies (FAWCETT et al. 2018).

However, there are more subtle, important differences between the ecotypes. CAROLL et al. (2003) found, that among the macropters of the *Koelreuteria* ecotype there are much more individuals which never develop functional flight muscles than among the macropters of the *Cardiospermum* ecotype. If this result will prove consistent in many/most populations that means that the ratio among dispersing/non-dispersing forms is still somewhat adapted to the host plant characteristics (food availability) even if this is not obvious regarding the externally visible wing dimorphism. However, considering that the host plant change occurred only recently, it might be not surprising, if the real situation doesn't correspond exactly to the theoretical predictions.

From the breeding and rearing experiments of DINGLE and WINCHELL (1997) is known, that the wing dimorphism in *J. haematoloma* has a strong genetic background, as there are large differences among the macropter/brachypter ratios of the different lineages ("families") even if raised under the same conditions. Wing morph determination is very likely polygenic at *J. haematoloma* (DINGLE and WINCHELL, 1997; FAWCETT et al., 2018).

Among the environmental factors affecting the wing form, the effect of photoperiod, nymphal density and food quantity has been documented; temperature doesn't seem to affect the wing form (DINGLE and WINCHELL, 1997; CAROLL et al., 2003). Both high nymphal density and low food quantities induce a larger proportion of macropters. However, there are large differences between the different lineages (families): the threshold values of the key environmental factors affecting the wing morph – especially the quantity of food – are very different, and this difference is heritable. There are large differences even between families belonging to the same ecotype, but the sensitive lineages are more common in the *Cardiospermum* ecotype than in *Koelreuteria* ecotype. Consequently, in general the ancestral *Cardiospermum* ecotype is reacting more readily the food scarcity with increased macropter ratio than the recently evolved *Koelreuteria* ecotype (DINGLE and WINCHELL, 1997; FAWCETT et al., 2018). FAWCETT et al. (2018) demonstrated with molecular experiments that the food level effects the wing morph involving the insulin-signalling metabolic pathway.

A surprising finding, that short-winged males has been found less fertile than the long-winged ones in the *Cardiospermum* ecotype. No difference has been found between the male fertility of the two wing forms in the *Koelreuteria* ecotype.

The closely related *Jadera aeola* (Dallas, 1852) is a neotropical bug, which seasonally aggregates and feeds on the fallen seeds of the plants of the soapberry family. Most populations of *J. aeola* are known to be monomorphic macropterous, but TANAKA and WOLDA (1987) found 2 dimorphic populations, with some sub-macropters. The earlier sexual maturation and greater fertility of the *J. aeola* sub-macropters has been experimentally proven. This dimorphism is known to be seasonal and environmentally induced as all the offspring of the short-winged adults became macropters. Nothing else is known about the wing dimorphism of this species. The authors suggest that the fast reproducing short-winged form is an adaptation to the rapid exploitation of the temporarily available abundant food resource (soapberry seeds) on the forest floor.

***Scaptocoris carvalhoi* (Digging bugs: Cydnidae)**

Scaptocoris carvalhoi Becker, 1967 is a neotropical, subterranean cydnid species, which exhibits wing dimorphism (NARDI et al. 2008). Only macropters can fly, but it is possible, that a portion of the macropters is also flightless. Both forms occur throughout the year, but the proportion of the macropters significantly increases before the beginning of the rainy season, when mass dispersal by flight (“swarming”) occurs.

***Leptoterna dolobrata* (Plant bugs: Miridae)**

The wing dimorphism of the meadow plant bug *Leptoterna dolobrata* (Linnaeus, 1758) was described by BRAUNE (1983) and reviewed by MUSOLIN and SAULICH (2021). Males of this species are all macropterous, while females are dimorphic. Usually brachypterous females are in majority, but a large number of macropterous females can be induced by exposing the nymph to high temperature and/or rearing them under crowded conditions. Brachypterous females mature earlier than the macropterous females.

Some related topics

Wing muscle reduction and self-mutilation (de-alation)

The effects of natural and artificial de-alation were mostly studied on crickets (Orthoptera, Gryllidae) and the main results are reviewed in TANAKA (1994). Some species of crickets usually shed their hind wings after an initial period, other cricket species do not. Natural self de-alation of the crickets usually occurs somewhat after that they start ovipositing, in some cases even after the peak oviposition period. In some crickets – including even species, where natural de-alation is unknown – artificial de-alation induces flight muscle histolysis and rapid egg production. However, different injuries (other than de-alation) are known to produce similar effect in some other insect species: for example, the amputation of some legs induces precocious sexual maturity in the migratory locust *Schistocerca gregaria* Forsskål, 1775. TANAKA (1994) concludes, that the natural de-alation in the crickets is rather a consequence than a causing factor of the transition from the migrating life period to the reproductive life period.

There are only a relatively few known cases of full or partial de-alation among Heteroptera.

Shedding of the wings is reported to be common in Enicocephalomorpha, Mesoveliidae, Veliidae, and occurring in some Aradidae (SCHUCH and SLATER, 1995).

According to HONĚK (1976a) macropters of the *Pyrrhocoris apterus*, the membrane tends to break off after the gonads have become active. Interestingly enough, this is the only record of the natural, partial de-alation in the vast literature of the *Pyrrhocoris* wing dimorphism. Macropters of *P. apterus* histolyse their flight muscles before the maturation of the ovaries (see above), so presumably – like in the crickets – de-alation is not the natural causal factor of the flight muscle histolysis and ovarian maturation. However, more accurate data about the frequency and timing of the *P. apterus* natural de-alation would be very informative.

Artificial de-alation of macropterous *P. apterus* right at the beginning of the adult stage causes the significant shortening of the pre-oviposition period (SOCHA, 2007). Simultaneously, de-alation also accelerated the histolysis of the flight muscles (SOCHA and ŠULA, 2008), so most probably the flight muscle histolysis and the ovarian development are also physiologically linked in *P. apterus*, and presumably in many other heteropteran species.

However – as known in some other insects as well – different other injuries, like sham operations have similar effect on *P. apterus* macropters (HODKOVÁ and SOCHA, 2006; SOCHA and ŠULA, 2008) The injury signal is transmitted to the neuroendocrine complex via the nervous system. It induces a higher food intake necessary for repairing and healing of the injured tissues, and subsequently removes the inhibition of the corpus allatus, which was temporarily suppressed in spontaneously fasting macropterous adults via the nervous connections from the brain (HODKOVÁ and SOCHA, 2006; SOCHA, 2007). It is important to note, that at *P. apterus* de-alation has a much stronger effect on flight muscle histolysis than the sham operations (SOCHA and ŠULA, 2008). It would be interesting to know, how specific is the physiological effect of de-alation on flight muscle histolysis and gonad development.

Older macropters of *Ischnodemus sabuleti* go through almost without exception in a partial de-alation process (GIDÓ, unpublished). That meant the elimination of the membrane, and serious damage of the hind wings. In Hungary the first de-alated individuals appear in early April and from the end of May hardly any full winged macropters occur. De-alated bugs survive until midsummer; they are active and mate frequently. Whether this de-alation is a result of an active self-mutilation (possibly rubbing the membrane with the hind legs) or it is simply the outcome of the vigorous flying activity is not known yet. Also, the possible connections of the de-alation with the flight muscle histolysis and gonad development are under investigation.

Wing dimorphism in agricultural pests

Among the wing-polymorphic blissids studied in detail the oriental chinch bug *Cavelerius saccharivorus* is a serious pest of sugarcane. The mixed dispersal strategy permits both the long-term survival of the low-density populations and also the the rapid expansion of the pest from the local outbreak centers. The southern chinch bug (*Blissus insularis*) is a pest of the St. Augustinegrass *Stenotaphrum secundatum* (Walter)Kuntze which is cultivated as a lawn in Florida.

The European *Ischnodemus sabuleti* has apparently a very similar dispersal strategy as *C. saccharivorus* and *Blissus insularis* but its primary host plants are mainly non-cultivated Poaceae (*Glyceria* spp.; *Ammophila* spp.; *Phragmites australis*, *Elymus* spp.). So, this species invades cereal fields only occasionally, when an unusually strong local outbreak forces the bugs to utilize also secondary host plants, including cultivated cereals (LAUENSTEIN and ÜBER, 1974).

The polyphagous wheat bug (*Nysius huttoni*) is an occasional pest of the maturing wheat and Brassica seedlings on drier summers in its native country, New Zealand. This bug was recently accidentally introduced to Western Europe, where it successfully established on different weed hosts, but until now no serious damage on European crops is attributed to this species. Its wing polymorphism (discussed above) has virtually no effect on its economic importance, as flight incapable brachypters form only a small minority of any population.

Scaptocoris carvalhoi is a polyphagous root parasite damaging different crops: soybean, cotton and pasture species in Brazil (NARDI et al, 2008). Its seasonal wing polymorphism helps this species in effective colonising of the new fields.

Discussion and conclusions

A general characterization of the Heteropteran wing dimorphism/polymorphism deduced from the published reviews and research articles.

Wing dimorphism/polymorphism among Heteroptera (like in most hemimetabolous insect groups) is in the most cases polyphenism, as different, specific environmental factors acting during the critical, sensitive period of the nymphal development strongly affect whether macropters or non-macropters emerge from the nymphs of a given genotype. However, environmentally unsensitive, strictly genetically determined cases of wing polymorphism also have been documented in the subfamily Lygaeinae

In the most cases the polyphenism has a strong, heritable genetic background, as different genotypes exposed to the same environmental factors during the nymphal development produce markedly different macropter/non-macropter ratios. This genetic variability is usually present and relevant both within the populations and among the different populations of the same species.

The normal, phylogenetically ancestral ontogenetic pathway is that one which leads to macroptery, and in the case of the wing polyphenic species this pathway can be diverted by different specific environmental cues, resulting non-macropterous individuals.

Genetic mutations can lead to exclusively non-macropterous genotypes (even species where all individuals have reduced wings are quite frequent among Heteroptera) or to genotypes with an altered sensitivity to the environmental factors influencing the wing form.

From functional point of view seasonal wing polymorphism and concurrent wing polymorphism can be distinguished. Seasonal wing polymorphism and concurrent wing polymorphism often co-occur and overlap in the same population, resulting a rather complex spatial and temporal pattern of macropter/non-macropter ratios.

Seasonal wing polymorphism is common in bi- and multivoltine populations, but it can be present even in the univoltine populations if the reproductive period is prolonged enough (a month or longer). The most important environmental factors causing seasonal polymorphism are the photoperiod and temperature experienced during the sensitive stage. Seasonal wing polymorphism – like other life history components e.g. voltinism, diapause, reproductive period etc. – often shows clear geographic trends which in most (but not all!) cases can be viewed as successful local adaptations.

The most often mentioned environmental factors affecting the concurrent wing polymorphism are nymphal density and/or the quantity and quality of food. Usually the high nymphal density and/or poor nutrition in the sensitive stage leads to an increased ratio of macropters, which allows mass emigration from the no longer favourable habitat spot.

The migration/reproduction trade-off (which means that individuals with better migration ability have inferior reproductive ability) has been demonstrated in many cases at the wing polymorphic Heteroptera. Usually, the macropterous individuals of both sexes require a longer time for sexual maturation, and sometimes even brachypterous females can produce less eggs than the non-macropters. Reproductive output of the males with different wing form has been less often investigated, but in some cases the greater mating success of the non-macropter form is documented. However, the earlier onset of reproduction of the non-macropterous form represents a considerable reproductive advantage in any cases.

Macropterous females of many insect species, including heteropterans, able and ready to fly when young, start the oviposition only after histolysing their flight muscles and losing their flight ability (“oogenesis – flight syndrome”, JOHNSON, 1969). This phenomenon occurs both in fully winged and wing dimorphic species (GUERRA, 2011, NAIR and PRABHU, 1985). In other cases (like at *Jadera haematoloma*) there are also macropterous individuals with never develop functional wing muscles. As being externally less apparent wing muscle polymorphism is much less documented than the externally visible wing dimorphism/polymorphism. However, its physiological and ecological significance might be the same or even larger. The frequent co-occurrence of the wing polymorphism and wing muscle polymorphism can easily lead to the functional misinterpretation of the former, if the latter is not considered.

In some species even macropters with functional flight muscles are unable or very reluctant to fly (FAIRBAIRN, 1986), while in other dimorphic species (like *P. apterus*) non-flying macropters are still the dispersing morph, being much more active walkers than the brachypters.

On evolutionary timescale wing-polymorphism can be a transitory stage of the pathway leading to the complete loss of flight ability or can be a state maintained by selection for its adaptive value in itself. On the evolutionary timescale wing polymorphism can be maintained by the frequent changing of environmental factors in space and time, which result that neither of the forms can maintain a long term advantage over the other/others. This condition favours both genetic diversity and fine-tuned developmental flexibility, which are both present at the wing dimorphic/polymorphic Heteroptera.

Comparisons between different lineages and between different trophic groups

Wing dimorphism/polymorphism is present in most of the heteropteran families; however, it is not evenly distributed across the different lineages. Wing dimorphism/polymorphism is quite common in several families (e.g. Nabidae, Gerridae, Blissidae), while it is rare or absent in other speciose families (e.g. Pentatomidae, Tingidae) (SCHUCH and SLATER, 1995). Considering either the occurrence of wing dimorphism/polymorphism in various distant lineages, either the morphologically or physiologically different forms, it is almost certain, that wing polymorphism appeared multiple times independently among Heteroptera.

In the most well documented cases the wing polymorphism is an environmentally affected polyphenism. Strictly genetically determined polymorphism has been documented only in Lygaeinae subfamily of Lygaeidae. It would be interesting to know, if this is a real peculiarity of the Lygaeinae subfamily (or of the Lygaeidae family) or rather there are plenty of undocumented cases of genetically strictly determined wing dimorphism in various other lineages, too. (Cases of the sexual wing dimorphism – which are of course genetically determined – are not considered here).

Some species rich lineages known to contain many wing dimorphic/polymorphic species (e.g. Nabidae, Reduviidae, Miridae) are very much underrepresented in the research of wing dimorphism/polymorphism, which might indicate, that the overall knowledge on heteropteran wing dimorphism/polymorphism is not only incomplete but also possibly biased.

An apparent seasonal wing dimorphism/polymorphism exists in most of the documented cases: as the northern temperate fauna is very much overrepresented in this research area, this is not surprising at all.

Effects of the nymphal density and food quantity/quality on the concurrent wing dimorphism/polymorphism are better known at some phytophagous species than in any of non-phytophagous ones. At gerrids the knowledge on the environmental factors affecting the concurrent wing dimorphism/polymorphism is scarce and ambiguous (see in GIDÓ, 2023).

Among phytophagous Heteroptera there is a well identifiable pattern of the concurrent wing polymorphism where the high frequency of the macropters is associated with the local population outbreaks: all documented blissid examples (*C. saccharivorus*, *I. sabuleti*, *D.*

japonicus, *B. insularis*) and *L. dolobrata* (and possibly many more undocumented cases of wing dimorphic mirid species) belong here. All these species feed on live plants, are gregarious and are able to damage seriously their food plants at high population density. The wing dimorphism of these species is highly sensitive both to the nymphal density and to the food quality. This pattern is also common in other hemipteran groups (like Delphacidae) with the same lifestyle (DENNO and PETERSON, 2000).

However, not all phytophagous, wing dimorphic/polymorphic Heteroptera fall in this category. The wing morph of the seed predator *J. haematoloma* is also sensitive to the food quantity and nymphal density, however unlike in the cases of the above-mentioned outbreak species, the percentage of the macropters in *J. haematoloma* is fairly high even at normal/low population densities. In the other well investigated cases of seed predator species, neither nymphal crowding, neither food quality/quantity effects the genetically determined wing form of *H. gibbicollis*, while it is not clear whether they have a significant effect on the wing morph of *P. apterus*.

In the future both deepening a widening of our knowledge in the field of insect wing dimorphism/polymorphism (including heteropterans) is needed. Deepening means the detailed (molecular level) understanding of the genetic and epigenetic causal factors and regulation of wing dimorphism/polymorphism of some “model species” selected from different heteropteran lineages. (For example, the exact roles of insect hormones -e.g. the juvenile hormone- in the wing form regulation are still not clarified). Widening meant the study of wing dimorphism/polymorphism also in the neglected phylogenetic lineages and also at the tropical species. Much more studies on wing muscle polymorphism are required as the understanding of insect dispersal polymorphism requires the simultaneous consideration of the wing polymorphism, the wing muscle polymorphism, and the behavioural polymorphism.

References

- ANDERSEN, N. M. (2000): The evolution of dispersal dimorphism and other life history traits in water striders (Hemiptera: Gerridae). *Entomological Science*, 3, 187–199.
- BRAUNE, H.J. (1983): The influence of environmental factors on wing polymorphism in females of *Leptopterna dolobrata* (Heteroptera, Miridae). *Oecologia*, 60, 340–347. <https://doi.org/10.1007/BF00376849>
- CARROLL, S. – MARLER, M. – WINCHELL, R. – DINGLE, H. (2003): Evolution of cryptic flight morph and life history differences during host race radiation in the soapberry bug, *Jadera haematoloma* Herrich-Schaeffer (Hemiptera: Rhopalidae). *Annals of the Entomological Society of America*, 96, 135–143. [https://doi.org/10.1603/0013-8746\(2003\)096\[0135:EOCFMA\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2003)096[0135:EOCFMA]2.0.CO;2)
- CHERRY, R. (2001). Seasonal wing polymorphism in southern chinch bugs (Hemiptera: Lygaeidae). *The Florida Entomologist*, 84, 737–739. <http://dx.doi.org/10.2307/3496417>
- CHERRY, R. – WILSON, A. (2003): Morphology and fertility of wing polymorphic adults of southern chinch bugs (Hemiptera: Lygaeidae). *Journal of Entomological Science*. 38, 688–691. <http://dx.doi.org/10.18474/0749-8004-38.4.688>
- DENNO, R. - PETERSON, M. (2000). Caught Between the Devil and the Deep Blue Sea, Mobile Planthoppers Elude Natural Enemies and Deteriorating Host Plants. *American Entomologist*. 46, 95–109. <https://doi.org/95-109>. 10.1093/ae/46.2.95
- DINGLE, H. - WINCHELL, R. (1997): Juvenile hormone as a mediator of plasticity in insect life histories. *Archives of Insect Biochemistry and Physiology*, 35, 359–373. [https://doi.org/10.1002/\(SICI\)1520-6327\(1997\)35:4<359::AID-ARCH2>3.0.CO;2-N](https://doi.org/10.1002/(SICI)1520-6327(1997)35:4<359::AID-ARCH2>3.0.CO;2-N)

- FAIRBAIRN, D. (1986): Does alary dimorphism imply dispersal dimorphism in the waterstrider, *Gerris remigis*? *Ecological Entomology*, 11, 355–368. <https://doi.org/10.1111/j.1365-2311.1986.tb00314.x>
- FAWCETT, M. M. – PARKS, M. C. – TIBBETS, A. E. – SWART, J.S. – RICHARDS, E.M. – VANEGAS, J. C. – CENZER, M. – CROWLEY, L. – SIMMONS, W. – HOU, W. – ANGELINI, D. (2018). Manipulation of insulin signaling phenocopies evolution of a host-associated polyphenism. *Nature Communications*, 16999. DOI: <https://doi.org/10.1038/s41467-018-04102-1>
- FUJISAKI, K. (1985): Ecological significance of the wing polymorphism of the oriental chinch bug, *Cavelerius saccharivorus* Okajima (Heteroptera: Lygaeidae). *Researches on Population Ecology*, 27, 125–136. <https://doi.org/10.1007/BF02515485>
- FUJISAKI, K. (1986a): Genetic variation of density responses in relation to wing polymorphism in the oriental chinch bug, *Cavelerius saccharivorus* Okajima (Heteroptera: Lygaeidae). *Researches on Population Ecology*, 28, 219–230. <https://doi.org/10.1007/BF02515451>
- FUJISAKI, K. (1986b): Reproductive properties of the oriental chinch bug, *Cavelerius saccharivorus* Okajima (Heteroptera: Lygaeidae), in relation to its wing polymorphism. *Population Ecology*, 28, 43–52. <https://doi.org/10.1007/BF02515534>
- FUJISAKI, K. (1989a): Morphometric traits of adults of the oriental chinch bug, *Cavelerius saccharivorus* OKAJIMA (Heteroptera : Lygaeidae), in relation to its wing polymorphism. *Applied Entomology and Zoology*, 24, 20–28. <https://doi.org/10.1303/aez.24.20>
- FUJISAKI, K. (1989b): Wing form determination and sensitivity of stages to environmental factors in the oriental chinch bug, *Cavelerius saccharivorus* Okajima (Heteroptera : Lygaeidae). *Applied Entomology and Zoology*, 24, 287–294. <https://doi.org/10.1303/aez.24.287>
- FUJISAKI, K. (1992): A male fitness advantage to wing reduction in the oriental chinch bug, *Calvellerius saccharivorus* Okajima (Heteroptera: Lygaeidae). *Population Ecology*, 34, 173–183. <https://doi.org/10.1007/BF02513529>
- GIDÓ, Z. (2023): Wing dimorphism/polymorphism in true bugs (Heteroptera) from a functional viewpoint: a review. Part I: Non-phytophagous species. *Journal of Central European Green Innovation*, 11, 39–54. <https://doi.org/10.33038/jcegi.4491>
- GUERRA, P.A. (2011): Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. *Biological Reviews of the Cambridge Philosophical Society*, 86, 813–835. <http://dx.doi.org/10.1111/j.1469-185X.2010.00172.x>
- HARRISON, R.G (1980) Dispersal polymorphisms in insects. *Annual Review of Ecology and Systematics*, 11, 95–118. <http://dx.doi.org/10.1146/annurev.es.11.110180.000523>
- HODKOVÁ, M. – SOCHA, R. (2006): Endocrine regulation of the reproductive arrest in the long-winged females of a flightless bug, *Pyrrhocoris apterus*. (Heteroptera, Pyrrhocoridae). *European Journal of Entomology*, 103, 523–529. <https://doi.org/10.14411/eje.2006.068>
- HONĚK, A. (1974): Wing polymorphism in *Pyrrhocoris apterus* (L.) (Heteroptera: Pyrrhocoridae): Influence of photoperiod. *Věstník Československé zoologické společnosti* 38, 241–242.
- HONĚK, A. (1976a): Factors influencing the wing polymorphism in *Pyrrhocoris apterus* (Heteroptera: Phyrhocoridae). *Zoologische Jahrbucher, Abteilung fur Systematik, Okologie und Geographie der Tiere*, 103, 1–22.
- HONĚK, A. (1976b): The regulation of wing polymorphism in natural populations of *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae). *Zoologische Jahrbucher, Abteilung fur Systematik, Okologie und Geographie der Tiere*, 103, 547–570.
- HONĚK, A. (1979). Independent response of 2 characters to selection for insensitivity to photoperiod in *Pyrrhocoris apterus*. *Experientia*, 35, 762–763.

- HONĚK, A. (1981): Temperature and wing polymorphism in natural populations of *Pyrrhocoris apterus* L. (Heteroptera: Pyrrhocoridae). *Zoologische Jahrbucher, Abteilung fur Systematik, Okologie und Geographie der Tiere*, 108, 487–501
- HONĚK, A. (1985): Ecophysiological differences between brachypterous and macropterous morphs in *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *Acta Entomologica Bohemoslovaca*, 82, 347–354.
- HONĚK, A. (1986a): Body size and fecundity in natural populations of *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae). *Zoologische Jahrbucher, Abteilung fur Systematik, Okologie und Geographie der Tiere*, 113, 115–140.
- HONĚK, A. (1986b): Inheritance of wing form in *Pyrrhocoris apterus*. *Journal of Heredity*, 77:465–467. <https://doi.org/10.1093/oxfordjournals.jhered.a110283>
- HONĚK, A. (1987): Wing polymorphism in *Pyrrhocoris apterus* (Heteroptera, Pyrrhocoridae): penetrance of recessive macropterous homozygotes and duration of larval development. *Genetica*, 73, 211–215. <https://doi.org/10.1007/BF00055276>
- HONĚK, A. (1995): Factors and consequences of a non-functional alary polymorphism in *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *Population Ecology*, 37, 111–118. <https://doi.org/10.1007/BF02515768>
- JOHNSON, C. G. (1969): Migration and dispersal of insects by flight. London, 763 pp.
- KLAUSNER, E. – MILLER, E.R. – DINGLE, H. (1981): Genetics of brachyptery in a lygaeid bug island population. *The Journal of Heredity*, 72, 288–289. <http://dx.doi.org/10.1093/oxfordjournals.jhered.a109502>
- KODRIK, D. – SOCHA, R (1999): A Mediterranean population of *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae) exhibits wing morph-related differences in adipokinetic response. *European Journal of Entomology*, 96, 327–330. <https://www.eje.cz/artkey/eje-199903-0014.php>
- LAUENSTEIN, G. – ÜBER, B. (1974): Occurrence of the bug, *Ischnodemus sabuleti* (Fallen) (Heteroptera, Blissinae) as an insect pest of cereals. *Gesunde Pflanzen*, 26, 229–231.
- MUSOLIN, D.L. – SAULICH, A.K. (2021): Seasonal development of plant bugs (Heteroptera, Miridae): subfamily Orthotylinae, Tribes Halticini and Orthotylini. *Entomological Review*, 101, 743–754. <https://doi.org/10.1134/S0013873821060026>
- NAIR, C. R. M. – PRABHU, V.K.K. (1985): Entry of proteins from degenerating flight muscles into oocytes in *Dystdercus cingulatus* (Heteroptera: Pyrrhocoridae). *Journal of Insect Physiology*, 31:383–88.
- NARDI, C. – FERNANDES, P. – BENTO, J. M. (2008): Wing Polymorphism and Dispersal of *Scaptocoris carvalhoi* (Hemiptera: Cydnidae). *Annals of the Entomological Society of America*, 101, 551–557. [https://doi.org/10.1603/0013-8746\(2008\)101\[551:WPADOS\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2008)101[551:WPADOS]2.0.CO;2)
- SAKASHITA, T. – FUJISAKI, K. – NAKASUJI, F. (1995): Environmental factors affecting wing length variation of a stink bug, *Pyrrhocoris sibiricus* (Heteroptera: Pyrrhocoridae). *Applied Entomology and Zoology*, 30, 303–308. <https://doi.org/10.1303/aez.30.303>.
- SAKASHITA, T. – NAKASUJI, F. – FUJISAKI, K. (1996): Definition of Wing Form and Morphometric Traits of the Adult Stink Bug, *Pyrrhocoris sibiricus* (Heteroptera: Pyrrhocoridae). *Applied Entomology and Zoology*, 31, 551–556. <https://doi.org/10.1303/aez.31.551>
- SAKASHITA, T. – NAKASUJI, F. – FUJISAKI, K. (1998a): Correlated response of nymphal period to selection for wing forms in the pyrrhocorid bug, *Pyrrhocoris sibiricus* (Heteroptera: Pyrrhocoridae). *Applied Entomology and Zoology*, 33, 143–145. <https://doi.org/10.1303/aez.33.143>

- SAKASHITA, T. – NAKASUJI, F. – FUJISAKI, K. (1998b): Seasonal variation in wing polymorphism of the pyrrhocorid bug, *Pyrrhocoris sibiricus* (Heteroptera: Pyrrhocoridae). *Applied Entomology and Zoology*, 33, 243–246. <https://doi.org/10.1303/aez.33.243>.
- SASAKI, R. – NAKASUJI, F. – FUJISAKI, K. (2002): Environmental factors determining wing form in the lygaeid bug, *Dimorphopterus japonicus* (Heteroptera: Lygaeidae). *Applied Entomology and Zoology*, 37, 329–333. <https://doi.org/10.1303/aez.2002.329>
- SASAKI, R. – NAKASUJI, F. – FUJISAKI, K. (2003): Seasonal changes in wing dimorphism of the lygaeid bug *Dimorphopterus japonicus* (Heteroptera: Lygaeidae) in relation to environmental factors. *Entomological Science*, 6, 63–70. <https://doi.org/10.1046/j.1343-8786.2003.00009.x>
- SCHUCH, R. T. – SLATER, J.A. (1995): True bugs of the World (Hemiptera, Heteroptera). Classification and Natural History. Cornell University Press; Ithaca & London, 337 pp.
- SMYKAL, V. – PIVARČI, M. – PROVAZNÍK, J. – BAZALOVÁ, O. – JEDLIČKA, P. – LUKŠAN, O. – HORÁK, A. – VANĚČKOVÁ, H. – BENEŠ, V. – FIALA, I. – HANUS, R. – DOLEŽEL, D. (2020): Complex Evolution of Insect Insulin Receptors and Homologous Decoy Receptors, and Functional Significance of Their Multiplicity. *Molecular Biology and Evolution*, 37, 1775–1789. <https://doi.org/10.1093/molbev/msaa048>
- SOCHA, R. (1993): *Pyrrhocoris apterus* (Heteroptera): a model species: a review. *European Journal of Entomology*, 90, 241–286.
- SOCHA, R. (2004): Decreased mating propensity of macropterous morph in a flightless wing-polymorphic insect, *Pyrrhocoris apterus* (Heteroptera). *European Journal of Entomology*, 101, 539–545. <http://dx.doi.org/10.14411/eje.2004.077>
- SOCHA, R. (2006): Endocrine control of wing morph-related differences in mating success and accessory gland size in male firebugs, *Animal Behaviour*, 71, 273–281, <https://doi.org/10.1016/j.anbehav.2005.07.029>
- SOCHA, R. (2007). Factors terminating ovarian arrest in long-winged females of a flightless bug, *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *European Journal of Entomology*, 104, 15–22. <https://doi.org/10.14411/eje.2007.003>
- SOCHA, R. (2008). Wing morph and age-related differences in fertilization success of adult males of a flightless bug, *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *European Journal of Entomology*, 105, 93–98. <https://doi.org/10.14411/eje.2008.013>
- SOCHA, R. (2013a): Latitudinal gradient in response of wing polymorphism to photoperiod in a flightless bug, *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *European Journal of Entomology*, 98, 167–169. <https://doi.org/10.14411/eje.2001.030>
- SOCHA, R. (2013b): Do long- and short-winged adult females of the bug *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae) differ in lifespan and reproductive capacity? *European Journal of Entomology*, 110, 115–121. <https://doi.org/10.14411/eje.2013.016>
- SOCHA, R. – KODRIK, D., (1999): Differences in adipokinetic responses of *Pyrrhocoris apterus* (Heteroptera) in relation to wing dimorphism and diapause. *Physiological Entomology* 24, 278–284. <https://doi.org/10.1046/j.1365-3032.1999.00143.x>
- SOCHA, R. – ŠULA, J. (1996): Differences in haemolymph proteins in relation to diapause and wing dimorphism in *Pyrrhocoris apterus* (L.) (Heteroptera: Pyrrhocoridae). *Journal of Comparative Physiology B* 166, 382–387. <https://doi.org/10.1007/BF02336921>
- SOCHA, R. – ŠULA, J. (2006): Flight muscles polymorphism in a flightless bug, *Pyrrhocoris apterus* (L.): developmental pattern, biochemical profile and endocrine control. *Journal of Insect Physiology*, 52, 231–9. <https://doi.org/10.1016/j.jinsphys.2005.10.009>
- SOCHA, R. – ŠULA, J. (2008): Regulation of the development of flight muscles in long-winged adults of the flightless bug *Pyrrhocoris apterus* (Heteroptera: Pyrrhocoridae). *European Journal of Entomology*, 105, 575–583. <http://dx.doi.org/10.14411/eje.2008.077>

- SOCHA R. – ŠULA, J. – KODRÍK, D. (2001): Sexual activity in macropterous and brachypterous males of a flightless bug, *Pyrrhocoris apterus* (Heteroptera). *European Journal of Entomology*, 98, 19–24. <https://doi.org/10.14411/eje.2001.003>
- SOCHA R. – ŠULA, J. – KODRÍK, D. (2004): Wing morph-related differences in developmental pattern of accessory gland proteins in adult males of *Pyrrhocoris apterus* (L.) and their endocrine control. *Journal of Insect Physiology*, 50, 893–901. <https://doi.org/10.1016/j.jinsphys.2004.07.001>
- SOCHA R. – ŠULA J. – ZEMEK R. (1997): Feeding, drinking and digestive enzyme activities in long- and short-day females of *Pyrrhocoris apterus* (Heteroptera). *Physiological Entomology*, 22, 161–169. <https://doi.org/10.1111/j.1365-3032.1997.tb01153.x>
- SOCHA R. – ŠULA J. – ZEMEK R. (1998): Feeding behaviour, digestive physiology and lipid content in macropterous females of *Pyrrhocoris apterus* (L.) (Heteroptera: Pyrrhocoridae). *Physiol. Entomol.* 23, 91–96. <http://dx.doi.org/10.1046/j.1365-3032.1998.2310091.x>
- SOCHA, R. – ZEMEK, R. (2000a): Wing Movement Behavior in Long- and Short-Winged Morphs of the Flightless Bug *Pyrrhocoris apterus* L. (Heteroptera: Pyrrhocoridae). *Journal of Insect Behavior*. 13, 741–750. <https://doi.org/10.1023/A:1007800212347>
- SOCHA, R. – ZEMEK, R. (2000b): Locomotor activity in adult *Pyrrhocoris apterus* (Heteroptera) in relation to sex, physiological status and wing dimorphism. *Physiological Entomology*. 25, 383–389. <http://dx.doi.org/10.1111/j.1365-3032.2000.00209.x>
- SOCHA, R. – ZEMEK, R. (2003): Wing morph-related differences in the walking pattern and dispersal in a flightless bug, *Pyrrhocoris apterus* (Heteroptera). *Oikos*, 100, 35–42. <https://doi.org/10.1034/j.1600-0706.2003.12100.x>
- SOCHA, R. – ZEMEK, R. (2004a): Mating behaviour and wing morph-related differences in the sexual activity of a flightless bug, *Pyrrhocoris apterus* (L.) (Heteroptera). *Ethology Ecology & Evolution*, 16, 217–229. <https://doi.org/10.1080/08927014.2004.9522633>
- SOCHA, R. – ZEMEK, R. (2004b): Wing morph-related differences in the pattern of mating activity in a flightless bug, *Pyrrhocoris apterus* (L.) (Heteroptera), *Invertebrate Reproduction & Development*, 46,1, 11–18, <https://doi.org/10.1080/07924259.2004.9652600>
- SOLBRECK, C. (1986): Wing and flight muscle polymorphism in a lygaeid bug, *Horvathiolus gibbicollis*: determinants and life history consequences. *Ecological Entomology*, 11, 435–444. <http://dx.doi.org/10.1111/j.1365-2311.1986.tb00322.x>
- SOLBRECK, C. – ANDERSON, D.B. (1989): Wing reduction; its control and consequences in a lygaeid bug *Spilostethus pandurus*. *Hereditas*, 111, 1–6. <https://doi.org/10.1111/j.1601-5223.1989.tb00368.x>
- ŠULA J. – KODRÍK D. – SOCHA R. (1995): Hexameric haemolymph protein related to adult diapause in the red firebug, *Pyrrhocoris apterus* (L.) (Heteroptera). *Journal of Insect Physiology*, 41, 793–800. [https://doi.org/10.1016/0022-1910\(95\)00025-P](https://doi.org/10.1016/0022-1910(95)00025-P)
- ŠULA, J. – SOCHA, R. – ZEMEK, R. (1998): Wing morph-related physiological differences in adults of temperate population of *Pyrrhocoris apterus* (L.) (Heteroptera: Pyrrhocoridae). *Comparative Biochemistry and Physiology*, 121, 365–73. [https://doi.org/10.1016/s1095-6433\(98\)10145-9](https://doi.org/10.1016/s1095-6433(98)10145-9)
- TANAKA, S. (1994): Evolution and physiological consequences of de-alation in crickets. *Researches on Population Ecology*, 36, 137–143. <http://dx.doi.org/10.1007/BF02514928>
- TANAKA, S., – WOLDA, H. (1987): Seasonal wing dimorphism in a tropical seed bug: ecological significance of the shortwinged form. *Oecologia*, 73, 559–565. <http://dx.doi.org/10.1007/BF00379416>
- TISCHLER, W. (1960): Studien zur Bionomie und Ökologie der Schmalwanze *Ischnodemus sabuleti* Fall. (Hem., Lygaeidae). *Zeitschrift für Wissenschaftliche Zoologie*, 163, 168–209.

TISCHLER, W. (1963): Weitere Untersuchungen zur Ökologie der Schmalwanze *Ischnodemus sabuleti* Fall. (Hem., Lygaeidae). *Zoologischer Anzeiger*, 171, 339–349. <https://eurekamag.com/research/024/131/024131613.php>

VEPSÄLÄINEN, K. (1978): Wing dimorphism and diapause in *Gerris*: determination and adaptive significance. In: DINGLE, H. (eds) *Evolution of Insect Migration and Diapause*. p. 218–253. Proceedings in Life Sciences. Springer, New York, NY. https://doi.org/10.1007/978-1-4615-6941-1_10

WEI, Y. J. (2011): Wing polymorphism in *Nysius huttoni* White (Hemiptera: Orsillidae). *New Zealand Journal of Zoology*, 38, 1–14, <http://dx.doi.org/10.1080/03014223.2010.532860>

WEI, Y.J. (2014): Flight initiation of *Nysius huttoni* (Hemiptera: Orsillidae) in relation to temperature and wing forms. *Applied Entomology and Zoology*, 49, 119–127. <https://doi.org/10.1007/s13355-013-0231-1>

WINCHELL, R. – DINGLE, H. – MOYES, C. D. (2000): Enzyme profiles in two wing polymorphic soapberry bug populations (*Jadera haematoloma*: Rhopalidae). *Journal of Insect Physiology*, 46, 1365–1373. [https://doi.org/10.1016/s0022-1910\(00\)00055-x](https://doi.org/10.1016/s0022-1910(00)00055-x)

Author

Dr. Zsolt Gidó PhD

assistant professor

Department of Environmental Sustainability

Institute of Environmental Sciences

Hungarian University of Agriculture and Life Sciences

H-8360, Keszthely, Deák Ferenc utca 16.

gido.zsolt@uni-mate.hu

A műre a Creative Commons 4.0 standard licenc alábbi típusa vonatkozik: [CC-BY-NC-ND-4.0](https://creativecommons.org/licenses/by-nc-nd/4.0/).

