RANGE EXPANSION AND INVASIVE CAPACITY OF THE WING DI- AND POLYMORPHIC INSECTS: A SHORT REVIEW

ZSOLT GIDÓ

Abstract

In this review article the invasive potential of wing dimorphic and polymorphic insects is discussed by presenting two case studies and overviewing the general knowledge of the dispersal abilities of these insects. Flying morphs of the wing dimorphic rice planthoppers Nilaparvata lugens and Sogatella furcifera continuously re-invade the rice fields in Japan and Northern China, where subsequent generations of dimorphic populations build up, causing several economic damages. The rapid range expansion of the wing dimorphic bush cricket Metrioptera roeselii in Central and Northern Europe in the 2000s was documented and extensively studied. These case studies are analysed, and the general relation of wing dimorphism and polymorphism and invasive potential is briefly discussed using the extensive knowledge on the wing dimorphism and polymorphism present in different insect orders.
Keywords: *wing polymorphism, wing dimorphism, insects, range expansion, dispersal*

A DIMORF ÉS POLIMORF SZÁRNYÚ ROVAROK FÖLDRAJZI TERJESZKEDÉSE ÉS INVÁZIÓS POTENCIÁLJA: RÖVID ÁTTEKINTÉS

Összefoglalás

Ez az áttekintő közlemény a szárny dimorfizmust vagy polimorfizmust mutató rovarok inváziós potenciálját tárgyalja. Két esettanulmányt ismertet és áttekinti a dimorf és polimorf szárnyú rovarok terjedési képességeivel kapcsolatos ismereteinket. A Nilaparvata lugens és a Sogatella furcifera dimorf szárnyú kabócafajok röpképes formái rendszeresen újrakolonizálják Japán és Észak-Kína rizsföldjeit, ahol aztán további dimorf szárnyú generációk fejlődnek ki, jelentős gazdasági kárt okozva. A Metrioptera roeselii (HAGENBACH, 1822) dimorf szárnyú szöcskefaj gyors közép- és észak-európai terjeszkedése a 2000-es években jól dokumentált és sokoldalúan megvizsgált jelenség. Ez a közlemény elemzi az említett két esettanulmányt, továbbá röviden tárgyalja a szárny-dimorfizmus – polimorfizmus és az invazív potenciál összefüggéseit, támaszkodva a különböző rovarrendekben előforduló szárny dimorfizmus és polimorfizmus kiterjedt irodalmára.
Kulcsszavak: *szárny-polimorfizmus, szárny dimorfizmus, rovarok, földrajzi terjeszkedés, vándorlás*

Introduction

Wing polymorphism (including wing dimorphism) of the insects is one of the most striking example of the wider phenomenon known as dispersal polymorphism. This apparent phenomenon occurs in many insect orders, and it is quite common in some groups (e.g. aphids, blissid bugs, water striders, orthopterans). 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, 1963; ROFF, 1986; ROFF and FAIRBAIRN, 1991; ZERA and DENNO, 1997; RENAULT, 2020). Reviews covering 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) are still more numerous (ZERA, 2004; BRAENDLE et al., 2006; VENN, 2007; GUERRA, 2011, HARTFELDER and EMLEN, 2012; and many others).

Earlier works mainly used an ecological-evolutionary approach, while nowadays in the „genomic age" became possible the deeper understanding of the genetics and the molecular ontogeny of insect wing polymorphism. This knowledge is at the moment still very scarce, and available only in a few selected „model" species: like the pea and aphid cotton aphids (*Acyrthosiphon pisum* Harris 1776, *Aphis gossypii* Glover 1877) and the rice planthoppers *Nilaparvata lugens* and *Sogatella furcifera*. However, exponential growth is expectable also in this area of research, and a synthesis of all aspects of wing polymorphism will be possible then (OGAWA et al., 2012; OGAWA and MIURA, 2014; YU et al., 2014; JI et al., 2021; ZHANG et al., 2022;).

Some of the wing dimorphic and polymorphic insects are serious agricultural pests, like many species of aphids and planthoppers on many different crops, or the oriental chinch bug (*Cavelerius saccharivorus* Okajima, 1922) on sugarcane (FUJISAKI, 1989).

Range expansions, sometimes called as invasions are some of the focal points of the recent applied entomological research. Due to the climate change and the worldwide transport of agricultural goods, the number and the significance of successful insect range expansions is expected to grow further during the next decades (PEŇA, 2013). The problem caused by invasive agricultural pests is one of the serious challenges of the modern applied entomology.

However, there are not many documented examples of range expansions of wing dimorphic or polymorphic insect species. In this review some case studies are presented and invasive potential of the wing polymorphic insects is discussed.

Terminology and coverage: wing polymorphism, wing polyphenism, dispersal polymorphism
As used in this review, wing polymorphism means that at least two different wing types are present within the same species, and, in most cases even in the same population. (Winglessness is also considered to be a „wing form"). The most common case is, that two distinct wing forms co-exist in the population. This is called wing dimorphism. These wing forms usually markedly differ also in flight capacity. The wingless (apterous) and in most cases the short winged (brachypterous) forms are unable to fly, while the full winged (macropterous) form is capable of flying. There are some remarkable exceptions to this general rule: for example, all individuals of the red firebugs - *Pyrrhocoris apterus* (Linnaeus, 1758), including the full winged ones are flightless, but even this way the macropters are more active, and have a better dispersal capacity (SOCHA, 1993). Much more important is, that in many species the macropterous form is capable of flying only for a limited time, as – usually before the full development of the gonads – it histolyses the flight muscles and converts them to reproductive resources. This is one aspect of the well-known „oogenesis-flight syndrome" (JOHNSON, 1969) and it is well documented

on some groups like waters striders (Gerridae, VÄPSALÄINEN, 1978) but it may be much more widespread than documented, as wing muscles are not visible externally.

Multiple wing forms (more than two) within a population have also been reported in different insect orders, e.g. *Cavelerius saccharivorus* (Hemiptera, Blissidae, FUJISAKI, 1989) or *Tetrix tuerki* (Krauss, 1876) (Orthoptera, Tetrigidae, PUSHKAR, 2009). For these cases the term wing polymorphism is used. Wing polymorphism, however, is an inclusive term, wing dimorphism being a sub-category of wing polymorphism.

Considering that substantial differences might occur in flight capability or flight behaviour of the full winged individuals, wing polymorphism has to be treated as a special case of a wider phenomenon, the dispersal polymorphism (HARRISON, 1980; RENAULT, 2020). The other types of dispersal polymorphism are not discussed here.

There are many cases when one of the sexes (the male in the *Blastophaga* fig wasps, the female in the winter moth *Operophtera brumata* Hübner, 1825 or in the order Strepsiptera) is apterous or brachypterous and flightless, while the other sex is macropterous and has ability to fly. These cases are not considered here as wing polymorphism and are not discussed.

Caste polymorphism of the social insects – although it includes wing polymorphism as well among termites: (Isoptera) and ants (Formicidae) - is not covered by this review. Solitary and gregarious morphs of the migratory locusts are also considered a more complex form of dispersal polymorphism and are not discussed here (PENER and SIMPSON, 2009).

Some authors use the term „wing polymorphism" only in those cases, when the wing form is 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.

Results

Case study I: Maintenance of the wing dimorphic rice planthopper pest populations of temperate East Asia by regular mass imigration from south

Two wing dimorphic planthopper species: *Sogatella furcifera* (Horváth, 1899) and *Nilaparvata lugens* (Stål, 1854); Hemiptera, Delphacidae) are serious pests of the rice in South-East Asia. These species are unable to overwinter in the northern part of their range, including Japan, so the northern populations are re-founded repeatedly by mass emigration of the winged hoppers from the south (KISHIMOTO, 1971; WU et al., 1994; WATANABE et al., 2009). An important difference is that while both sexes are wing dimorphic in *N. lugens*, in *S. furcifera* only the females are wing dimorphic, while males are usually macropterous (MATSAMURA, 1996).

Planthoppers, as small insects are weak flyers, so the efficiency of the mass immigration is very strongly influenced by the weather conditions. However, the topic of forecasting the annual damage expectable using the meteorological data and computer simulations is not discussed here (WATANABE et al., 2009).

All windborne colonizers are full winged, but subsequent generations quickly build up on the fresh rice fields of Japan and Northern China. These hoppers are both brachypterous and macropterous. The brachypterous form dominates when the rice plants are still fresh and growing. When the rice plants enter upon the phase of senescence, a generation containing a large amount of macropterous specimen emerge. Some of these are carried back by the winds to south, where they can overwinter.

It is widely accepted, that – as usual among the wing dimorphic insects – the brachypterous form of both rice planthopper species has a reproductive advantage over the macropterous form (LIN et al., 2018). So, the alternating generations of brachypters and macropters are very well fitted into the life cycle of an invasive species with the periods of mass reproduction, followed by mass migration.

The genetic and ontogenetic base of the wing dimorphism of both *N. lugens* and *S. furcifera* has been studied for decades, and this research gained new momentum in the recent years (MATSAMURA, 1996, 1997; SAXENA et al., 1981; YU et al., 2014; LIANG et al., 2016; GAO et al., 2019). As it is expectable in the case of such a fine-tuned plasticity, wing dimorphism of the rice hoppers is polyphenism. The development of macropters can be induced by different environmental effects experienced during the sensitive period of the nymphal growth. Macropter-inducing cues are: temperature, photoperiod, nymphal density and the quality of host plant (IWANAGA et al., 1985; IWANAGA and TOJO, 1986; LIN et al., 2017), the latter two are considered as most important. These ensure the mass appearance of the migrating form not only at the end of the growing season, but also, when and where a population outbreak devastates the host plants.

However, this polyphenism has a rather complex genetic background. The different genotypes co-existing in both *N. lugens* and *S. furcifera* are not equally sensitive to the above mentioned environmental cues (MATSAMURA, 1996; IWANAGA et al., 1986; ZHANG et al., 2022). As most genetic studies have been carried out in Japan and China, where the populations are consisted of a mixture of immigrants from different southern source populations (IWANAGA et al., 1986), it is still not clear how much relevant genetic variation exist within and between the self-sustaining tropical and subtropical populations. The intensity of the current research on these two economically significant planthopper species is very promising, and very likely it will reveal new, very interesting insights both from theoretical and practical viewpoints.

Case study II: Range expansion of the wing dimorphic Metrioptera roeselii bush cricket and some related species in Central and Northern Europe

The recent range extension of the wing dimorphic bush cricket, *Metrioptrera roeselii* (Hagenbach, 1822*)* in Central and Northern Europe got much attention (KINDWALL et al., 1998; BERGGREN, 2001; BERGGREN & al., 2001; BRUNZEL, 2002; SIMMONS and THOMAS, 2004; GARDINER, 2009; HOCHKIRH and DAMERAU, 2009; PONIATOWSKI and FARTMANN, 2009; WISSMANN et al. 2009; CASSEL-LUNDHAGEN et al. 2011; PONIATOWSKI et al. 2011 a, b; KANUCH et al. 2013, 2014; SZANYI et al., 2014; BECKMANN et. al., 2015), and revealed very interesting aspects of the dispersal biology of wing dimorphic insects.

PONIATOWSKI and FARTMANN (2009) have demonstrated experimentally that high nymphal density induces the high percentage of macropterous specimen also in *M. roeselii.* However, SIMMONS and THOMAS (2004) suggested, that there should be also a significant genetic component. Conclusive data on the interaction of genetic and epigenetic factors determining the wing morph of *M. roeselii* are still missing.

Range expansion of *M. roeselii* includes three different processes. There is a slow and steady penetration into the nearby habitats across the range borders without flight. This is performed by both brachypterous and macropterous individuals (WISSMANN et al. 2009). The steady dispersal by walk can be very effective through more or less continuous landscape but is unable to cross the natural and artificial barriers (forests, rivers, highways) (BERGGREN et al., 2001). Multiple, successful, unintended human introductions of *M. roeselii* far northwards from its former range with the transport of agricultural products have been demonstrated also by genetic

surveys (KANUCH et al., 2013). Of course, artificially introduced populations if once established, can rapidly expand further on their own.

The range expansion by flight performed by macropters is much more successful in crossing barriers, than the dispersal by walking. However, macropters are rare (several percentages) during most of the time in most of the populations. A certain density of migrating individuals is necessary for successful colonization, as less than 8-30 individuals arriving simultaneously in the same new habitat patch have very little chance to establish a new population (BERGGREN, 2001). So, natural range expansion across barriers is mostly expectable in the years of outbreaks, when the high population densities induce a high percentage of macropters. Such an event was documented in Germany, where the heat wave in the summer of 2003 resulted in rapid range expansion by flight of *M. roeselii* (HOCHKIRCH and DAMERAU, 2009). Thus, climate change facilitates in two ways the spread of *M. roeselii*: by creating new suitable habitats in Northern Europe and by increasing the number of the dispersing, macropterous form.

Wing dimorphic populations on the expanding range frontier seem to have some special characteristics as well. Newly established frontier populations contain an unusually high percentage of macropters, even if the population density is not high (SIMMONS and THOMAS, 2004; PONIATOWSKI and FARTMANN, 2011 b). However, this effect is temporary: after 5-10 years after colonisation the percentage of the macropters falls back to the former low level. The same pattern was also found at *Conocephalus discolor* (Thunberg, 1815), another wing dimorphic bush cricket, which has also been expanded its range (KLEUKERS et al., 1996; SIMMONS and THOMAS, 2004).

It is still not clear, why this pattern emerges in frontier populations. SIMMONS and THOMAS (2014) suggest, that macroptery has also a genetic component, and new populations established only by macropters produce more macropterous offspring as well. The return to the usual state can be explained by two distinct processes: the reproductive advantage of the brachypters over the macropters and the higher emigration rate of the macropters. A further possible advantage of the returning to the predominance of brachyptery in older populations is, that isolated populations, especially if they are also frontier populations can better adapt to the local optimum than interconnected populations (CASSEL-LUNDHAGEN et al., 2011).

Comparative data available about the related wing dimorphic species which are not invasive also hold some special interest. No high percentage of macropters in the field populations of *Metrioptera brachyptera* (Linnaeus, 1761), a closely related bush-cricket, have been ever documented. However, under experimental conditions, overcrowding caused an even higher percentage of macropters in *M. brachyptera* than in *M. roeselii* (PONIATOWSKI and FARTMANN, 2009). Seemingly, under the current environmental conditions *M. brachyptera* - unlike *M. roeselii* - cannot produce such population outbreaks, which might enable it to expand its range by producing a large number of macropterous colonizers.

Are wing polymorphic insects strong dispersers?

Considering the efficiency of having a separate dispersal form and a non-dispersing, fast reproducing form induced by the proper environmental cues, one might speculate, that wing dimorphic insects are very efficient dispersers. However, there are not too many known examples of invasive wing dimorphic or polymorphic insect species. (Invasive aphids might represent an exception, but the immense literature of invasive aphids does not link the invasive capacity with the wing dimorphism. Perhaps, because wing dimorphism is taken as a granted integral part of the complex aphid life cycle).

To understand, why wing polymorphic insects are not much better represented among the invasive species, one should consider that most of insect species are in fact wing monomorphic flyers, which meant, that most insects species are good or very good dispersers. For the majority

of insects, flight is not only necessary for long distance dispersal, but also to carry out the everyday tasks of collecting food (e.g. pollinators, dung and carrion feeders, aerial predators and some parasites, like mosquitos), escaping predators and/or finding sexual partners and/or proper places (e.g. host plants) for oviposition. Wing polymorphism is only an option for those insects which are able to carry out the above-mentioned tasks without flight and use the flight only for long distance dispersal.

One can even speculate, that even the macropterous morphs of the wing polymorphic species might be weaker and/or more reluctant flyers compared to their wing monomorphic macropterous relatives. The scarcity of data does not allow such a bold generalisation, but there are some results corroborating this hypothesis. MATALIN (2003) had shown with morphometric analysis that all-macropterous carabid species in Eastern Europe are stronger flyers, than the macropterous individuals of the wing dimorphic species. Moreover, the former species mostly retain their flight ability during their whole life, while macropters of the dimorphic species usually fly only during the young adult stage.

Sometimes the appearance of the wing dimorphism or polymorphism in a macropterous species can be even the first stage of the evolutionary process leading to the total loss of flying ability (DEN BOER et al., 1980). The existence of wing polymorphic, but entirely flightless species, like the familiar red firebug (*Pyrrhoris apterus*) clearly demonstrates this evolutionary pathway. Documented appearances of brachypterous, flightless mutants in monomorphic macropterous populations belonging to different insect species (e.g. KLAUSNER et al., 1981; SOLBRECK and ANDERSON, 1989, NISHIDE and TANAKA, 2013) also can mark the first step of this evolutionary processes. However, the wealth of the examples of fine-tuned wing polyphenisms adjusted properly to the environmental conditions especially among the hemimetabolous insects (see the reviews cited in Introduction) leaves no doubt, that wing polymorphism is not always a transitory stage towards the total loss of the flight ability, rather it can be also a highly adaptive life history strategy on its own.

Finally, it has to be mentioned, that many flightless insect species had been proved to be efficient dispersers (VENN, 2007).

So, wing dimorphic and polymorphic insects cannot be considered as exceptionally good dispersers among insects.

Are wing polymorphic insects resilient colonists?

Good dispersing abilities are far not enough for a species to be a successful invader. The survival and expansion abilities of the small, vulnerable founder populations are crucial for any range expansion.

Considering the above analysed case studies and many other examples from the reviews cited in the Introduction, the environmentally fine-tuned wing polyphenism can be highly adaptive, giving a considerable advantage for wing polymorphic populations to survive and expand.

However, other, less conspicuous forms of the dispersal polymorphism might be much more common, and at least equally effective than the externally also apparent wing polymorphism. For example, globally invasive fire ant species *Solenonopsis geminata* (Fabricius, 1804) and *S. invicta* Buren, 1972 show dispersal polymorphism of the reproductive queens. These species have heavier claustral queens and lighter parasitic queens, the latter is able to fly much longer distances (HELMS and GODFREY, 2016). The silent switch from the „dispersal phase" to the „reproductive phase", including the histolysis of the flight muscles is documented in many insect orders, and it can be very widespread (see the reviews in the Introduction). A marked flight-muscle dimorphism is also documented in some fully macropterous species (VENN, 2007). Behavioural polymorphism – the differences in the readiness to take flight and cover large distances – can be also very marked, but much more difficult to detect. A detailed discussion of this topic is presented by RENAULT (2020).

At the present stage of knowledge, it can be suggested, that a proper form of dispersal polymorphism – including wing dimorphism or polymorphism in some cases – can help the small founding populations in survival and expansion. Much further research is needed to clarify the role of wing dimorphism in the wider context of dispersal dimorphism.

Wing polymorphism is expected to persist in discontinuous environments, where the suitable habitat patches are not very much isolated, as too much isolation favours the complete loss of the dispersal flight (DENNO et al., 1996; AHLROTH et al., 2010). The temporary character of the habitats has an ambiguous effect, as favours full macroptery instead of wing polymorphism, but wing polymorphism instead of full brachyptery (DEN BOER et al., 1980; ANDERSEN, 2000).

Strong positive correlation was found in the great majority of the wing polyphenic insects between the high population density and the mass appearance of macropters (orthopterans, true bugs, planthoppers, aphids – see the reviews mentioned in the Introduction). So, the rapid spread out from the local outbreak centres is greatly enhanced by the wing polyphenism. Contrary, no density-induced macroptery was documented among the wing-polymorphic carabid beetles, where the wing form is primarily genetically determined (VENN, 2016).

It is suggested that many wing dimorphic and polymorphic species are in some way pre-adapted to the successful population establishment in the range frontiers, and if the other circumstances are favourable, can expand their range quickly and efficiently.

Pest management and wing polymorphism

The damage caused by the wing dimorphic and polymorph agricultural pests (aphids, planthoppers, blissid bugs) is strongly related to their dispersal capacity. Many of the serious wing dimorphic and polymorphic pests (rice planthoppers, oriental chinch bug) are gregarious species with local population outbreaks, and density dependent production of the migrating form (KISHIMOTO, 1979; IWANAGA et al., 1985; FUJISAKI, 1989; IWANAGA and TOJO, 1986; BRAENDLE et al., 2006; LIN et al., 2017). Monitoring the local outbreaks can be used or the prediction of mass migration waves, and prevention or at least the reduction of the local outbreaks can effectively hinder the invasions and range expansions.

There is not much knowledge on the direct effects of the agricultural management practices on the wing polymorphism of pest species, and other insects. The paper published of BAO et al., (2009) has a special interest, as the authors demonstrate that sub-lethal doses of some insecticides induce the production of macropters in the brown rice planthopper, *Nilaparvata lugens*, helping this way the spread of the pest species. As different physiological stresses are known to induce the production of macropters in different wing dimorphic and polymorphic insect species (see the above-mentioned reviews) similar side effects of the pest management practices can be more widespread, than one might assume.

Conclusions

Wing polymorphism and the biology of range expansions are complex phenomena on their own. Both topics have an immense research history, but their relation is still only partially understood. Deeper understanding of the genetics and the physiology of the wing polymorphism of some focal species (pea aphid, rice planthoppers) is progressing very rapidly. As the range of many species is expected to expand due to both climate change and the anthropogenic introductions, one can expect many more revealing case studies in the appropriate future. The role of wing polymorphism has to be evaluated, however, in the wider context of general dispersal polymorphism. More research on possible effects of the pest

management practices on the wing form determination of the wing polymorphic pest species is also needed.

References

AHLROTH, P. – ALATALO, R.V. – SUHONEN, J. (2010): Reduced dispersal propensity in the wingless waterstrider Aquarius najas in a highly fragmented landscape. *Oecologia,* 162, 323–330. DOI: https://doi.org/10.1007/s00442-009-1457-z

ANDERSEN, N. M. (2000): The evolution of dispersal dimorphism and other life history traits in water striders (Hem. Gerridae). *Entomological Science*, 3, 187–199. Conference paper.

BAO, H. – LIU, S. – GU, J. – WANG, X. – LIU, Z. (2009): Sublethal effects of four insecticides on the reproduction and wing formation of brown planthopper, *Nilaparvata lugens*. *Pest Management Science,* 65, 170–174. DOI: http://dx.doi.org/10.1002/ps.1664

BECKMANN, C.B. – PURSE, B.V. – ROY, D.B. – ROY, H.E. – SUTTON, P.G. – THOMAS, C.D. (2015): Two Species with an Unusual Combination of Traits Dominate Responses of British Grasshoppers and Crickets to Environmental Change. *PLoS ONE,* 10, e0130488. DOI: http://dx.doi.org/10.1371/journal.pone.0130488

BERGGREN, A. (2001): Colonization success in Roesel's bush-cricket *Metrioptera roeseliii*: The effects of propagule size. *Ecology,* 82, 274–280. DOI: http://dx.doi.org/10.2307/2680102

BERGGREN, A. – CARLSON, A. – KIINDVALL, O. (2001): The effect of landscape composition on colonization success, growth rate and dispersal in introduced bush-crickets Metrioptera roeseliii. *Journal of Animal Ecology*, 70, 663–670. DOI: http://dx.doi.org/10.1046/j.1365-2656.2001.00525.x

BRAENDLE, C. – DAVIS, G. K. – BRISSON, J. A. – STERN, D. L. (2006): Wing dimorphism in aphids. *Heredity,* 97, 192–199. DOI: http://dx.doi.org/10.1038/sj.hdy.6800863

BRUNZEL, S. (2002): Increased dispersal rates, distances in density-stressed bush crickets (Metrioptera brachyptera (L., 1761) (Saltatoria: Tettigoniidae). *Beitrage zur Entomologie,* 52, 241–253. DOI: http://dx.doi.org/10.21248/contrib.entomol.52.1.241-253

CASSEL-LUNDHAGEN, A. – KANUCH, P. – LOW, M. – BERGRENN, A. (2011): Limited gene flow may enhance adaptation to local optima in isolated populations of the Roesel's bush cricket (Metrioptera roeselii). *Journal of Evolutionary Biology,* 2, 381–390. DOI: http://dx.doi.org/10.1111/j.1420-9101.2010.02174.x

DEN BOER, P. J. – VAN HUIZEN, T. H. P. – DEN BOER-DAANJE, W. – AUKEMA B. – DEN BIEMAN, C. F. M. (1980): Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process (Coleoptera: Carabidae). *Entomologia Generalis,* 6, 107–134. DOI: http://dx.doi.org/10.1127/entom.gen/6/1980/107

DENNO, R. F. – RODERICK, G. K. – PETERSON, M. A. – HUBERTY, A. F. – DOBEL, H. G. – EUBANKS, M. D. – LOSEY, J. E. – LONGOLETTO, G. A., (1996): Habitat Persistence Underlies Intraspecific Variation in the Dispersal Strategies of Planthoppers (1996). *Biology Faculty and Staff Publications,* 45. DOI: https://doi.org/https://cedar.wwu.edu/biology_facpubs/45

FUJISAKI, K. (1989): 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. DOI: https://doi.org/10.1303/aez.24.20

GAO, X. – FU, Y. – AJAYI, O.E. – GUO, D. – ZHANG, L. – WU, Q. (2019): Identification of genes underlying phenotypic plasticity of wing size via insulin signaling pathway by network-based analysis in *Sogatella furcifera. BMC Genomics,* 20, 396. DOI: https://bmcgenomics.biomedcentral.com/articles/10.1186/s12864-019-5793-z

GARDINER, T. (2009): Macropterism of Roesel's bushcricket Metrioptera roeselii in relation to climate change and landscape structure in eastern England. *Journal of Orthoptera Research*, 12, 95–102. DOI: http://dx.doi.org/10.1665/034.018.0110

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. DOI: http://dx.doi.org/10.1111/j.1469-185X.2010.00172.x

HARRISON, R. G. (1980). Dispersal polymorphism in insects. *Annual Reviews of Ecology and Systematics*, 11, 95–118. DOI: http://dx.doi.org/10.1146/annurev.es.11.110180.000523

HARTFELDER, K. – EMLEN, D. J. (2012): Endocrine Control of Insect Polyphenism. *Insect Endocrinology*, 11, 464–522. DOI: http://dx.doi.org/10.1016/B0-44-451924-6/00045-4

HELMS, J.A. IV – GODFREY, A. (2016) Dispersal Polymorphisms in Invasive Fire Ants. *PLoS ONE,* 11, e0153955. DOI: https://doi.org/10.1371/journal.pone.0153955

HOCHKIRCH, A. – DAMERAU, M. (2009): Rapid range expansion of a wing-dimorphic bush-cricket after the 2003 climatic anomaly. *Biological Journal of the Linnean Society*, 97, 118–127. DOI: http://dx.doi.org/10.1111/j.1095-8312.2008.01199.x

IWANAGA, K. -TOJO, S. (1986): Effects of juvenile hormone and rearing density on wing dimorphism and oöcyte development in the brown planthopper, *Nilaparvata lugens. Journal of Insect Physiology*, 32, 585–590. DOI: https://doi.org/10.1016/0022-1910(86)90076-4

IWANAGA, K. – TOJO, S. – NAGATA, T. (1985): Immigration of the brown planthopper, Nilaparvata lugens, exhibiting various responses to density in relation to wing morphism. *Entomologia Experimentalis et Applicata*, 38. DOI: http://dx.doi.org/10.1111/j.1570-7458.1985.tb03505.x

JOHNSON, C. G. (1969): Migration and dispersal of insects by flight. London, 763 pp.

JI, J. – HUANGFU, N. – LUO, J. – GAO, X. – NIU, L. – ZHANG, S. – CU, J. (2021): Insights into wing dimorphism in worldwide agricultural pest and host-alternating aphid *Aphis gossypii. Journal of Cotton Research* 4, 5. DOI: https://doi.org/10.1186/s42397-021-00080-w

KANUCH, P. – BERGGREN, A. – CASSEL-LUNDHAGEN, A. (2013): Colonization history of Metrioptera roeselii in northern Europe indicates human-mediated dispersal. *Journal of Biogeography,* 40, 977–987. DOI: http://dx.doi.org/10.1111/jbi.12048

KANUCH, P. – BERGGREN, A. – CASSEL-LUNDHAGEN, A. (2014): Genetic diversity of a successful colonizer: isolated populations of Metrioptera roeselii regain variation at an unusually rapid rate. *Ecology and Evolution*, 4, 1117–1126. DOI: http://dx.doi.org/10.1002/ece3.1005

KISHIMOTO, R. (1971): Long Distance Migration of Planthoppers, *Sogatella Furcifera* and *Nilaparvata Lugens. Japan International Research Center for Agricultural Sciences* 5, 201–216. DOI: https://doi.org/ tars5-_201-216.pdf (jircas.go.jp)

KINDVALL, O. – VESBY, K. – BERGGREN, A. – HARTMAN, G. (1998): Individual mobility prevents an Allee effect in sparse populations of the bush cricket Metrioptera roeselii: an experimental study. *Oikos,* 81, 449–457. DOI: http://dx.doi.org/10.2307/3546766

KLAUSNER, E. – MILLER, E. R. – DINGLE, H. (1981): Genetics of brachyptery in a lygaeid bug island population. *Journal of Heredity,* 72, 288–289. DOI: http://dx.doi.org/10.1093/oxfordjournals.jhered.a109502

KLEUKERS, R.M. – DECLEER, K. – HAES, E.C.M. – KOLSHORN, P. – THOMAS, B. (1996): The recent expansion of Conocephalus discolor (Thunberg) (Orthoptera: Tettigoniidae) in Western Europe. *Entomologist's Gazette,* 47:37–49.

LIANG, Z.Q. – SONG, S.Y. – LIANG, S.K. – WANG, F.H. (2016): Analysis of Differential Proteins in Two Wing-Type Females of Sogatella furcifera (Hemiptera: Delphacidae). *Journal of Insect Science*16(1):35. DOI: http://dx.doi.org/10.1093/jisesa/iew024

LIN, X. – XU, Y. – JIANG, J. – LAVINE, M. – LAVINE, L. C. (2018): Host quality induces phenotypic plasticity in a wing polyphenic insect. *Proceedings of the National Academy of Sciences*, 115, 7563–7568. DOI: http://dx.doi.org/10.1073/pnas.1721473115

MATALIN, A. V. (2003): Variations in flight ability with sex and age in ground beetles (Coleoptera, Carabidae) of south-western Moldova. *Pedobiologia* 47, 311–319. DOI: http://dx.doi.org/10.1078/0031-4056-00195

MATSAMURA, M. (1996): Genetic analysis of a threshold trait: density-dependent wing dimorphism in Sogatella furcifera (Horváth) (Hemiptera: Delphacidae), the whitebacked planthopper. *Heredity,* 76, 229–237 DOI: http://dx.doi.org/10.1038/hdy.1996.36

MATSAMURA, M. (1997): Correlated responses of life history traits, wing length, and flight propensity to wing-form selection in the whitebacked planthopper, Sogatella furcifera (Horvath) (Hemiptera: Delphacidae). *Applied Entomology and Zoology* 32. (3): 437–445. DOI: http://dx.doi.org/10.1303/aez.32.437

NISHIDE, Y. – TANAKA, S. (2013): The occurrence in the migratory locust, Locusta migratoria (Orthoptera: Acrididae), of a short-winged morph with no obvious fitness advantages over the long-winged morph. *European Journal of Entomology,* 110, 577–583, DOI: http://dx.doi.org/10.14411/eje.2013.078

OGAWA, K. – MIURA, T. (2014): Aphid polyphenisms: trans-generational developmental regulation through viviparity. *Frontiers in Physiology,* 5, 1. DOI: http://dx.doi.org/10.3389/fphys.2014.00001

OGAWA, K. – ISHIKAWA, A. – KANABE, T. – AKIMOTO, S. – MIURA, T. (2012): Male-specific flight apparatus development in Acyrthosiphon pisum (Aphididae, Hemiptera, Insecta): comparison with female wing polyphenism. *Zoomorphology*, 131, 197–207. DOI: https://doi.org/10.1007/s00435-012-0154-3

PEŇA, J. E. (2013): Potential invasive pests of agricultural crops. Vol. 3. CABI, 440 pp.

PENER, M. P. – SIMPSON, S. J. (2009): Locust Phase Polyphenism: An Update. *Advances in Insect Physiology* 36: 1–272. DOI: http://dx.doi.org/10.1016/S0065-2806(08)36001-9

PONIATOWSKI D. – FARTMANN, T. (2009): Experimental evidence for density-determined wing dimorphism in two bushcrickets (Ensifera: Tettigoniidae). — *Europe J. Entomol.* 106: 599–605. DOI: http://dx.doi.org/10.14411/eje.2009.075

PONIATOWSKI, D. – FARTMANN, T. (2011a) Does wing dimorphism affect mobility in Metrioptera roeselii? *European Journal of Entomology*, 108, 409–415. DOI: http://dx.doi.org/10.14411/eje.2011.052

PONIATOWSKI, D. – FARTMANN, T. (2011b): Weather-driven changes in population density determine wing dimorphism in a bush-cricket species. *Agriculture, Ecosystems & Environment* 145(1), 5–9. DOI: http://dx.doi.org/10.1016/j.agee.2010.10.006

PUSHKAR, T. I. (2009): Tetrix tuerki (Orthoptera, Tetrigidae): Distribution in Ukraine, ecological characteristic and features of biology. *Vestnik zoologii*, 43(1). DOI: http://dx.doi.org/10.2478/v10058-009-0001-2

RENAULT, D. (2020): A Review on Dispersal Polymorphism in Wing-Dimorphic, Mono-Morphic, Wingless, and Range-Expanding Insects, and Experimental Designs for Sorting out Resident and Disperser Phenotypes. *Insects, 11*(4), 214. DOI: 10.3390/insects11040214

ROFF, D. A. (1986): The evolution of wing dimorphism in insects. *Evolution,* 40, 1009–1020. DOI: http://dx.doi.org/10.1111/j.1558-5646.1986.tb00568.x

ROFF, D. A. – FAIRBAIRN, D. J. (1991): Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. *Integrative and Comparatory Biology*, 31, 243–251. DOI: http://dx.doi.org/10.1093/icb/31.1.243

SAXENA, R. C. – OKECH, S. H. – LIQUIDO, N. J. (1981): Wing Morphism in the Brown Planthopper, *Nilaparvata Lugens. International Journal of Tropical Insect Science* 1, 343–348. DOI: http://dx.doi.org/10.1017/S1742758400000631

SIMMONS A.D. – THOMAS C.D. (2004): Changes in dispersal during species range expansions. *The American Naturalist* 164, 378–395. DOI: http://dx.doi.org/10.1086/423430

SOCHA, R. (1993): Pyrrhocoris apterus (Heteroptera): a model species: a review. *European Journal of Entomology* 90, 241–286.

SOLBRECK, C. – ANDERSON, D.B. (1989). Wing reduction; its control and consequences in a lygaeid bug, Spilostethus pandurus. *Hereditas,* 111, 1–6. DOI: http://dx.doi.org/10.1111/j.1601-5223.1989.tb00368.x

SZANYI, A. – NAGY, A. – RÁCZ, I.A. – VARGA, Z. (2014): Contrasting patterns of macroptery in Roeselís bush cricket Metrioptera roeselii (Orthoptera, Ensifera). *Estonian Journal of Ecology*, 63, 4. DOI: https://doi.org/10.3176/eco.2014.4.07

VENN, S. (2007): Morphological responses to disturbance in wing-polymorphic carabid species (Coleoptera: Carabidae) of managed urban grasslands. *Baltic Journal of Coleopterology* 7, 51–59.

VENN, S. (2016): To fly or not to fly: Factors influencing the flight capacity of carabid beetles (Coleoptera: Carabidae). *European Journal of Entomology*, 113, 587–600. DOI: http://dx.doi.org/10.14411/eje.2016.079

VÄPSALÄINEN, K. (1978): Wing dimorphism and diapause in Gerris: determination and adaptive significance. *Evolution of Insect Migration and Diapause*, 218–253. DOI: http://dx.doi.org/10.1007/978-1-4615-6941-1_10

WATANABE, T. – MATSUMURA, M. – OTUKA, A. (2009): Recent occurrences of long-distance migratory planthoppers and factors causing outbreaks in Japan. *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia.* 179–189.

WISSMANN, J. – SCHIELZETH, H. – FARTMANN, T. (2009): Landscape-scale expansion of Roesel's bush-cricket Metrioptera roeselii at the North-western range limit in Central Europe (Orthoptera: Tettigoniidae). *Entomologia Generalis* 31, 317–326. DOI: https://doi.org/10.1127/entom.gen/31/2008/317

WU, G.R. – YU, X. P. – TAO, L.Y. – REN, Z. J. (1994): Wing dimorphism and migration in the brown planthopper, *Nilaparvata lugens* Stål. In: *Insect life-cycle polymorphism* pp. 263–275. DOI: https://doi.org/10.1007/978-94-017-1888-2_13

YU, J.-L. – AN, Z. F. – LIU, X. (2014): Wingless gene cloning and its role in manipulating the wing dimorphism in the white-backed planthopper, Sogatella furcifera. *BMC molecular biology*. DOI: https://doi.org/10.1186/1471-2199-15-20

ZERA, A. J. (2004): The endocrine regulation of wing polymorphism: State of the art, recent surprises, and future directions. *Integrative and Comarative. Biology,* 43: 605–606. DOI: https://doi.org/10.1093/icb/43.5.607

ZERA A. J. – DENNO R. F. (1997): Physiology and ecology of dispersal polymorphism in insects. *Annual Review of Ecology Evolution and Systematics*. 42, 207–230. DOI: https://doi.org/10.1146/annurev.ento.42.1.207

ZHANG, C. – MAO, M.S. – LIU, X.D. (2022): Relative contribution of genetic and environmental factors to determination of wing morphs of the brown planthopper *Nilaparvata lugens. Insect Science*. Epub ahead of print. DOI: http://dx.doi.org/10.1111/1744-7917.13037

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