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WING DIMORPHISM/POLYMORPHISM IN TRUE BUGS (HETEROPTERA) FROM A FUNCTIONAL VIEWPOINT: A REVIEW. PART I: NON-PHYTOPHAGOUS SPECIES

A SZÁRNY DIMORFIZMUS/POLIMORFIZMUS A POLOSKÁKNÁL (HETEROPTERA) FUNKCIONÁLIS NÉZŐPONTBÓL: ÁTTEKINTÉS. ELSŐ RÉSZ: NEM FITOFÁG FAJOK

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Abstract

In this review article the available information on the wing dimorphism/polymorphism occurring at non-phytophagous Heteroptera is reviewed from a functional viewpoint. This meant practically the information about the wing dimorphism/polymorphism of the superfamily Gerroidea, as hardly anything has been published on this theme of other non-phytophagous Heteroptera. Seasonal and concurrent wing dimorphism/polymorphism are treated and discussed separately. Heritability and phenotypical plasticity of the wing form, and the effects of different modifying environmental factors are briefly reviewed and discussed. The superior reproductive ability of the non-macropterous form is well documented at female gerroid bugs; there are less available data on the males. The seasonal wing polymorphism directed by photoperiod and affected by temperature is usually well adapted to the current environmental conditions. The effects of the population density and that of the food quantity and quality on wing form of the gerroid bugs have not been well understood yet; and it is arguable, whether the macropterous/non macropterous ratio of the natural gerroid populations corresponds to the temporal stability of their actual habitats in an adaptive way. Wing dimorphism/polymorphism has to be evaluated within the wider concept of dispersal polymorphism, which includes other related phenomena like wing muscle polymorphism and behavioural differences.

Keywords: *wing dimorphism/polymorphism; Heteroptera; Gerroidea; dispersal polymorphism; migratory syndrome*

Összefoglalás

Ezen áttekintő közlemény a nem fitofág poloskák (Heteroptera) szárny dimorfizmusát/polimorfizmusát funkcionális nézőpontból összegzi és elemzi a szakirodalom alapján. Ez gyakorlatilag a Gerroidea főcsalád szárny dimorfizmusának/polimorfizmusának tárgyalását jelenti, mivel szinte semmit nem közöltek az egyéb, nem fitofág poloskacsoportok szárny dimorfizmusáról/polimorfizmusáról. A közlemény az évszakos és az egyidejű szárny dimorfizmust/polimorfizmust elkülönítve kezeli és tárgyalja. Ismerteti a szárnyforma öröklődését és fenotipikus plaszticitását, beleértve a különböző módosító környezeti tényezők hatását. A nem-makropter forma szaporodási előnye jól dokumentált a Gerroidea főcsaládba tartozó poloskák nőstényeinél; jóval kevesebb adat áll rendelkezésre a makropter és nem-

makropter hímek reproduktív teljesítményéről. A fényperiódus által vezérelt és a hőmérséklet által befolyásolt évszakos szárny dimorfizmus/polimorfizmus általában megfelelő alkamazkodást mutat az aktuális környezeti feltételekhez. A populációsűrűség illetve a táplálék mennyiségének és minőségének a hatása a dimorph/polimorf Gerroideák szárnyformájára még nem tekinthető megfelelően tisztázottnak. Vitatható, hogy a természetes Gerroidea populációkban tapasztalható makropter/nem makropter arányok mennyiben tekinthetőek az aktuális élőhely időbeli stabilitására adott adaptív válasznak. A szárny dimorfizmus/polimorfizmus a vándorlási polimorfizmus tágabb összefüggésében értelmezendő, amely olyan jelenségeket is magába foglal mint a szárnyizom-polimorfizmus illetve a vándorlási hajlam.

Kulcsszavak: *szárny dimorfizmus/polimorfizmus, Heteroptera, Gerroidea, vándorlási polimorfizmus, vándorlási szindróma*

Introduction

Wing polymorphism (including wing dimorphism) of the insects is one of the most striking examples of the wider phenomenon known as dispersal polymorphism. Wing polymorphism has attracted the interest of the entomologists since the beginning of the scientific enterprise. Research on wing polymorphism yielded many important results, and still there are some unanswered questions left. The accumulation of knowledge is marked by the series of review articles published from the mid-twentieth century till nowadays (JOHNSON 1969; ROFF 1986; ROFF and FAIRBAIRN 1991; ZERA and DENNO 1997; RENAULT 2020;). Reviews that cover only a selected taxonomic group (*e.g.* aphids, carabid beetles) and/or a narrower topic (*e.g.* endocrinology of wing polymorphism, dispersal -reproduction trade off, , range expansion and invasive capacity of wing polymorphic insects) are still more numerous (some of the more recent and important are: BRAENDLE et al. 2006; GUERRA 2011, HARTFELDER and EMLEN 2012; VENN 2016; LIN and LAVINE 2018; GIDÓ 2022).

The suborder Heteroptera (true bugs) is a worldwide distributed insect group with appr. 40 000 species (SCHUH and SLATER 1995). Many species have serious economic impact as agricultural pests, a few also as human parasites and disease vectors. As wing polymorphism is quite widespread among different heteropteran lineages and very common in some groups (Nabidae, Gerridae, “Veliidae”, Blissidae), a considerable, although strongly biased research material has been accumulated on the heteropteran wing polymorphism. Most of the research has been done on some focal groups or species, like on the northern temperate species of the family Gerridae, or on the red firebug, *Pyrrhocoris apterus* (Linnaeus 1878) while virtually nothing has been published on the wing polymorphism of the other heteropteran groups.

Most heteropterans have well developed fore and hind wings and are able to fly. However, the partial or total reduction of the fore- and hind wings is common in different heteropteran lineages, thus many species have reduced wings and are unable to fly. When the different wing forms co-exist in the same species it is called wing dimorphism or polymorphism. In most cases – but not necessarily – it implies also flight dimorphism/polymorphism.

This paper reviews the published literature on heteropteran wing dimorphism from a functional viewpoint. The material has been divided in two parts for practical reasons. This first part discusses the information on the wing-polymorphism of non-phytophagous heteropteran groups, which practically meant the information on the wing dimorphism of the semi-aquatic bug superfamily Gerroidea due to the lack of the information about the other groups. The second part, discussing the wing dimorphism/polymorphism of the phytophagous Heteroptera is in preparation.

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. SCHUH and SLATER (1995) distinguish sub-macroptery, coleoptery, brachyptery, 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 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.

Review of the wing dimorphism/polymorphism of the different taxonomic groups

Superfamily Gerroidea: Gerridae + "Veliidae"

These two families form a distinct phylogenetic lineage which diverged from the rest of the gerromorph families during the mid-Triassic, around 200 million years ago (ARMISÉN et al., 2022). (According to the same work, the family Veliidae is not monophyletic, so it is not a valid family.) Wing polymorphism is very widespread among the Gerridae and "Veliidae", and it received considerable attention focused mostly on gerrids: EKBLOM 1941; GUTHRIE 1959; ANDERSEN 1973, 1993, 2000; VEPSÄLÄINEN 1971, 1974 a,b, 1978; VEPSÄLÄINEN and KRAJEWSKI 1974; JÄRVINEN and VEPSÄLÄINEN 1976; ZERA 1981, 1984; ZERA et al.1983 ; FAIRBAIRN 1986, 1988; SPENCE 1989; FAIRBAIRN and BUTLER 1990; KAITALA and HULDÉN 1990; ZERA and TIEBEL 1991; HARADA 1992; KAITALA and DINGLE 1992, 1993; HARADA and NUMATA 1993; INOUE and HARADA 1997; HARADA et al. 1997, 2005, 2011; HARADA and TANEDA 1998; HARADA and SPENCE 2000; AHLROTH et al. 2001; KISHI et al. 2003; SPENCE and ANDERSON 2003; PFENNING and POETHKE 2006; GOODWYN-FUJISAKI 2007; HARADA and NISHIMOTO 2007; PFENNING et al. 2007, 2008; FAIRBAIRN and DESRANLEAU 2008; FAIRBAIRN and KING 2009; HAN 2020; HYUN and HAN 2021; and somewhat less on "veliids" : MURAJI et al. 1989; MURAJI and NAKASUYI 1998; ARNQUIST et al. 2007; DITRICH et al. 2008; DITRICH and PAPÁCEK 2009; CIANFERONI and SANTINI 2012; MATSUSHIMA and YOKOI 2022;. Part of this immense research material has been briefly reviewed by ČERMAKOVÁ and DITRICH 2009.

Palearctic and Nearctic gerromorph species are very much overrepresented in the research of wing polymorphism. Unfortunately, very little had been published on wing polymorphism of the tropical gerrids and “veliids”: SELVANAYAGAM and RAO 1986; NUMMELIN 1997; ARNQUIST et al. 2007; KOVAC and KROCKE 2013; CUNHA et al. 2020.

The most recent and comprehensive phylogenetic analysis (ARMISÉN et al. 2022) corroborates the hypothesis that the ancestral state of the gerrid-veliid lineage was wing polymorphism (ANDERSEN 1993, 2000). Wing polymorphism appeared at least once more independently among gerromorph bugs, in the family Mesoveliidae.

Among gerrids and “veliids” there are macropters, brachypters, micropters and apters, depending on the species. SUN et al. (2018) described gene expression differences between the macropterous and brachypterous form of the gerrid *Gigantometra gigas* Hungerford & Matsuda, 1958.

Unfortunately, there isn’t any comprehensive knowledge on the genetic and ontogenetic processes leading to the wing polymorphism of any gerromorph species. Experimental works have been demonstrated that a considerable part of the wing polymorphism of different gerrid species is heritable (VEPSÄLÄINEN 1974a, 1978: ZERA et al. 1983; SPENCE and ANDERSON 2003). The large differences in macropter/non-macropter ratio among the different co-existing water strider species (VEPSÄLÄINEN 1974b; JÄRVINEN and VEPSÄLÄINEN 1976; SPENCE 1989;) and part of the strong geographic differences between the different populations of the same species (ALHROTH et al. 2001; FAIRBAIRN and KING 2009) are very likely explained by the genetic differences. Also, large part of the concurrent wing polymorphism (see above) can be probably explained with the individual, within-population genetic diversity, although the use of the term “genetic polymorphism” as a synonym of the “concurrent polymorphism” is not justified in the present state of knowledge.

Most of the genotypes present in natural populations show considerable phenotypic plasticity, as different environmental cues acting during the sensitive period of the nymphal development greatly affect whether macropterous or non-macropterous individuals emerge. Unlike in aphids (BRISSON 2010), but like in any other wing dimorphic/polymorphic insects (orthopterans, delphacids etc.) no maternal effects on the wing form are known among the heteropterans. The most important environmental factor affecting the wing form in gerromorph bugs is the photoperiod (VEPSÄLÄINEN 1971; ZERA et al. 1983; MURAJI et al. 1989; HARADA and NUMATA 1993; ZERA and TIEBEL 1991; INOUE and HARADA 1997; PFENNING and POETHKE 2006; GUDMUNDS et al. 2022;) which results an apparent seasonal polymorphism, well documented in some northern temperate species (VEPSÄLÄINEN 1974b; JÄRVINEN and VEPSÄLÄINEN 1976; PFENNING and POETHKE 2006; PFENNING et al. 2008). Critical daylength thresholds can differ greatly between different species, between different populations of the same species and – possibly – even between the different individuals of the same population. The effect of photoperiod can be modified by temperature and some other environmental factors causing a rather complex outcome. However – at least for the wing dimorphic, northern temperate gerromorph species – a general pattern of the seasonal wing polymorphism is identifiable.

Voltinism of the gerrid species depends on the climatic conditions of their actual distribution areas. So, generation numbers can change as a function of latitudinal gradients. As most of gerrids overwinter away from the water, the overwintering generation (which is the only generation in Northern Europe) is in the most cases fully macropterous (or at least predominantly macropterous), while the summer breeding generation (existing only in Central and Southern Europe) is wing dimorphic (JÄRVINEN and VEPSÄLÄINEN 1976). As demonstrated by PFENNING and POETHKE (2006) univoltine and bivoltine populations of the same wing dimorphic species – *Gerris lacustris* (Linnaeus, 1958) – can even co-exist very close to each other, due to the microclimatic differences. In Bavaria, Germany, sun-exposed warm ponds hold bivoltine, while shaded, cool forest ponds hold univoltine *G. lacustris* populations. While the adaptive value of the macroptery of the overwintering generation is quite easily understandable, considering the necessity of the migration to and from the overwintering sites, the great number of brachypters in the summer generation, when many of the ponds dry out is less easy to explain. PFENNING and POETHKE (2006) demonstrated, that *G. lacustris* brachypters develop considerably faster than their macropterous conspecifics, and so in Bavaria the length of the season available for activity, breeding and development allows two generations/year only if one of the generations is brachypterous, and this way reaches the reproductive age earlier.

However, this elegant model is not universally applicable to all wing dimorphic gerrids and "veliids", not even for all the northern temperate species. For example – like at *Gerris lacustris* – macropters of *Limnoporus canaliculatus* (Say,1832) has been reported to overwinter more successfully than the non-macropters (ZERA 1984), but at *Gerris asper* (Fieber, 1861) and *Aquarius najas* (De Geer, 1773) the opposite is recorded (EKBLOM 1941; AHLROTH et al., 1999). *A. najas* is even fully apterous in Northern Europe, while is wing dimorphic (with a small percentage of macropters) in Central and Southern Europe (AHLROTH et al. 1999). The apterous morph is the overwintering form also in *Microvelia douglasi* Scott, 1874 (MURAJI et al. 1989). No difference has been found between the overwintering success of the different wing forms at *Aquarius remigis* (Say, 1832) (AHLROTH et al. 1999).

FAIRBAIRN and KING (2009) demonstrated that the unusual high percentage of the macropterous *Aquarius remigis* in montane regions of California is induced by the temperature differences, independent of the photoperiod (as the photoperiod differences between the lowland and montane habitats of the same region are negligible).

The effects of the environmental factors on the concurrent wing polymorphism have been less clarified at Gerromorpha. Experimental tests on the effect of the food limitation are rare: PFENNING et al. (2007) reported that when food is limited, more brachypterous and less macropterous *G. lacustris* adults emerge. GUDMUNDS et al. (2022) found no effect of food quantity on the wing form of *Gerris buenoi* Kirkaldy, 1911.

Positive correlation between the ratio of macropters and the nymphal rearing density has been found at *Aquarius paludum* (Fabricius, 1794) (HARADA et al. 1997), *Microvelia douglasi* (MURAJI et al. 1989) and at the mesoveliid *Mesovelia furcata* Mulsant & Rey, 1852 (DITRICH and PAPÁCEK 2009). No effect of the nymphal density on the wing form has been demonstrated at *Limnoporus canaliculatus* (ZERA et al. 1983), while at *Gerris buenoi* the results are contradictory: both negative (HARADA and SPENCE 2000) and positive (GUDMUNDS et al. 2022) correlation of the nymphal density and the ratio of the macropters has been reported.

Up to the moment no effect of the nymphal habitat desiccation on the resulting wing form has been demonstrated, although it was only tested at *A. paludum* (KISHI et al. 2003) and at *Velia caprai* (Tamanini, 1947) (DITRICH and PAPÁCEK 2009).

The applicability of these experimental results for the natural conditions of the gerromorph bugs is also unclear. There isn't sufficient knowledge on how, when, where, how much and how often the population density affects the development and reproduction of the gerromorph bugs in the natural populations. Some authors (JÄRVINEN and VEPSÄLÄINEN 1976; PFENNING et al. 2007) suggest that natural gerrid populations are seriously food limited at least in a certain period of the year (late summer-early autumn in Europe). However, GUDMUNDS et al. (2022) found, that – unlike in the known cases of phytophagous hemipterans, including the heteropteran *Pyrrhocoris apterus* (Linnaeus, 1758) – the nutrition sensitive insulin signalling metabolic pathway is not involved in the ontogeny of the wing form of *Gerris buenoi*. The latter authors suggest that the wing form of predatory gerromorph bugs might be much less affected by the quantity and quality of the available food – and perhaps also by population density – than the wing form of phytophagous Heteroptera. Further research is needed to clarify this topic. It has to be remarked, that if kept under starvation, macropterous individuals of *Aquarius paludum* retain their flight muscles, which under natural conditions allows them to leave the unfavourable environment (HARADA and NISHIMOTO 2007).

The general model stating the reproductive superiority of the brachypterous females over the macropterous ones (ZERA and DENNO 1997) has been widely confirmed at the gerromorph bugs. Macropterous females are not necessarily inferior considering the lifelong fecundity, but in almost all cases examined, they start the oviposition later, than the faster developing brachypterous females (ZERA 1984; SPENCE 1989; HARADA, 1992; HYUN and HAN, 2021).

The usual life cycle of the northern temperate, bivoltine and trivoltine gerroid bugs, with the short-winged/dimorphic direct breeding generation(s) and the predominantly macropterous autumn generation which oviposits only after the diapause and migration to and from the overwintering sites adds a new aspect to the fertility differences of the gerroid wing morphs (HARADA and NUMATA 1993; HARADA and TANEDA 1998). INOUE and HARADA (1997) demonstrated at *Aquarius paludum insularis* that both the wing form and the direct breeding *versus* diapausing state are determined by photoperiod, but they are physiologically de-coupled, having different sensitive periods and threshold-values for the photoperiodic stimulus. This phenomenon allows a greater flexibility of life history and reproduction for the species, and probably is widespread among gerrids.

Many macropterous gerrid females histolyse their flight muscles, mostly before the full maturation of their ovaries (JÄRVINEN and VEPSÄLAINEN 1976; ANDERSEN 2000; KAITALA and HULDÉN 2008). More detailed quantitative information on many different species would be very useful in this regard.

The reproductive superiority of the brachypterous over the macropterous males is less often demonstrated, although the fierce and apparent sexual competition of gerroid males had been intensively studied. Mating superiority of the non-macropterous males has been explicitly demonstrated only in *Aquarius remigis* (KAITALA and DINGLE 1993) and *Microvelia horvathi* Lundblad, 1933 (MATSUSIMA and YOKOI 2022). HAN (2020) demonstrated at *Tenagogerris euphrosyne* (Kirkaldy, 1902) that under experimental conditions nymphal crowding leads to a larger proportion of macropters among the males than among the females. It is tempting to explain this difference with the supposedly much stronger intra-specific competition of the males, due to the strong sexual competition. This way emigrating from the crowded habitats it is probably more advantageous for the males than for the females. This should be also dependent on the sex ratio, as sexual competition among the males highly increases if the males outnumber the females.

A highly exceptional assortative mating system is described by ARNQUIST et al. (2007) in the Australian "Zeus bugs" (*Phoreticovelia rotunda* Polhemus and Polhemus, 2000 and *P. disparata* Polhemus and Polhemus, 2000, Veliidae). Apterous and macropterous morphs of the Zeus bugs strongly differ also in size and in reproductive behaviour; and in most cases apters mate with apters and macropters mate with macropters. There is no information on the fecundity differences between the two morphs, or on the extent of the gene flow among them. Except the *Phoreticovelia* species, assortative mating of the different wing morphs is not known to be characteristic to the wing dimorphic/polymorphic insects, including gerroid bugs.

It is tempting to link the adaptive value of the gerroid wing forms with the temporal stability of their aquatic habitats. Not surprisingly this has been discussed by many authors: JÄRVINEN and VEPSÄLÄINEN (1976); SPENCE (1989); ANDERSEN (2000). There is a widely accepted large-scale perspective, which works more or less well on species level and above. According to that view, long-term habitat stability (representative above all to marine habitats, but also to most of the lotic habitats and great ponds/lakes) favours the monomorphic (or almost monomorphic) non- macropterous species due to the reproductive advantages of the non-macropterous morph. Highly temporal aquatic habitats in contrast favour the exclusively macropterous species for obvious reasons (ANDERSEN 2000). However, there are also some exceptions. For example, FAIRBAIRN and KING (2009) reports, that the permanent high mountain streams in California (which can be considered as temporally relatively stable lotic habitats) are populated by an almost exclusively macropterous *Aquarius remigis* population, while the percentage of the brachypters on the temporary less stable streams at lower elevations is much higher. The authors explain this “anomaly” with the supposedly high adaptive value of the upstream compensatory migration by flight for the populations inhabiting the fast-flowing mountain streams with frequent torrential floods. It is worthy to note, that in California, even in the lowland regions, the percentage of *A. remigis* macropters is higher than in other parts of North America. As streams and rivers dry out less frequently in the temperate regions compared to California, this pattern fits well with the above-described general model of the wing form relation to the temporal stability (FAIRBAIRN and KING, 2009).

It is also not difficult to attribute an adaptive value to the seasonal polymorphism, providing a faster reproducing brachypterous/dimorph summer generation and a slower reproducing but more efficiently dispersing macropterous autumn generation of gerrids. The macroptery of the autumn generation is also an adaptation to the hibernation away from the water.

More challenging and interesting is to explain the maintenance of the genetic diversity underlying the concurrent polymorphism, which requires, that on an evolutionary timescale neither morph can have a long-term fitness advantage over the other. Rare macropters might persist in a large population for a long time, even if they have a fitness disadvantage (ROFF 1994). However, the long-term maintenance a more balanced proportion of macropterous and non-macropterous morph requires a more or less accurate fitness compensation on evolutionary timescale: the fitness gain of better dispersal ability must equate the fitness loss by inferior reproductive output of the macropters. Both from theoretical (ROFF 1994) and empirical or combined viewpoint (JÄRVINEN and VEPSÄLÄINEN 1976; SPENCE 1989; ANDERSEN 2000) is widely held, that these conditions occur when the habitat is discontinuous, the suitable habitat patches are moderately disconnected, and the temporal stability of the habitat patches is intermediate. (Too much isolation of the habitat patches favours monomorphic non-macroptery, as the chance of a successful immigration is very low).

Realising the considerable epigenetic plasticity of the wing form (discussed above), one might speculate a “properly flexible genotype” which is superior in any environment, as – reacting to the proper environmental signals – develops to a macropter or a brachypter, according to which one is favourable at that time in that habitat. Regarding the seasonal polymorphism, there is good evidence of a proper, highly adaptive, environmentally fine-tuned photoperiod specific plasticity of wing morphs, moreover HARADA et al. (2005) demonstrated, that the photoperiodic sensitivity of *Aquarius paludum insularis* can adapt rapidly and successfully to the climate change.

However, is not clear at all, whether gerroid nymphs show any adaptive wing morph plasticity regarding the temporary or permanent state of their habitat. In the few examined cases (see above) the desiccation of nymphal habitat had no effect on the wing form of the developing adults. Even results on the effects of the density-dependent or potentially density dependent factors on the wing form (nymphal density, food related effects) are few and equivocal (ČERMAKOVÁ and DITRICH 2009). Definitely much more and more precise empirical data is needed, but one might suppose that there is no effective phenotypical plasticity which adjusts the ratio of the gerroid wing forms to the temporary or permanent character of their actual habitat.

The “decision” of developing or not developing, and later of retaining or histolysing the wing muscles (“wing muscle polymorphism”) might or might not be more properly adjusted to the desiccation of the habitat and/or the density dependent effects. The few results available on the environmental plasticity of gerrid flight muscle polymorphism (KAITALA et al. 1989; KAITALA and HULDÉN 1990; HARADA et al. 1997; HARADA and NISHIMOTO 2007) are highly interesting, but too limited to be conclusive. These suggest that the gerrid wing muscle polymorphism is sensitive to density dependent (or at least potentially density dependent) factors (food availability, population density itself), and also that the environmental factors experienced both during the past nymphal development and during the current adult stage affect whether the wing muscles of the adults will be retained or not. Further research regarding this topic is desperately needed.

The fact, that many gerrid species are habitat generalists regarding the temporal stability of their habitats makes the real situation more complex and more stochastic. The landscape for a habitat generalist gerrid species is a mosaic of different lentic and lotic water bodies with different degrees of temporal stability. A flying macropterous gerrid female searching for a habitat to live and reproduce might observe the current size of the water surface, the amount of emergent and floating vegetation, perhaps might have a cue on the water depth (as might see or not see the light reflected from the bottom) the shaded or sunny character of the habitat, and – after the arrival to the surface – she experiences the temperature, the current velocity and the presence/absence of conspecifics. Any of these factors might affect her decision to enter, stay and reproduce there or leave that habitat. Either, because the scarcity of the suitable habitats, either because of the poor judgment of the real habitat quality, frequently many populations of generalist species end up in sub-optimal habitats. FAIRBAIRN (1985) convincingly demonstrated that the colonising *Aquarius remigis* individuals in Canada deliberately preferred the shaded cool stream environment to the sunny, warm pond environment, however they reproductive output of the stable pond population was considerably larger. It would be extremely interesting to know, if there is any genetic linkage between the wing form and active habitat choice among gerrids.

As the phenotypic plasticity of the wing form is probably not directly adjusted to the temporal stability of the habitat (KISCHI et al. 2003; DITRICH and PAPÁCEK 2009) and many gerrid populations live in sub-optimal habitats, one can suppose that the actual ratio of the macropters and non-macropters in a given habitat often strongly differs from that, what would be the local optimum.

Investigating several wing-monomorphic and dimorphic gerrid species has been found that the ratio of the macropters within a given species is positively correlated with the readiness of flight of the macropterous individuals. Also, macropters are less ready to histolyse their flight muscles in the gerrid species where the macropter form is in majority (FAIRBAIRN and DESRANLEAU 1987; FAIRBAIRN and BUTLER 1990). Similar phenomenon has been recorded also on intraspecific level: if numerous macropters of *Aquarius paludum* have been induced experimentally by high nymphal rearing density, then these macropters were more likely to retain their flight muscles than the usual, less abundant macropters (HARADA et al. 1997). The correlation of different aspects of dispersal capacity has been emphasised mainly by FAIRBAIRN (1994) who named it “migratory syndrome”. The “migratory syndrome” has also been documented in some other insect groups, like in carabid beetles (MATALIN 2003).

Even when the temporally stable environment clearly favours the non-flyer morph, maintenance of a very low percentage of macropters might be still advantageous, at least at population level. Rare macropters occur indeed in many, predominantly brachypterous, micropterous or apterous populations of gerromorph bugs and other, non-phytophagous heteropterans (e.g. Reduviidae). However, if they became already rare, macropterous genotypes can be easily lost, either simply by genetic drift or due to their fitness disadvantages on individual level. The result is the widespread occurrence of completely flightless heteropteran species in suitable habitats for a more sedentary lifestyle (SCHUH and SLATER 1995).

Other non-phytophagous groups

Although many wing dimorphic/polymorhic species are known to occur worldwide in various heteropteran lineages, including such predatory groups as Naucoridae, Nabidae or Reduviidae, almost nothing has been published on the biology of the wing dimorphism/polymorphism of non-phytophagous Heteroptera other than Gerroidea.

MONTEITH (1969) described the wing dimorphism of a New Guinean aradid species, *Caecicoris microcerus* (Walker, 1873). Aradids are fungal feeders. According to the author full winged aradid species usually occur under the bark of large dead tree trunks (spatially isolated and transient habitats) while the fully apterous ones live in the litter of the moist tropical forests (spatially continuous and permanent habitat). The author also speculates, that the apterous form is probably better camouflaged in its more open habitat. However, the habitat partitioning of the monomorphic macropterous and monomorphic apterous tropical aradid species is not applicable for the dimorphic *C. microcerus*, as both forms co-exist in the forest litter.

FRIÁS-LASSERRE et al. (2017) described the non-functional wing dimorphism (even macropters are flightless) of the parasitic, blood-sucking reduviid bug *Mepraia spinolai* (Porter, 1934). This species is a health concern in Chile, being one of the so-called “kissing bugs” transmitting the Chagas disease to humans. All females of *M. spinolai* are apterous, while males are either apterous or macropterous. In spite of their lack of flying ability, macropterous males still represent the dispersing morph, as they are much more active than the apterous males and females. (Very much as in non-functional wing dimorphic, phytophagous *Pyrrhocoris apterus*, except that in the latter, both sexes are wing dimorphic). So, despite their low infection rate, macropterous males are probably the main vectors of Chagas disease, because they are the most frequent visitors of the human houses.

Discussion

The externally visible macroptery does not necessarily imply the ability or the willingness to fly. Along the above discussed gerroid and reduviid examples many other cases are known among the non-phytophagous Heteroptera where the fully winged adults lack the flight muscles and thus, they are flightless (*e.g.* YOUNG 1965). Even if the macropters can fly, sometimes they are very reluctant to disperse by flight (FAIRBAIRN 1986). However – as seen in the case of the reduviid *Mepraia spinolai*, or at the phytophagous *Pyrrhocoris apterus* (GIDÓ, in prep.) – the flightless macropterous morph still can be the dispersal form of the species, macropters being much more agile walkers than the brachypters. Thus, the externally visible, and so, better documented wing dimorphism/polymorphism should be evaluated in the wider concept of dispersal polymorphism (RENAULT 2020).

At the state of art facts on wing dimorphism/polymorphism of non-phytophagous Heteroptera correspond fairly well with the general characteristics of the wing dimorphism/polymorphism in other hemipteran and hemimetabolous insect groups. However, the occurrence of wing dimorphic/polymorphic species in many distant heteropteran lineages (SCHUH and SLATER 1995) indicates that wing dimorphism evolved many times independently and quasi-independently among Heteroptera. Morphologically, genetically and functionally different kinds of wing polymorphisms may exist even on infraspecific level (for example the rare micropterous form of the *Pyrrhocoris apterus* along the common brachypterous and macropterous forms, SOCHA 1993). So, the study of the emerging model species for the hemipteran wing dimorphism – the brown rice planthopper, *Nilaparvata lugens* (Stål, 1854) (Delphacidae) and the pea aphid, *Acyrtosiphon pisum* Harris, 1776 (Aphididae) – might give some insight into the heteropteran wing dimorphism as well, but important differences are already known (ZHANG et al. 2019; SMYKAL et al. 2020; GUDMUNDS et al. 2022) and still many more will be likely revealed soon, as the knowledge on the genetic and physiological backgrounds of the different wing dimorphisms/polymorphisms grows. So, every specific case of wing polymorphism/dimorphism, interesting either from theoretical or economical point of view needs a case study on its own, to see where and how corresponds or does not correspond to the general tendencies deduced from the already known case studies.

For a more detailed and more accurate general view, comparative data on different heteropteran lineages is necessary. As reflected in this review, data on the wing dimorphism/polymorphism of non-phytophagous Heteroptera is very strongly biased taxonomically. Of course, from the immense taxonomical literature the occurrence of wing dimorphic and polymorphic species among the different heteropteran lineages is fairly well known. But, as seen above, while there are a plenty of papers on different aspects of gerroid wing dimorphism/polymorphism, almost nothing specific is known about the other non-phytophagous wing dimorphic/polymorphic groups. This is probably because few non-phytophagous heteropterans have considerable economic effects (the few human and livestock parasites are an exception). Gerroids represent a remarkable exception, as various aspects of their biology, including wing dimorphism/polymorphism attracted considerable research attention despite their complete economical insignificance.

As there isn't relevant information on the wing dimorphism on the other non-phytophagous heteropteran groups, one can compare the gerroids with the phytophagous Heteroptera, rather than comparing the non-phytophagous bugs with the phytophagous ones. Considering the phenotypic plasticity of the wing polymorphism (polyphenism) with a sensitive nymphal period, the reproductive disadvantage of the macropterous form, and the existence a seasonal polymorphism controlled by photoperiod and temperature there is a remarkable similarity between the gerroids and the phytophagous Heteroptera. However, these patterns are more or less generally widespread among the wing dimorphic/polymorphic Hemiptera and also in other wing-dimorphic/polymorphic hemimetabolous insects (like certain orthopteran species).

It is not clear, how much and how often the nymphal crowding and the food quality and quantity effects the wing form of the gerrids, while these effects are known to be very influential at the typical phytophagous wing dimorphic/polymorphic hemipterans like planthoppers (DENNO and PETERSON 2000), aphids (BRISSON 2010) or blissid bugs (FUJISAKI 1989). The dividing line might be not among the phytophagous and non-phytophagous heteropterans, as the wing form of the phytophagous seed predator, *Pyrrhocoris apterus* also doesn't seem to show strong connection with the population density or food quantity and quality. This question will be discussed more in details in GIDÓ (in prep.).

Conclusions

Further research should proceed in two directions. First of all, some of the neglected non-phytophagous lineages with many known cases of wing dimorphism/polymorphism (Nabidae and/or Reduviidae might be good candidates) should be examined in detail to see in which aspects their wing dimorphism corresponds to and differs from that of the gerroids and that of some better known phytophagous heteropteran species like *Pyrrhocoris apterus* or *Cavelerius saccharivorus* (Okajima, 1922). The other direction is – which is already in process – the deepening of our knowledge and understanding on the wing dimorphism/polymorphism of the gerrids. The great strength of the already existing knowledge on gerrid wing dimorphism/polymorphism is that we have comparative information on a handful of different gerroid species from Europe, Japan, and North America. On the other hand, there isn't an outstanding "model species" (like *Pyrrhocoris apterus* among phytophagous, wing dimorphic

Heteroptera) which has been very intensively studied from many various aspects. In-depth studies of physiology and molecular biology require such model species, and soon one or a few focal gerrid species will apparently emerge as models.

For the real understanding of the functional role of the wing dimorphism/polymorhism another aspects of the dispersal polymorphism – first and foremost the externally invisible flight muscle polymorphism and also the behavioural issues – also have to be studied in detail and evaluated together with the wing dimorphism/polymorphism.

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