



UNIVERSITY OF PANNONIA
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The ecology of mosquito and sandfly vectors and their pathogens in a changing environment

A szúnyog, lepkeszúnyog vektorok és patogénjeik ökológiája a változó környezetben

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ABBREVIATIONS

AGCC	Anthropogenic Global Climate Change
IPCC	Intergovernmental Panel on Climate Change
THB(s)	thermal bridge(s)
UI	Urbanisation Intensity
UHI	Urban Heat Intensity
USDA	United States Department of Agriculture
VBD(s)	Vector-borne disease(s)
VBORNET	European Network for Arthropod Vector Surveillance for Human Public Health
WNF	West Nile fever
WNV	West Nile fever virus

Taxonomic names and their abbreviations

Both nomenclature and taxonomy were based on the Fauna Europea zoological taxonomic index database (operated by Museum für Naturkunde Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany). The species names are never abbreviated in the main titles and the names of genera are written in full at the beginning of the sentences. The abbreviations for genera and subgenera of Culicidae (Diptera) were performed according to the recommendations of Reinert (2001). The abbreviations of the genera are as follows:

- *Anopheles* Meigen, 1818 = *An.*
- *Aedes* Meigen, 1818 = *Ae.*
- *Culex* Linnaeus, 1758 = *Cx.*
- *Culiseta* Felt, 1904 = *Cs.*
- *Ochlerotatus* Lynch-Arribálzaga, 1891 = *Oc.*

The abbreviation of the genera of sandfly vectors and some important pathogens are as follows:

- *Dirofilaria* Railliet & Henry, 1911 = *D.*
- *Leishmania* Borovsky, 1898 (Ross, 1903) = *L.*
- *Phlebotomus* Loew, 1845 = *Ph.*
- *Plasmodium* Marchiafava & Celli, 1885 = *P.*

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CONTRIBUTIONS TO THE RESEARCH

GIS maps were made by **Ákos Bede-Fazekas PhD** (MTA Centre for Ecological Research, Institute of Ecology and Botany; MTA Centre for Ecological Research, GINOP Sustainable Ecosystems Group), **Tamás Hammer** (Veszprém District Office, Department of Environmental Protection, Nature Conservation Department, a former colleague of University of Pannonia, Department of Limnology), and **Kinga Farkas-Iványi PhD** (a former colleague of Centre for Ecological Research, Hungary and Department of Restoration and Animal Ecology).

Antal Rengei DVM and his colleagues (**Kisállat-Ambulancia Ltd.**, Szeged) collected the canine dirofilariasis data. The serological investigation of the collected blood samples was partly carried out by **Éva Fok PhD** and her colleagues (University of Veterinary Medicine Budapest, Department of Parasitology and Zoology).

Technical drawings were designed by **Péter Juhász PhD** (a former colleague of Department of Engineering Geology and Geotechnics, former Department of Construction Materials and Engineering Geology). Temperature measurements were performed by **Lilla Mlinárik PhD** (Department of Engineering Geology and Geotechnics).

ABSTRACT IN ENGLISH

The factors of seasonality, dispersal, distribution and presence of vectors in anthropogenic environments are in the focus of the current investigations of vector-borne diseases predominantly. Therefore, the basic aims of the present dissertation are as follows:

- (a) to investigate the seasonality of mosquito vectors and mosquito-borne diseases. Within this topic, the following aims were set:
 - (i) to model the changing seasonality of *Anopheles maculipennis* larvae under climate change in the North Balkan and the Carpathian Basin;
 - (ii) to study the diversity, seasonal abundance and potential vector status of the cave-dwelling mosquito fauna of the Bakony-Balaton Region.
- (b) to study the dispersal factors of invasive mosquitos. Within this topic, the following aim was set:
 - (i) to estimate the total and passive dispersal per generation of *Aedes albopictus*;
- (c) to study the distribution and survival of vectors and vector-borne diseases in anthropogenic environments. Within this topic, the following aims were set:
 - (i) to study the influence of urbanisation level and proximity to standing waters on the spatial distribution of canine dirofilariasis;
 - (ii) to investigate how the anthropogenic heat emission influence the urban occurrence of sandfly species in Budapest and
 - (iii) to model the future potential distribution of *Phlebotomus neglectus* and *Phlebotomus mascittii* in Budapest.

For these purposes, the seasonality, the dispersal factors, the distribution and the presence in anthropogenic environments of vectors and mosquito- and sandfly-borne diseases were investigated based on field collections, monographic data and the public databases of governmental panels.

- (a) The major conclusions for topic 1 are as follows:
 - (i) The complete main *Anopheles maculipennis* larva season will increase by two months in Southeast Hungary and at least 1 month in the other parts of the South Pannonian Ecoregion, in the North Balkan region including South Romania and North Bulgaria for

2041-2070.

- (ii) In caves, male mosquitos can be found only in the second half of the year, while female individuals both in the first and the second half of the year. Both the relative abundance of males and females exhibited an increasing trend between August and November. The infected *Culex pipiens pipiens* mosquitos starting their diapause in the autumn can serve as the potential vectors of the West Nile virus in the next year.
- (b) The major conclusions for topic 2 are as follows:
 - (i) The active dispersal of female *Aedes albopictus* mosquitos may play only a secondary role in determining the rate of areal expansion and, in contrast, passive factors play a primary role.
 - (ii) Based on similar average values of the passive dispersal distances of the mosquito in Florida and Italy, the anthropogenic component can be well estimated at large spatial scales.
- (c) The major conclusions for topic 3 are as follows:
 - (i) Most of the canine dirofilariasis cases are related to locations with a medium to high urbanisation index, although the proximity of mosquito-bearing waters also plays important role in the observed spatial infection patterns. It was found that the distance from potential mosquito habitats and the urbanisation intensity determine together the abundance of dirofilariasis in urban environments.
 - (ii) The anthropogenic heat emission of big cities may explain the observed isolated northward populations of *Phlebotomus* species.
 - (iii) The present-day relatively small, extrazonal urban populations of the sandfly species will become the source of their more rapid expansion than we might expect on the basis of the recent zonal distribution of this species.

KIVONAT MAGYARUL

A vektorok által terjesztett megbetegedésekkel kapcsolatos jelenlegi kutatások fókuszában elsősorban a vektorok szezonálisát, terjedését, elterjedését és az ember alkotta környezetben való előfordulását meghatározó tényezők állnak. A jelen kutatás alapvető céljai a következők voltak:

(a) Vizsgálni a szúnyogok és az általuk terjesztett betegségek szezonálisát.

Ebben a témában a következő célok kerültek kitűzésre:

- (i) modellezni az *Anopheles maculipennis* szúnyog faj klímaváltozás hatására várhatóan változó lárvaszezonálisát az Észak Balkánon és a Kárpát-medencében;
- (ii) meghatározni a barlangokat látogató szúnyog fajok diverzitását, évszakos abundanciáját és vektor kompetenciáját a Bakony-Balaton régióban.

(b) Tanulmányozni az invazív szúnyog fajok terjedését meghatározó tényezőket.

Ezeknek elérése érdekében az alábbi cél került kitűzésre:

- (i) megbecsülni az *Aedes albopictus* aktív és passzív terjedését.

(c) Elemezni a vektorok és a vektorok által terjesztett megbetegedések előfordulását és fennmaradását városi környezetben. Az előbb leírtak vizsgálata céljából a következő részletes célok kerültek kitűzésre:

- (i) elemezni a dirofilariasis városi előfordulását a kisvizek távolsága és az városiasodottság fokának függvényében;
- (ii) annak vizsgálata, hogy az antropogén hőemisszió mennyiben határozza meg a lepkeszúnyog fajok fennmaradását városi környezetben;
- (iii) valamint modellezni a *Phlebotomus mascittii* és *Phlebotomus neglectus* jövőben várható előfordulását Budapesten.

Ennek érdekében a szúnyog és lepkeszúnyog fajok és az általuk okozott betegségek szezonális, diszperziós és elterjedési tényezői, valamint az ember építette környezetben való előfordulásuk került vizsgálatra terepi gyűjések, monografikus adatok, valamint kormányzati panelek nyilvános adatbázisait igénybe véve.

- (a) Az első kérdéskör kapcsán az alábbi fő megállapításokra jutottam:
- (i) A 2041-2070-es évekre Dél-Magyarországon az *Anopheles maculipennis* lárvaszezonja kb. 2 hónappal fog megnyúlni, ugyanakkor a szezonhossz növekedése a Dél-Pannon ökorégió más területein, az Észak-Balkánon és Dél-Romániában is mindenhol várhatóan legalább 1 hónap növekedést fog mutatni.
 - (ii) A barlangokban hímivarú szúnyog egyedek csak az év második, nőivarú szúnyogok viszont az év mindekét felében előfordulnak. Augusztus és november hónapok között mindkét nemhez tartozó egyedek száma növekedést mutat a barlangokban. Azon fertőzött, nőtény *Culex pipiens pipiens* egyedek, melyek ősszel megkezdik nyugalmi időszakukat a barlangokban, a következő évben a Nyugat-nílusi láz vírus forrásaivá válhatnak.
- (b) A második kérdéskörben a következő eredményeket nyertem:
- (i) Az *Aedes albopictus* nőtényeinek terjedésében az aktív terjedés másodlagos szerepet játszik a passzív terjedéshez képest, ami azt jelenti, hogy a faj migrációjának sebességét a passzív komponens határozza meg elsősorban.
 - (ii) Tekintve, hogy a Floridai-félsziget és az Appennin-félsziget esetében is nagyon hasonló értékek adódtak a passzív komponensre, ez azt jelenti, hogy a passzív komponens nagy léptékű terjedési modellekben jól becsülhető.
- (c) A harmadik kérdéskörben a következő megállapításokat tettem:
- (i) A kutya dirofilariasis esetek zöme magasan vagy mérsékelten urbanizált területekhez volt köthető. Ugyanakkor a szúnyogok szaporodási helyeit jelentő vizes élőhelyektől való távolság is erősen meghatározza annak térbeli előfordulását. Ezek alapján kijelenthető, hogy a két tényező együttesen determinálja a kutya dirofilariasis térbeli eloszlását.
 - (ii) Az antropogén hőemisszió megmagyarázza a lepkeszúnyogok kis populáció méretű, extrazonális városi előfordulásait.
 - (iii) A jelenlegi, viszonylag kis méretű, extrazonális városi lepkeszúnyog populációk a jövőben a fajok gyorsabb terjedésének forrásaivá válhatnak, mint amit a zonálisan előforduló populációk alapján várhatnánk.

RESUMEN EN ESPAÑOL

Los factores de estacionalidad, dispersión, distribución y presencia de vectores en ambientes antropogénicos se encuentran en el foco de atención de las investigaciones actuales sobre enfermedades transmitidas por vectores, principalmente. Por lo tanto, los objetivos básicos de la presente tesis son los siguientes:

(a) Las principales conclusiones del primer tema son:

(a) investigar la estacionalidad de los mosquitos vectores y las enfermedades transmitidas por mosquitos. Dentro de este tema, se establecieron los siguientes objetivos:

- (i) modelar la estacionalidad cambiante de las larvas de *Anopheles maculipennis* debido al cambio climático en los Balcanes del Norte y la Cuenca de los Cárpatos.
- (ii) estudiar la diversidad, la abundancia estacional y el posible estado vectorial de la fauna de mosquitos que habitan en cuevas en la región de Bakony-Balaton.

(b) estudiar los factores de dispersión de los mosquitos invasores. Dentro de este tema, se estableció el siguiente objetivo:

- (iii) estimar la dispersión total y pasiva por generación de *Aedes albopictus*.

(c) estudiar la distribución y supervivencia de vectores y enfermedades transmitidas por vectores en ambientes antropogénicos. Dentro de este tema, se establecieron los siguientes objetivos:

- (i) estudiar la influencia del nivel de urbanización y la proximidad a las aguas estancadas sobre la distribución espacial de la dirofilariasis canina.
- (ii) investigar cómo la emisión de calor antropogénico influye en la presencia urbana de especies de flebotomos en Budapest
- (iii) y modelar la distribución futura potencial de *Phlebotomus neglectus* y *Phlebotomus mascittii* en Budapest.

Para estos fines, la estacionalidad, los factores de dispersión, la distribución y la presencia en ambientes antropogénicos de vectores y enfermedades transmitidas

por mosquitos y flebótomos se investigaron sobre la base de colecciones de campo, datos monográficos y bases de datos públicas de paneles gubernamentales.

- (a) Las principales conclusiones del segundo tema son:
 - (i) La temporada principal de larvas de *Anopheles maculipennis* aumentará en dos meses en el sudeste de Hungría y al menos un mes en las otras partes de la Ecorregión del sur de Panonia, en la región de los Balcanes del Norte incluyendo Rumanía del Sur y Bulgaria del Norte para 2041-2070.
 - (ii) En las cuevas, los mosquitos machos solo se pueden encontrar en la segunda mitad del año, mientras que las hembras, tanto en la primera como en la segunda mitad del año. Tanto la abundancia relativa de hombres como mujeres mostraron una tendencia creciente entre agosto y noviembre. Los mosquitos *Culex pipiens pipiens* infectados, que comienzan su diapausa en el otoño, pueden ser los vectores potenciales del virus del Nilo Occidental durante el próximo año.
- (b) Las principales conclusiones del segundo tema son:
 - (i) La dispersión activa de mosquitos hembra *Aedes albopictus* desempeña un papel secundario en la determinación de la tasa de expansión territorial y, por el contrario, los factores pasivos pueden desempeñar un papel principal.
 - (ii) Con base en valores promedio similares de las distancias de dispersión pasiva del mosquito en Florida e Italia, que en grandes escalas espaciales el componente antropogénico puede ser bien estimado.
- (c) Las principales conclusiones del tercer tema son:
 - (i) La mayoría de los casos de dirofilariasis canina están relacionados con localizaciones con un índice de urbanización de medio a alto, aunque la proximidad de las aguas que contienen mosquitos también juega un papel importante en los patrones de infección espacial observados. Se encontró que la distancia de los hábitats potenciales de los mosquitos y la intensidad de la urbanización determinan

conjuntamente la abundancia de dirofilariasis en los entornos urbanos.

- (ii) La emisión de calor antropogénico de las grandes ciudades puede explicar las poblaciones aisladas observadas hacia el norte de especies de *Phlebotomus*.
- (iii) Las poblaciones urbanas relativamente pequeñas y extrazonales actuales de las especies de flebótomos se convertirán en la fuente de su expansión más rápida de lo que cabría esperar sobre la base de la distribución zonal reciente de esta especie.



Sir Ronald Ross (13 May 1857 - 16 September 1932), British medical doctor, Nobel laureate in Physiology or Medicine (1902). He was the person who found the connection between mosquitos and malaria and the first one who prepared a scientific mathematical model of a human mosquito-borne disease. Also, he introduced the name of the causative agent of leishmaniasis, *Leishmania* that is currently accepted taxonomically.

MOTTO

'Science is the differential calculus
of the mind. Art the integral
calculus; they may be beautiful when
apart, but are greatest only when
combined.'

(Sir Ronald Ross - Quoted in The Complete Poems of Hugh MacDiarmid 1920-1976 (1978), Vol. 2, 1360).

CHAPTER I

Review of the topic of
Diptera vectors and the
transmitted diseases

The topics of this chapter:

- **The global diversity and brief natural history of Diptera**
- **Diptera vectors and their pathogens**

1. THE GLOBAL DIVERSITY AND BRIEF NATURAL HISTORY OF DIPTERA

Diptera, with about 125,000 described species, is one of the largest of the insect orders, constituting almost 12.5% of known insect taxa and 8.3% of all known animal life-forms. New species are discovered frequently (Mayhew, 2007). So far, more than 3,500 species of the Culicidae have already been described (Harbach, 2011). In the recent dissertation I will focus on the ecology of some Culicidae and Phlebotominae vectors and their pathogens. Both Culicomorpha and Psychodomorpha, infraorders of Nematocera, belong to the old lineages of Diptera. Although the recent phylogenetic studies do not support clearly the classic division of Diptera into Nematocera and Brachycera (Wiegmann et al., 2011), mosquitos and sandflies can be classified in the suborder Nematocera based on their anatomical features and phylogenetic position. Still, the older clades of Diptera belong to Nematocera (including Ptychopteromorpha, Culicomorpha, Blephariceromorpha, Bibionomorpha, Psychodomorpha, Tipuloidea) and the younger clades (from Stratiomyomorpha to Acalyptrata) belong to Brachycera according to their anatomy and appearance (Yeates et al., 2003; *Fig.1*).

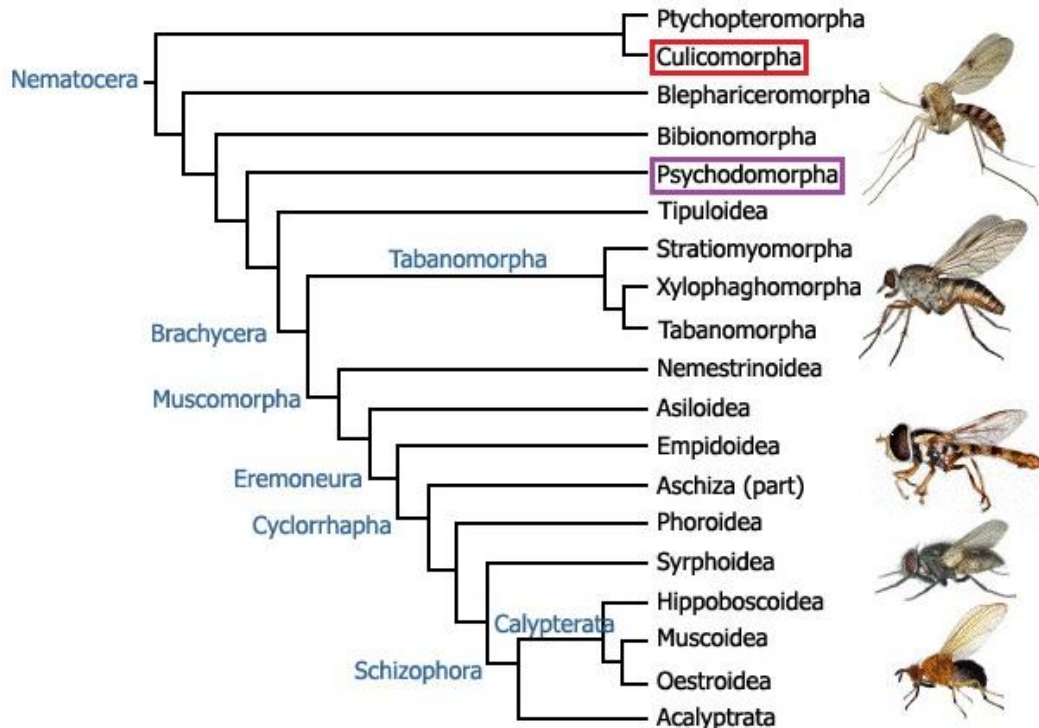


Figure 1. Phylogeny of Diptera (Yeates et al., 2003) with the phylogenetic position of Culicomorpha (red frame) and Psychodomorpha (purple frame).

The origin of Diptera from Permian Mecoptera is suggested (Shcherbakov et al., 1995). The oldest Diptera fossils were discovered in the Vosges Mts. (France, Alsace) and these are dated to the turn of Lower to Middle Triassic (Gall and Grauvogel, 1966). However, the morphological diversity of the earliest dipteran taxa indicates that the branching off the Mecoptera had happened earlier, probably in the end of the Permian or the beginning of the Triassic (Krzemiński and Krzemińska 2003). The suborder Nematocera may have evolved in the early Triassic period around the P/T mass extinction event, 252 million years ago (Krzemiński and Krzemińska 2003). Certainly, the first member of Culicomorpha lived in the late Triassic period (Rhaetian period; Krzemiński and Krzemińska, 2003). A phylogenetic study found that temporal divergence of Anophelinae and Culicinae occurred 226 million years ago, in about the Upper Triassic (Reidenbach et al., 2009). The oldest member of Psychodidae was found in late Triassic sediments. The first *Phlebotomus* species lived in the late Cretaceous period (Stebner et al., 2015). The first Culicinae species (including *Coquillettidia*, *Culex* and *Culiseta* genera) appeared only in the Eocene fossil record between the Lutetian and the Priabonian ages, about 48.6-33.9 million years ago (Szadziewski and Gilka 2011; Harbach and Greenwalt 2012). In the Tertiary-Quaternary period, mosquitos and other Nematocera species were the common and important elements of the insect fauna (Fig.2).



Figure 2. Subfossil mosquito-like Diptera from copal (originating from resin of *Hymenaea verrucosa* (GAERTNER, 1791) OLIVER, 1871; Northeast Madagascar; photo by the Author, 2017).

2. DIPTERA VECTORS AND THEIR PATHOGENS

Many haematophagous Diptera species can transmit pathogens to animals or humans and several of them are only the passive vectors of different viruses, bacteria or fungi, which means that the reproduction of these pathogens does not require the body of insect hosts. Flies play key role in the dissemination of enteral pathogens carrying the agent directly on their legs, influencing the seasonality of certain enteral diseases (Trájer and Schoffhauzer, 2016). For example, the synantrop mothfly *Clogmia albipunctata* WILLISTON, 1893 (Diptera: Psychodidae), which can transmit nosocomial infections is commonly can be found in hospitals (Trájer and Juhász, 2017). This passive vector carries the pathogens on their body hair but the larvae of this mothfly themselves can cause human myiasis. In contrast, those pathogens, which obligately require the body of an arthropod (insect, tick, copepod crustacean) host, cause the true vector-borne diseases (hence: VBDs). Many of the insect vectors belong to the order Diptera. For example, certain members of black flies (genus *Simulium* - Diptera: Simuliidae) are the vectors the parasitic nematode *Onchocerca volvulus* BICKEL, 1982, which causes onchocerciasis that may result blindness in people in the tropical areas of Africa, Central - and South America (WHO, 2019A). Black flies are also the vectors of several other parasitic nematodes in several genera. Tsetse flies (genus *Glossina* - Diptera: Glossinidae) are the vectors of trypanosomes, which cause the animal trypanosomiasis (which is known as nagana pest; Soltys and Woo, 1977) and human sleeping sickness disease (the so-called African trypanosomiasis) in sub-Saharan Africa (WHO, 2019B, Knight, 1971). Some species of biting midges (genus *Culicoides* - Diptera: Ceratopogonidae) are the vectors of several arboviruses, protozoa and filarial worms. The Pigeon louse fly *Pseudolynchia canariensis* MACQUART, 1839 (Diptera: Hippoboscidae) can serve as the vector of pigeon malaria (Markus and Oosthuizen, 1972). Deer flies (e.g. the genus *Chrysops*, Diptera: Tabanidae) are the vectors of tularemia (Mörner, 1992), as well as the parasitic filarial nematode *Loa loa* COBBOLD, 1864 that causes loiasis in tropical Africa (Noireau et al., 1990). Eye gnats (Diptera: Chloropidae) can transmit yaws to humans (Barnard, 1952), vesicular stomatitis (Kramer et al., 1990) and the Brazilian purpuric fever (Machtinger and Kaufman, 2011) that is a potentially fatal illness of children (Brazilian Purpuric Fever Study Group, 1987). Mosquitos (genera *Aedes*, *Anopheles*, *Culex*, etc. - Diptera: Culicidae) are the

vectors of many pathogens such as malaria (Ross, 1910), yellow fever (Christophers, 1960), Chikungunya and Dengue fevers (Igarashi, 1978), West Nile virus (hence: WNV; Savage et al., 1999), filariasis (Wharton, 1962), Zika virus (Marchette et al., 1969), forming the deadliest animal family in the world in the aspect of mankind. Sandflies (genera *Phlebotomus* and *Lutzomyia* - Diptera: Psychodidae) are the primary vectors of cutaneous, mucocutaneous and visceral leishmaniasis (Adler and Ber, 1941), papataci fever (Sabin et al., 1944), bartonellosis (pathogen: *Bartonella bacilliformis* STRONG et al., 1913; Ihler, 1996) and Carrion's disease (Oroya fever) in South America (Hertig, 1942).

2.1. THE GLOBAL BURDEN OF MOSQUITO AND SANDFLY-TRANSMITTED DISEASES

About 40% of the people of Earth live in malaria endemic areas and only this VBD infects more than 214 million and kill more than 440,000 people in each year, mostly in the sub-Saharan Africa and Asia, Latin America (Olupot-Olupot and Maitland, 2013; Caminade et al., 2014; WHO, 2017). The causative agents are different *Plasmodium* parasites; the vectors are *Anopheles* species. Despite all efforts, the *Plasmodium falciparum* WELCH, 1897 caused malaria remained the most important mortality factor for children under 5 years of age in the Sub-Saharan Africa throughout the entire 20th century (Craig et al., 1999). Another pathogen, the Dengue fever virus infect more than 100 million humans during a year causing the death of approximately 10,000-22,000 people (Carabali et al., 2015; Bhatt et al., 2013; Stanaway et al., 2016). The caused disease is the Dengue fever; the vectors are *Aedes* mosquitos. Yellow fever virus infects about 200,000 and kills 30,000 in a year in the tropical areas of Africa and Latin America (WHO, 2013). The virus is carried by *Aedes* mosquitos. Chikungunya virus infects one to 2 million but kills less than 1,000 people a year (WHO, 2016). This virus also carried by *Aedes* mosquitos. Lymphatic filariasis occurs in the Sub-Saharan Africa and Asia. It is generally not fatal, but more than 100 million people suffer from this distorting illness in the Earth (GBD, 2015). The vectors are different *Culex*, *Anopheles* and *Aedes* mosquitos. The Japanese encephalitis virus infects 68,000 and kills 16,000 people in each year (WHO, 2015). The virus is transmitted by *Culex* mosquitos. *Leishmania* protozoans infect about 2 million and kill approximately 20,000-50,000 deaths in each year (WHO, 2014; Barrett and Croft, 2012). The vectors are sandfly (*Phlebotomus*) species. It can be concluded that mosquitos are the most dangerous

multicellular organisms for mankind in the Earth (Fig.3).

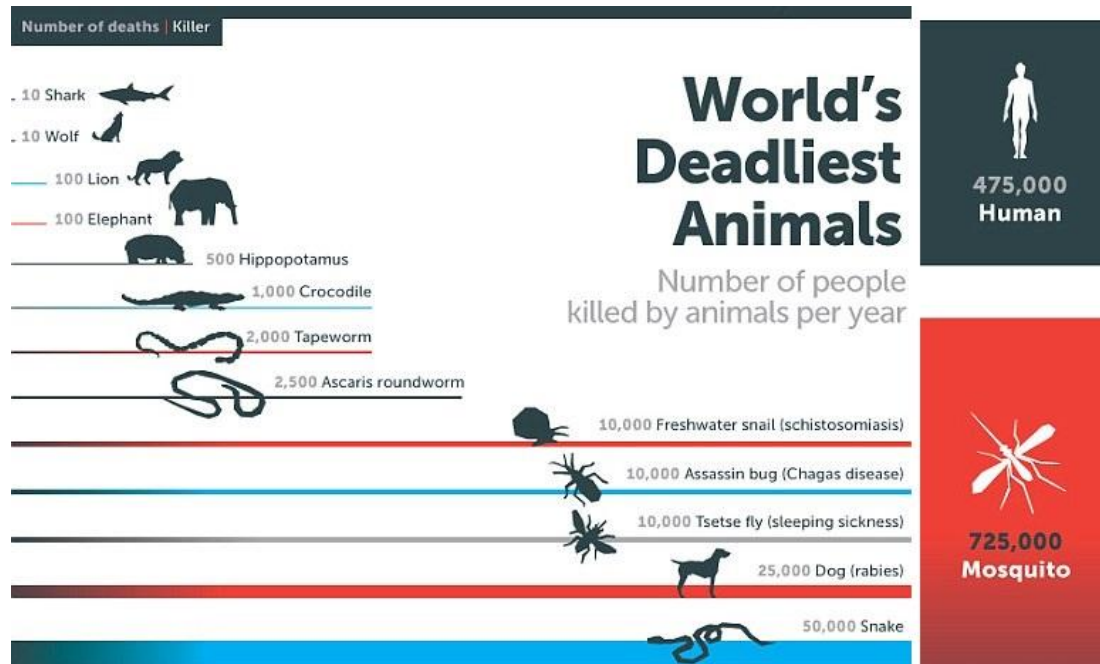


Figure 3. ‘The deadliest animal in the World’. (Infographics of Bill Gates, posted in April 25, 2014; Gates, 2014).

2.2. THE POTENTIAL EFFECT OF CLIMATE CHANGE ON ARTHROPOD VECTORS

The phenomenon of Anthropogenic Global Climate Change (hence: AGCC) has been accepted to a quite broad extent. There is a great amount of climate models based on the IPCC SRES climate scenarios, and free access is provided for them. The models are reliable enough and have good temporal and horizontal resolution for studying the potential future distribution of plant and animal vector species. Thus, the maps created by the model have importance not only for landscape architects and botanists (Saliné Czinkóczy and Bede-Fazekas, 2012), but also for epidemiologists. Regional climate models predict an increasing aridity of the Carpathian Basin by the end of the 21st century particularly in the vegetation period (Pieczka et al., 2011A, B; Bartholy et al., 2009; Bartholy and Gelybó, 2007). The simulated warming is typically between 1.5 °C and 2 °C in most parts of Europe in winter, summer temperatures are predicted to increase by more than 2.5 °C in the Mediterranean area, in Central Europe by less than 1.5 °C and in Eastern Europe by about 1 °C or less by 2050. Although the precipitation in the Mediterranean area decreases by up to 50%, the precipitation increases in large, even in the northern parts of Europe in autumn and winter. As expected, the climate in the Carpathian Basin will be warmer, more arid and will have extreme rainfalls more

frequently in the colder half-year (Bartholy et al., 2009). The rapid AGCC has the potential to change the fitness of the native plant populations and can trigger the area expansion of certain species (Trájer et al., 2016A; Huntley, 1991) dramatically altering community compositions (Jump and Peñuelas, 2005), and the degradation of the fragmented flora and fauna results in poor plant associations dominated by alien species (Gibbons et al., 2000). Vector-borne diseases are also sensitive to climatic conditions (Rogers and Randolph, 2006). Climate change will favor of the northward spreading of insect species (Roques et al., 2009; Ladányi and Horváth, 2010) and higher latitudes can cause the earlier flying activity of adult insects (Hufnagel and Kocsis, 2011). Based on these facts, an important impact of AGCC on human health is the increasing hazard of VBDs. The current importance of VBDs is less in Europe than in the countries of the low-income countries, particularly in the Sub-Saharan Africa. The protective role of cold winters in the temperate climate may lose its importance. Due to the AGCC, the importance of arthropod-borne diseases can increase by the end of the 21st century. Climate change can cause a shift in the geographical spread of insect populations (Ladányi and Horváth, 2010) by modifying the climatic conditions and seasonal patterns and affecting the reproduction and the length of annual activity of vector species. These changes can increase their population in the recently inhabited areas, and by moderating the climate in the temperate climate areas of Europe, they can facilitate the migration of these arthropod vectors to the north such as *Aedes albopictus* SKUSE, 1894 (e.g. Trájer et al., 2017A, 2014A; Benedict et al., 2007; Scholte and Schaffner, 2007). Changes in climatic patterns and in seasonal conditions may also affect disease behavior in terms of spread pattern, diffusion range, amplification and persistence in novel habitats. Higher temperatures can induce the earlier flight of adult insects, eg. in the case of Lepidoptera species (Hufnagel and Kocsis, 2011). Heat, humidity and enough organic matter are the main drivers of the larval development of sand flies (Naucke, 2002; Lindgren et al., 2006) while the increasing CO₂ levels are usually unfavourably affecting the development of the insect larvae (Hufnagel and Kocsis, 2011). The above described facts point to the investigation of the ecological relations of VBDs requires a complex, real interdisciplinary approach involving the work of climatologists, veterinarians, epidemiologists, microbiologists, etc.

2.3. THE ASIAN TIGER MOSQUITO

Aedes albopictus, also known as the Asian tiger mosquito is a competent vector for at least 22 arboviruses including Dengue virus, Chikungunya virus, Zika-virus, WNV, St. Louis encephalitis and Japanese encephalitis (Bonilauri et al., 2008; Grard et al., 2014; Hochedez et al. 2006; Gratz, 2004; Cancrini et al., 2003; Ibáñez-Bernal et al., 1997; Knudsen et al., 1996; Moore and Mitchell, 1997; Sardelis et al., 2002; Wong et al., 2013). This mosquito is also the vector of filarial nematodes e.g. *Dirofilaria* species (Hochedez et al., 2006; Cancrini et al., 2003). It was also confirmed that *Aedes albopictus* is one of the potential vectors of Zika-virus (Grard et al., 2014; Wong et al., 2013). *Ae. albopictus* is indigenous to the Hindustan Peninsula, to Southeast Asia, and to the islands of the Western Pacific and Indian Ocean. It was introduced to the Americas and Europe around the 1980s (Gratz, 2004). The rapid dispersal of *Ae. albopictus* was observed during the past few decades e.g. a northward expansion of the species and its hosted human parasites in the Mediterranean (Caminade et al., 2014, Benedict et al., 2007; Scholte and Schaffner, 2007; Schaffner and Karch, 2000; Knudsen et al., 1996; Mitchell, 1995). Since the first European appearance in Albania, the Asian tiger mosquito has demonstrated a remarkable invasive potential in the Mediterranean region (Urbanelli et al., 2000). The mosquito now occurs in each of the countries from Portugal to Greece, including such North Balkan countries as Slovenia and Croatia (Benedict et al., 2007; Kalan et al., 2011; Klobučar et al., 2006; Merdić, 2011; Petrić et al., 2006, 2001; Scholte and Schaffner, 2007; Fig.4).

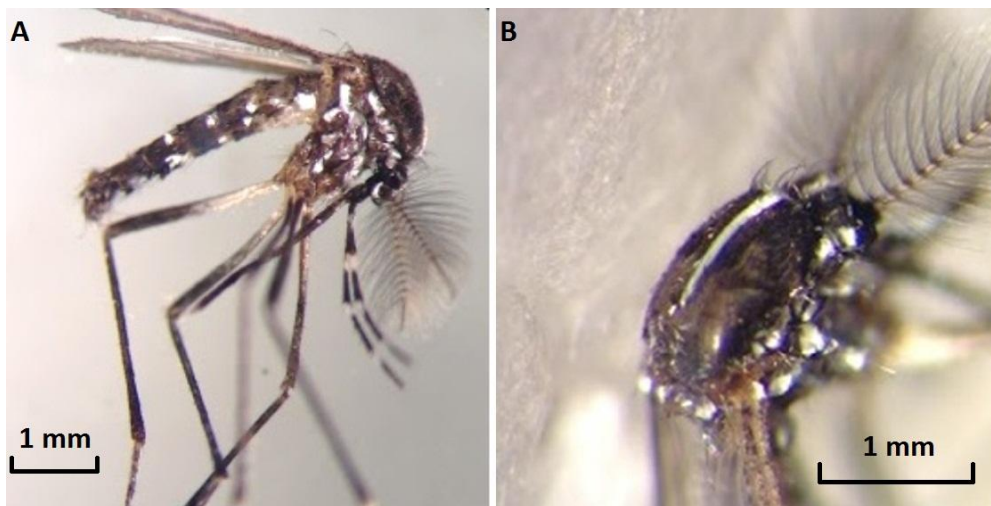


Figure 4. The lateral and dorsal view of a male *Ae. albopictus* (it was collected by Attila J. Trájer and Balázs Tánzos in 2014, Zagreb. Photo by Máté Vass and the Author, 2014).

2.4. SANDFLY VECTORS AND LEISHMANIASIS

Phlebotomus species are important or the only vectors of several arthropod-borne diseases as leishmaniasis and different arbovirus-caused infections. Solely the incidence of leishmaniasis is more than 0.7-1.2 million new cases per year and about 20.000-40.000 death occur every year due to leishmaniasis in the world (Alvar et al., 2012). In the subtropics and tropics, leishmaniasis is one of the most important human VBDs with more than 12 million infected people (Naderer et al., 2006). *Leishmania infantum* NICOLLE, 1908 is the most notable causative agent of leishmaniasis both in humans and the reservoir animals in Europe. Members of the genus *Phlebotomus* are the main vectors of the unicellular eukaryote parasite genus *Leishmania* in Eurasia and Africa. Other sandfly vectors of *Leishmania* parasites can be found in the subgenera *Larroussi* and *Adlerius* (Killick-Kendrick, 1990). In Southern Europe, leishmaniasis is mostly a zoonosis because the main hosts of *Leishmania* parasites are dogs and cats; however, foxes, rodents and horses can also be reservoirs (García et al., 2000; Pennisi, 2002; Köhler et al., 2002; Solano-Gallego et al., 2003; Shaw et al., 2009), and a human-to-human transmission cycle is also possible (Alvar et al., 1997). The observed distribution of the cases of leishmaniasis in dogs (CanL) is similar to the human leishmaniasis' current occurrence (Lindgren et al., 2006; Solano-Gallego et al., 2011). In case of the coinfection with HIV, the manifestation of the symptoms of leishmaniasis is much more serious than in case of 'simple' infections with the parasites (Desjeux and Alvar, 2003). Most of the *Phlebotomus* species can be found in the Mediterranean and peri-Mediterranean areas in Europe, although certain sandfly species such as *Phlebotomus major* subsp. *neglectus* Tonnoir, 1921 (hence simply: *Ph. neglectus*) can be found as high as 47-49° N in Hungary and Germany, as well (Tánczos et al. 2012; Naucke et al., 2008). Some species are restricted to the west or to the east part of the Mediterranean Basin. *Phlebotomus* species are active in temperate regions during summer and in hot tropical and subtropical regions throughout the entire year (Abonnenc, 1972). The most important limiting factors of sandfly distribution, reproduction and survival are winter temperature and summer precipitation (Trájer et al., 2013; Fig.5).



Figure 5. A trapped male *Ph. neglectus* individual (it was collected by Attila J. Trájer and Balázs Tánzos in 2014, Nagyharsány, Hungary. Source: Trájer et al., 2018. Photo by Máté Vass and the Author, 2014).

2.5. DIROFILARIASIS

One of the causative agents of canine heartworm infection, *Dirofilaria immitis* LEIDY, 1856 is a mosquito-transmitted filaroid nematode, which infects mammals, usually dogs (Vörös et al., 2000). Human *D. immitis* infections sporadically present in the European Union (Muro et al., 1999) mainly in the Mediterranean region (Jelinek et al., 1996). Literature provides several human medical aspects of *D. immitis* infection which can be the source of serious diagnostic errors in the human medicine (Ciferri, 1982; Ro et al., 1989) e.g. unnecessarily performed thoracotomy for the removal of the supposed lung tumor (Merrill et al., 1980) or the infection of the spermatic cord (Theis et al., 2001) and intra-ocular infections (Moorhouse, 1978). *Dirofilaria repens* RAILLIET & HENRY, 1911 cause subcutan and ocular infections in humans. Dirofilariasis is one of the most important emerging parasitic, mosquito-borne diseases in the oceanic and temperate climate areas of Europe (Raccurt, 1999; Pampiglione et al., 2001) and North America with serious veterinary and human medical consequences (Macêdo et al., 1998; Pampiglione et al., 1999; Traversa et al., 2010). In the Americas, Iran, Turkey and Australia *D. immitis* is the sole causative agent of canine dirofilariasis, while in China, North Central Europe and South Africa *D. repens* is the parasite responsible for the

disease. In several countries of South Europe and in Hungary both *D. immitis* and *D. repens* cause infection in dogs (Simón et al., 2012; Fig.6).

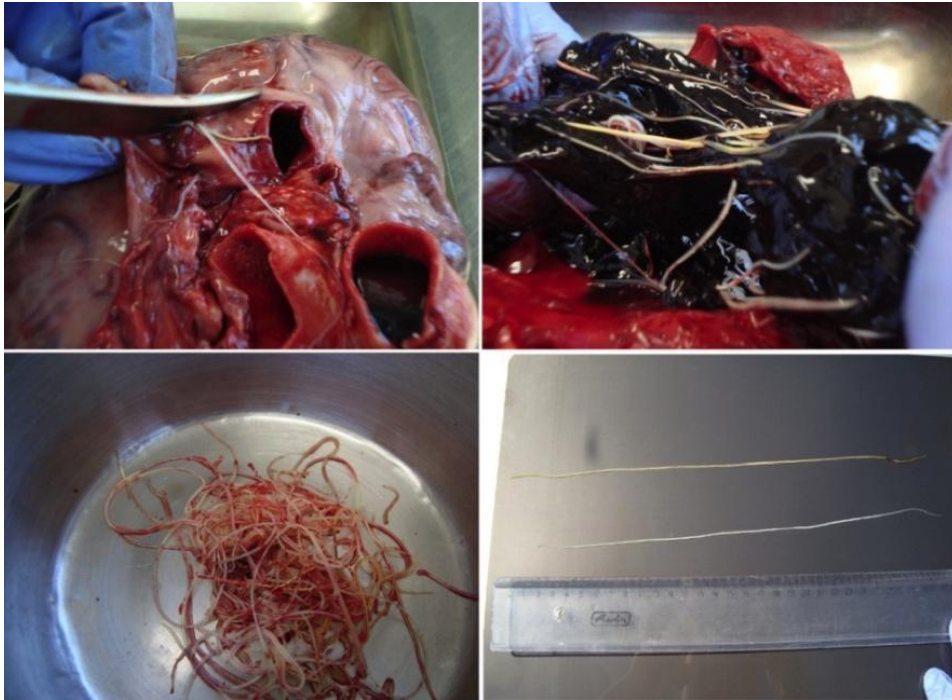


Figure 6. Adult *D. immitis* filarioid worm in the right ventricle, *in situ* photograph and adult *D. immitis* nematodes, *ex situ* photograph (the dog was dissected in 2013. Source: Trájer et al., 2015A. Photo by Antal Rengei, 2013).

Heartworm disease is an emerging parasitosis among dogs in Europe. Within a single decade (from 2001 to 2011), canine dirofilariasis became endemic in seven European countries (Albania, Bulgaria, Croatia, the Czech Republic, Hungary, Romania and Serbia) and in a Russian federal state (Morchón et al., 2012). The first imported dirofilariasis case caused by *D. immitis* was reported from Hungary in 1982 (Boros et al., 1982) and the first autochthonous case was observed only in 2007 (Jacsó et al., 2009). Serological studies conducted in Hungary demonstrated that about 2.4% of dogs are infected by *D. immitis* (Farkas et al., 2014).

2.6. WEST NILE FEVER

West Nile fever (hence: WNF) is an important mosquito-borne infection in the temperate regions of the Northern Hemisphere. The first WNF cases were detected in Europe (Albania) in 1958. Notable outbreaks were recorded already in the 1960's, the 70's and the 90's on the Old Continent (Bardos, 1959). Now, WNF is prevalent in the entire Mediterranean region and the continental parts of Eastern Europe (Hubálek and

Halouzka, 1996), but it is also an emerging disease in North America and North Africa. It is very plausible that the range of the disease will extend in Europe due to AGCC predominantly in East Central and Eastern Europe (Trájer et al., 2014A). West Nile virus, the etiologic agent of WNF (Goldblum et al., 1954) was first isolated in Uganda, in 1937 (Barzon et al., 2015; Kuno et al., 1998). The virus is the member of Flaviviridae, belonging to the Japanese encephalitis antigenic group of Flavivirus. Based on the glycoprotein envelope of the virus, two major human pathogenic lineages were distinguished: Lineage-1 and Lineage-2 strains (Kemenesi et al., 2014; Pachler et al., 2014; Bakonyi et al., 2006). In 20–30% of the cases, WNV causes flu-like symptoms after a 2 to 14-day latency period, although about 70–80% of the cases is asymptomatic, and neurological symptoms appear in less than 1% of the cases. Individuals above the age of 65 have higher risk for morbidity and neurological manifestations (Barzon et al., 2015; Hayes et al., 2005). The most serious manifestation of the diseases is the rare lethal encephalomyelitis in humans. The case fatality rate is about 10% in the neurological infections (CDC, West Nile virus, Symptoms & Treatment). The virus is transmitted by mosquitos from avian hosts in most of the cases. The predominant vectors of WNV are different culicid mosquitos (Koopmans et al., 2007).

2.7. MALARIA AND ITS ANOPHELINE VECTORS

Malaria is one of the most important VBDs in the world affecting at least 3.2 billion people (WHO-World Malaria Report, 2017) and causing about 700.000 to 2.7 million people deaths per a year (Patz and Olson, 2006). The disease is caused by different *Plasmodium* species and transmitted by several *Anopheles* mosquitos. About 40% of the mankind live in malaria endemic areas (Mendis et al., 2001). Once in the wide areas of Europe, malaria was endemic, however, due to the active eradication programs of the 20th century, malaria became a non-endemic or rare disease in the old continent. Based on the risk classification of Gething et al. (2011), in 1900, malaria was mesoendemic in the Balkan (excluding the high Dinarids and the Rodope Mountains) and hypoendemic in the other areas of Eastern and Central Europe. Prior to the 1950s, malaria was endemic to Hungary (Szénási et al., 2003; Lőrincz, 1937). The incidence of malaria was relatively high, because for example, in 1937, the total number of the cases would

exceed the 4,000 in the country (Lőrincz, 1937), that was at least equal to 44 cases per 100,000 inhabitants in this year. The members of the *Anopheles maculipennis* complex were the main vectors of malaria based on the contemporary investigations (Lőrincz, 1937). In Hungary, *Anopheles algeriensis* THEOBALD, 1903, *Anopheles atroparvus* VAN THIEL, 1927, *Anopheles maculipennis sensu stricto* MEIGEN, 1818 (hence: *An. maculipennis*) and *Anopheles messeae* FALLERONI, 1926 were plausibly the main potential malaria vectors. The current geographic range of malaria is much smaller than the range of the potential mosquitos, which phenomena is called as ‘Anophelism without malaria’ (Jetten et al., 1996). The range of malaria is strongly determined by the occurrence of the anopheline vectors and the seasonal activity patterns of both larvae and imagos of malaria mosquitos. Hackett and Missiroli (1935) already in 1935 recognized that the length of the *An. maculipennis* season is determined by latitude which correlates to the spatial patterns of temperature conditions. Kuhn et al. (2002) found significant relationships between climatic factors as precipitation, temperature and the presence of the most important malaria vectors in Europe. The effect of AGCC on the distribution of malaria mosquitos is not a fiction: in the period of 1973–2012, the expansion of *An. maculipennis* was observed in Northeastern Europe and Northwestern Asia (Novikov and Vaulin, 2014). Parallel to the spread of the vectors, one of the possible results of elevated temperature conditions is the increasing worldwide burden and distribution of malaria (Lindsay and Birley, 1996; Loevinsohn, 1994). Martens et al. (1999) predicted that the greatest potential consequences of AGCC are that malaria will occur in temperate zones, where the anopheline mosquito vectors are present but the recent cooler climate does not allow the transmission of the parasites. Kuhn et al. (2002) showed that AGCC can significantly increase the abundance of the European *Anopheles* species.



CHAPTER II

Seasonal patterns

The topics of this chapter:

- **Changing seasonality of *Anopheles maculipennis***
- **Diversity, seasonal abundance and potential vector status of the cave-dwelling mosquito fauna of the Bakony-Balaton region**

1. CHANGING SEASONALITY OF *ANOPHELES MACULIPENNIS*¹

1.1. INTRODUCTION

The activity of malaria vectors and the seasonal transmission probability of *Plasmodium* species are highly sensitive to climatic conditions (Martens et al., 1995) – mainly the changes of temperature (van Lieshout et al., 2004). Similarly to the larvae of other anopheline mosquitos, the larvae of *Anopheles maculipennis* also develop through four instars, after which they metamorphose into pupae. The time of development is the function of water temperature where larvae develop, and it indirectly depends on the ambient air temperature. Paz and Albersheim (2008) concluded that ‘elevated ambient temperature increases the growth rates of mosquito vector populations, since the full ontogeny time of mosquitos depends on temperature’. The larvae of *An. maculipennis* can inhabit the water of smaller watercourses, marshes, brooks, rainwater puddles, and the littoral part of small lakes, or they can live even in dendrotelmata, phytotelmata, technotelmata, or malakotelmata. In the Bakony-Balaton region, Hungary, larvae were continuously collected from the beginning of April to mid-October, and the main swarming season of imagos occurred from late June to the end of September (Tóth, 2006). The species avoid the salt lakes of the Hungarian Great Plain (Tóth, 2004). Climate models predict the resurgence and worldwide increasing risk of malaria transmission due to the anthropogenic climate change (Martens et al., 1999). It was found that small increases in temperature at low temperatures can increase the risk of malaria transmission substantially (Lindsay and Birley, 1996), although the potential effect of the changing climatic patterns is strongly influenced by socioeconomic developments and malaria control programs (Martens et al., 1995). For example, in the East African highlands, the warming trend from 1950 to 2002 caused the parallel increases in malaria incidence. The rapid response of malaria to the changing temperature patterns is understandable as *Anopheles* mosquitos are highly sensible for the meteorological conditions, particularly to the air temperature.

¹This chapter was published in Időjárás:

Trájer, A.J., Hammer, T. (2018). Expected changes in the length of *Anopheles maculipennis* (Diptera: Culicidae) larva season and the possibility of the re-emergence of malaria in Central and Eastern Europe and the North Balkan region. Időjárás/Quarterly Journal of the Hungarian Meteorological Service, 122(2), 159-176.

Temperature determines the time of the ontogeny and the questing activity of female mosquitos (McDonald, 1957; Jetten and Takken, 1994). In addition, the highly complex ontogeny of *Plasmodium* parasites is also the function of the ambient temperature. For example, it is known that the lower temperature threshold of the ontogeny of *Plasmodium vivax* GRASSI & FELETTI, 1890 and *P. falciparum* are 14.5-16 and 18 °C, respectively (McDonald, 1957). Even Hackett and Missiroli (1935) showed that the pattern of malaria season is in correlation with the latitude of a malaria endemic area, since the latitude essentially determines the annual temperature conditions with other factors, e.g., as the distance from the oceans and the altitude conditions. Before the 20th century, the 15 °C July isotherm appointed the northeast occurrence of the endemic malaria cases (Menne and Ebi, 2006). Precipitation is also an important factor of the malaria cases determining, with the temperature conditions, the dominance of the *Anopheles* species in Europe (Kuhn et al., 2002). In the Atlantic and continental climate zones of Europe, as the Central European region, *An. atroparvus* in Eastern Europe, *An. messeae* and in the Balkan Peninsula *Anopheles superpictus* GRASSI, 1899 are the main potential vectors of the human pathogen *Plasmodium* species.

Recently, seven *Anopheles* species are known from Hungary, although the presence of *Anopheles sacharovi* FAVRE, 1903 is also possible in the southern border areas (Sáringér-Kenyeres et al., 2018). In Hungary, *An. atroparvus*, *An. maculipennis*, and *An. messeae* are the plausible potential vectors of the *Plasmodium* parasites according to the historical data (Szénási et al., 2003). It is also known that before the eradication of the malaria in Hungary, *P. vivax* caused the 90% and *P. falciparum* the 10% of the malaria cases. The resurgence of malaria in Europe is more than a fiction: *Plasmodium*-infected people introduced tropical malaria during the 1997 heat-wave in Germany (Krüger et al., 2001) and Italy (Baldari et al., 1998), when local female *Anopheles* mosquitos bite infected passengers returning from endemic areas. The reverse case is also known, when introduced, infected malaria vectors caused malaria infection in the airport staff or the people living in the neighborhood of the airport (Giacomini et al., 1997). However, the well-developed simulations provide information of the vector potential of the *Anopheles* species in the near future; there are no well-based evidences about the potential seasonality of malaria in the continental areas as the Carpathian Basin. In turn, seasonality and the determinants of the annual run of the disease season

can be more important factors of the possibility of reemergence of malaria than the simple presence of the malaria vectors. Since either the tropical vectors or the parasites are not or only partly equivalent to their continental counterparts, the model results require further validation. According to the above described causes, only the historical data of an area in a temperate region can provide a reliable basis and model for the potential near future seasonality of malaria in the temperate regions, even the climate is changing. In contrast to the northern regions of Europe, where malaria spontaneously disappeared in the early 20th century (Bruce-Chwatt and de Zulueta, 1980), the malaria eradication was the consequence of the joint effort of public health services in Hungary (Szénási et al., 2003).

Objective. It was aimed to model the changing seasonality of *An. maculipennis* larvae due to climate change in Central and East Europe and the North Balkan region based on the scenarios of the REMO climate model (Kotlarski et al., 2005). We focused on the modeling of the start and end of the mosquito larva season of *An. maculipennis*.

Hypothesis. As above was mentioned, the annual abundance of *Anopheles* species (both of larvae and of imagos) follows the change of such climatic factors as the ambient temperature. Based on this observation, it was hypothesized that using the temperature-abundance correlation of *Anopheles* larvae, the season of malaria mosquito larva season can be modeled and projected for the future. It is well known that the seasonality of insects strongly depends on temperature which predicts that rising temperatures will cause the prolongation of the mosquito seasons.

1.2. MATERIALS AND METHODS

1.2.1. Climate data and its processing

Since the climatic and topographical conditions are very homogenous in the country, Hungary was considered in climatic sense as a homogenous unit. The daily temperature values were gained from the KNMI (Koninklijk Nederlands Meteorologisch Instituut) Climate Explorer (Klein Tank et al., 2002), E-OBS model (1950-now; Haylock et al., 2008). Average values were calculated from the 0.5° grid within the domain including almost the entire Hungary. The latitudinal range was 45.50°N-48.50°N, while the longitudinal was 16.00°E-23.00°E. The monthly mean temperature values were derived

from the period of January 1970 to December 1999. The daily data was converted into monthly mean temperature values.

It was thought that ambient air temperature can be handled as the principal factor of *An. maculipennis* seasonality with specific regard to the start and end of the mosquito larva season, and consequently, temperature can strongly influence the total length of the larva season. This presumption was based on the observations that the poikilothermic *An. maculipennis* mosquitos breed in small lakes, small lake-like reservoirs, litoprofundal shallow lakes, and swamp-like natural waters (Tóth, 2004), which have low heat storage capacity due to the combination of extent water surface and relatively low water depth. This geometry is expressly true for the narrow littoral zone of the waters, where the larvae of *An. maculipennis* can be found.

Two climate data sources were used:

1) The REMO model provided climatic analysis for the reference period and two future periods (2011-2040 and 2041-2070) for modeling purposes.

2) Since the collection period of mosquito larvae (from the 1960s to the end of the 1990s - which practically means the period of 1961-1999 in the present analysis) does not completely overlap the reference period of the REMO model (1961–1990), the E-OBS climate model (from 1950 to now) was used for performing correlation between monthly relative mosquito larva abundances and monthly mean temperature values.

European climate data were obtained from the regional climate model REMO, which was developed in Hamburg (Jacob and Podzun, 1997; Jacob, 2001). The horizontal resolution of the used grid is 25 km×25 km. The model REMO is based on the ECHAM5 global climate model (Roeckner et al., 2003, 2004) and the IPCC SRES A1B scenario. The A1B scenario supposes very fast economic increase, a worldwide population peak in the middle of the 21st century, and the introduction of innovative and efficient technologies (Nakicenović et al., 2000). The reference period of REMO is 1961-1990, the two future periods of modeling are 2011-2040 and 2041-2070. Although the entire European continent is within the domain of REMO, only a part of the grid covering the studied area was used. For the abundance modeling, only one variable, the monthly mean temperature (°C) was used. To perform the correlation between the relative (%) abundance values and mean temperatures, mean temperature values of the period 1961-1999 were gained from the E-OBS model. The monthly ambient

temperature values were averaged according to monthly temporal resolution. The following grid was used which covers almost the whole area of Hungary: from 45.75 to 48.50N and from 16.00 to 23.00 E. The spatial resolution was $0.25^\circ \times 0.25^\circ$.

1.2.2. Mosquito data

The relative abundance, RA (in %), value of the female imago individuals of *An. maculipennis* s.s. was gained from the three decades (1970s, 1980s, and 1990s) covering countrywide mosquito collecting data of Tóth (2004). This monograph contains the data of different mosquito larvae, pupae, and adults based on the literature of the former mosquito collection efforts in Hungary and the author's own surveys. The monograph was based on the data of collections, which were performed basically in the 1960s, 1970s, 1980s, and the 1990s. The abundance data of larvae of *An. maculipennis* were used in monthly temporal distribution. The absolute number of larvae was converted to relative monthly abundance values according to Eq.1. If the total annual value is 100%, relative monthly abundance value is

$$A_{rm} = \frac{N_m}{N_a} \times 100 \quad (1)$$

where A_{rm} is the relative abundance of a month, N_m is the number of the total collected larvae according to a given month, and N_a is the total number of the collected larvae representing the entire period.

The number of collected female mosquitos was assorted according to the months of the year and used the summarized monthly female mosquitos in the model. The number of the collected mosquitos was termed as a relative abundance (RA). Since the monthly value of RA depends on the number of monthly trapping occasions, we used the quotient of RA and the number of the trapping occasions (termed as the normalized relative abundance value, NRA ; Eq.2):

$$NRA = \frac{RA_i}{N_t} \quad (2)$$

where NRA is the normalized relative abundance, RA_i is the normalized relative abundance of the i th month of the year and N_t is the number of trapping occasions in the i th month of the year. Since this number is based on the summarized number of collected mosquitos, this data was utilized to build only a relative model predicting the seasonal run of the malaria mosquito season.

1.2.3. Modeling steps

Comparing the relative monthly abundance data of the larvae of *An. maculipennis* and the monthly mean temperature values, it was observed, that the annual abundance profile of the mosquito larvae starts to increase rapidly above the abundance value of 12% in May, and inversely, the main season ends, when the abundance decreases below this value after September in Hungary. The 12% monthly abundance value was handled as the frame of the main larva season of the mosquito. Only those months were involved into the analysis, when the monthly mean temperature of the period exceeded the 4 °C value, which empirically indicates the start/end of the larva season. ESRI ArcGIS 10.0 software (ESRI 10.0) was used for preparing climatic data, running the model, and displaying the model results. First step, the georeferenced climate data of REMO climate model were loaded to the program. Using the raster calculator function of ArcGIS, monthly temperature values were converted into monthly relative abundance values. The raster results were converted to polygon-type ESRI shapefile format. The order of the three layers - the modeled relative larva abundance values of the periods 1961-1990, 2011-2040, and 2041-2070 - determined that the result maps can show the mainly northward (spring), southward (autumn), or the seasonal altitudinal shifts of the relative abundance (or activity) of *An. maculipennis* larvae. To create color images, we linked the points with the calculated relative abundance values. The different values were assigned to the referred points and were sorted into attribute table. Then the climatic data were refined by the inverse distance weighted interpolation method of ESRI ArcGIS 10.0 software. Color codes of relative abundance values were selected according to a 0 to 12 (exactly to 12.24<) scale. Dark red color was used to mark the main season in the maps, when the modeled relative abundance values reach or exceed the 12% annual value; porcelain white color indicates the pre or post-season areas, where there are no active larvae in the natural waters.

1.2.4. Statistics

Simple linear correlation and regression were performed by the simple regression tool of VassarStats on-line statistical program (Lowry, 2004). Microsoft Office 2010 Excel was used in the visualization of the graphs. ArcGis 10.0 software was used in the performance of the spatial data.

1.3. RESULTS

1.3.1. Correlation between the larva abundances and temperature

The start of the main season was in April, while the threshold of the larval abundance of *An. maculipennis* was about 4 °C in Hungary in the reference period. In the end of the season, the monthly abundance value decreased below the 12% value which occurred in October, while the larval season ended in November in the reference period in Hungary, when the ambient mean temperature sank below 4 °C. Strong, significant linear correlation was found between the monthly relative abundances of larvae and the mean ambient temperature values ($r^2=0.94$, $p<0.0001$) from March to November (Eq.3):

$$A_{rm} = 1.3564 * T_m - 7.1749 \quad (3)$$

where is A_{rm} the relative (%) abundance of *An. maculipennis* larvae in a month, T_m is the mean monthly ambient temperature (°C). Eq.3 was used in the modeling if the projected abundance of the larvae (Fig.7).

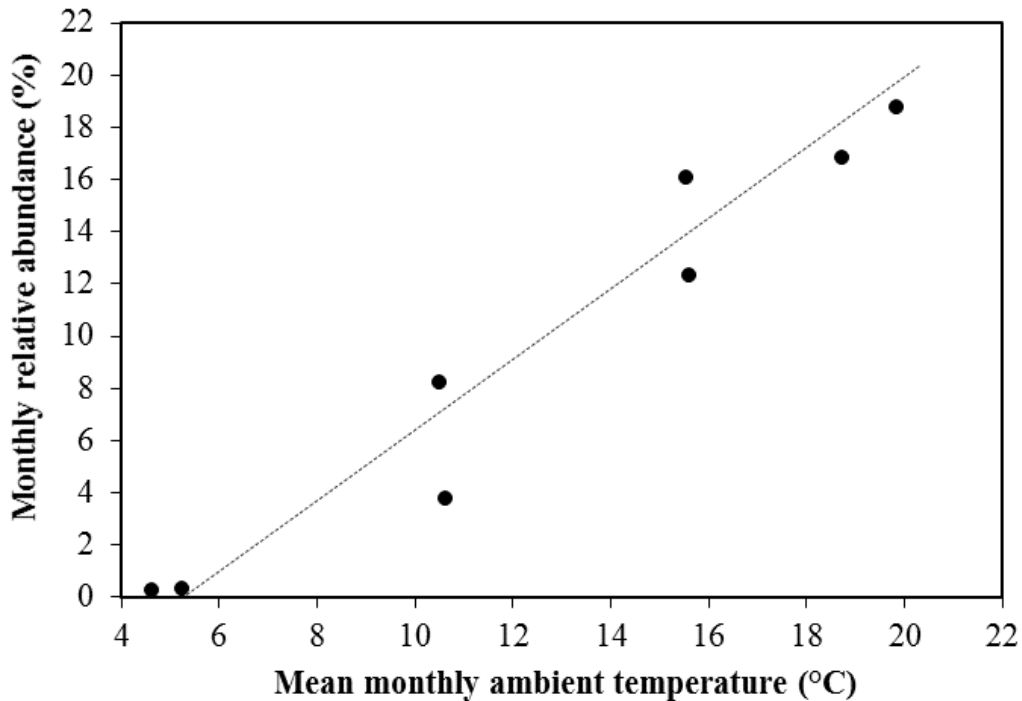


Figure 7. The correlation between the monthly relative abundances of *An. maculipennis* larvae and the mean monthly ambient temperatures in March to November.

1.3.2. Modeled starts of the seasons

The modeled relative abundance values of *An. maculipennis* larvae showed notable differences in the case of the three different 30-year periods. Comparing the modeled abundances for the reference periods 1961-1990, 2011-2040, and 2041-2070, the most notable spatiotemporal shifts in the main larval seasonality, including the start of the absolute and the main season, was observed in April based on the modeled relative abundances. It was modeled for the reference period, that the main larva season usually did not start until May in Central and East Europe and the North Balkan region except a Romanian lowland section of river Danube. In contrast, for the period 2011-2041, the model predicts, that the main season of the larvae of *An. maculipennis* will start in April in the areas of Vojvodina, Serbia and the Romanian Lowland. For the period 2041-2070, the model predicts the broader shift of the main season's start from May to April affecting almost the entire South Pannonian Ecoregion. In Southeast Hungary, East Croatia, North Serbia, South Romania, and North Bulgaria, the total main season will shift by 1 month to the period of 2041-2070. For 2041-2070, the model predicts that the start of the season of the mosquito's larvae in Southeast Germany, the Czech Republic, and the northeastern forelands of the Carpathian Mountains will start one month earlier compared to the reference period (Fig.8).

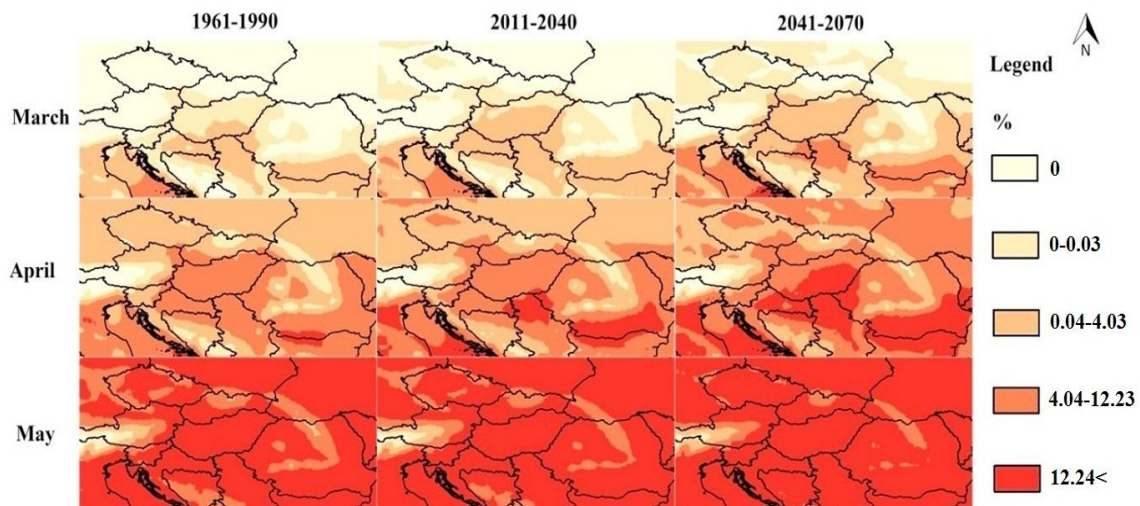


Figure 8. The predicted monthly relative abundance values of *An. maculipennis* larvae in Central and East Europe and the North Balkan in March, April and May for the periods of 1961-1990, 2011-2040, and 2041-2070.

1.3.3. Modeled ends of the seasons

The model predicts that the main season of *An. maculipennis* larvae will end one month later in 2041-2070, compared to the reference period, when it ends in October. For 2041-2071, the model predicts that the total season will not end until November in the northern part of Central Europe. For 2041-2070, the model predicts also that the main season of the mosquito's larvae will continue to the end of October in the entire North Balkan and South Pannonian Ecoregion to the end of October. In Hungary, the end of the main season will shift by plus 1 month for the period 2041-2070. Due to the high heat storage capacity of the sea water, the main season of *An. maculipennis* continues to November in the Adriatic coasts. For 2041-2070, the model predicts that the start of the season of the mosquito's larvae in South East Germany, the Czech Republic and the northeast forelands of the Carpathian Mountains will end one month later compared to the reference period. The model shows the vertical shift of the season, which is clearly visible in case of the Transylvanian Middle Mountains or in the Dinarid Ranges, where the main part of the season also predicted to start earlier and end later by 1-1 month (Fig.9).

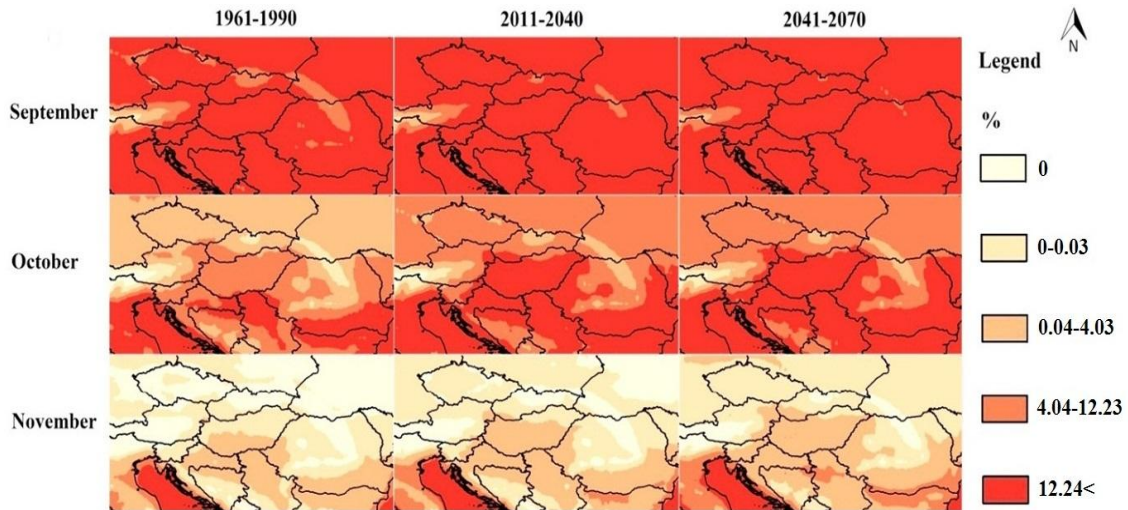


Figure 9. The predicted monthly relative abundance values of *An. maculipennis* larvae in Central and East Europe and the North Balkan in September, October and November for the periods of 1961-1990, 2011-2040, and 2041-2070.

1.4. DISCUSSION

The modeling of the larva seasons of *An. maculipennis* provided important additive information on the influencing climatic factors of the former temperate malaria. The potential malaria vector role of *An. maculipennis* sensu stricto can be proposed due to the high frequency of the species compared to the total mosquito material. *Anopheles maculipennis* or even *An. messeae* can be handled as the typical model species of the *An. maculipennis* complex. In the historical times, up to the middle of the 20th century, *Plasmodium vivax* was the predominant cause of malaria in the temperate parts of Europe, and *P. falciparum* persisted only in the Mediterranean coastal regions of the old continent (de Zulueta, 1994). The possibility of the overwintering of *Anopheles* mosquitos is not theoretical, since the lethal temperature for some members of the genus is below -15 °C (Wallace and Grimstad, 2002). It is plausible that relatively cold-resistant *Plasmodium vivax* was the main infectious agent of malaria in Hungary (Szénási et al., 2003) This *Plasmodium* species accounts for more than 50% of all human malaria cases outside of Africa recently (Mendis et al., 2001). *P. vivax* infection is a re-emerging malaria disease in the eastern part of the Mediterranean Basin (Andriopoulos et al., 2013). The occurrence of malaria is strictly limited by precipitation and temperature thresholds. For example, the temperature threshold of the digestion of blood meal in case of *Anopheles maculipennis* is 9.9 °C, while the threshold temperature of the extrinsic incubation cycle of *Plasmodium vivax* is 14.5-15 °C (Martens et al., 1995). The absolute minimum limits of the start and the end of the malaria season were about at the 5 °C mean monthly temperature values which are lower than the recent known, at least 14.5 °C ontogeny threshold of the *Plasmodium* species (McDonald, 1957). In the light of these facts, it is interesting that it was found that the threshold of the larval abundance of *Anopheles maculipennis* is about 4 °C in Hungary that is very close to the former absolute temperature limit of malaria in Hungary. It is in accordance with the gained, also about 5 °C minimum activity threshold of adult female *An. messeae* individuals. These observations raise the possibility that the former malaria strains were colder tolerant in the temperate regions of Europe than the recent genetic lines in the tropical/subtropical regions. The larva seasonality model revealed an important factor of the possible re-emergence of malaria in Central and East Europe, since the length of the mosquito larva season also affects

the possibility of malaria transmission by several direct and indirect ways. In contrast to the recent tropical and subtropical examples, malaria in the temperate, continental climate of Hungary had mainly unimodal seasonality with a 3 to 4 months' winter diapause. It is also notable that the also mosquito-transmitted, in Hungary recently endemic WNF has a late summer - early autumn peak season with a very low and negligible case number in June (Trájer et al., 2014A).

The monthly relative abundance values of *An. messeae* larvae were modeled for 1961-1990, 2011-2040 and 2041-2070 in Central and East Europe and the North Balkan region based on the REMO climate model and the Hungarian monographic mosquito data of Tóth (2004). The results predict the notable elongation of the larva season for 2011-2040 and 2041-2070 compared to the reference period 1961-1990. The changes of the geographical patterns of the starting and ending months of the main and absolute seasons seem to be inhomogenous in the studied region. The fastest increase of the season's length will affect the areas, where large rivers and flood basins occur. The model predicts the most rapid elongation of the larva season of *An. maculipennis* in the central part of the Pannonian Ecoregion and the lower (Romanian and Bulgarian) section of the Danubian Plain. The model shows that the length of the main season is predicted to increase by 2 months for 2041-2070 in the southeastern part of the Hungarian Great Plain, while in the other parts of the Pannonian Ecoregion and the North Balkan, the length of the main season will elongate by less than two months for the second future period. These heterogenic predicted spatial-temporal changes of the activity of larvae can be the potential consequence of the faster warming climate of the Carpathian Basin.

Based on the modeled present and future larva seasonality it can be concluded that one of the most important factors of temperate malaria is the ambient temperature. Since increasing temperature also increase the length of the mosquito season and consequently enhance the number of annual generations and mosquito abundance, the modeled future elongation of the larva season may indicate the increasing risk of the re-surgence of malaria in the North Balkan and the Pannonian Ecoregion, including the territory of Hungary.

2. DIVERSITY, SEASONAL ABUNDANCE AND POTENTIAL VECTOR STATUS OF THE CAVE-DWELLING MOSQUITO FAUNA OF THE BAKONY-BALATON REGION²

2.1. INTRODUCTION

Swamps, puddles, techno- and dendrotelmata and other small aquatic habitats are the most frequently investigated mosquito breeding sites. In contrast, there is a limited knowledge about their shelters and overwintering habitats. Caves represent a potential natural shelter of mosquito species, but they cannot fully complete their life cycle in this environment. Kjærandsen (1993) concluded that most of the trogliphile Diptera species including mosquitos inhabit caves and cave systems only for hibernation. Mosquitos are the elements of the food chain in caves as prey for chiropterans and arachnid species. Trogliphile fauna is consisted of several relatively small, poikilotherm animals, while female mosquitos must feed on homeothermic (warm-blooded) birds and mammals. The only frequent, trogliphile, warm-blooded mammals in the temperate region belong to the order Chiroptera whose animals are the predators of mosquitos in caves. In contrast, the balanced, tempered and permanently humid air and wall of caves provide the opportunity of successful overwintering for the imagos. Mosquitos enter caves to escape of the outside existing unfavorable conditions as low air temperature or dryness and can avoid the great predation pressure by birds during daylight (Ives, 1938). Mosquitos inhabit the caves periodically in a certain part of the year. Whang (1961) found that the largest number of *Culex pipiens pipiens* L. (1758) mosquitos was collected from culverts and caves where the temperature and humidity were higher than in the surrounding environmental sites of this species concluding that the individuals of the mosquito hibernate as adults Whang (1961) found no larvae between November and April around the hibernating where shelters as caves are available.

²This chapter was published in Acta Zoologica Bulgarica:

Trájer, A.J., Schoffhauzer, J., Padisák, J. (2018). Diversity, seasonal abundance and potential vector status of the cave-dwelling mosquitoes (Diptera: Culicidae) in the Bakony-Balaton Region. Acta Zoologica Bulgarica, 70(2), 247-258.

The mean air temperature of caves corresponds to the mean annual temperature of a given area. In wide areas of the temperate zone, ambient temperature can be too low for the full development of mosquito species. Whang (1961) found that while in the coldest months the average temperature was below the freezing point, temperatures in the main hibernating sites (including caves) were usually above 0 °C. The difference between the temperatures of cave habitats and the ambient environment could be even 12-13 °C. Mosquitos, in general, can be found in the parahypogean region ('twilight zone') of caves, but according to the ambient conditions, they can change their position. Buffington (1972) observed an extensive movement of *Cx. pipiens* populations even during midwinter concluding that the changes of air current directions may have a significant effect on the movement of mosquitos on the cave wall.

The females of *Culex pipiens pallens* COQUILLET, 1898 e.g. can be found only near the entrance in summer but they move to the deeper parts of the cave in winter period (Shimogama and Takatsuki, 1967). Kűchlein and Ringelberg (1964) observed that *Cx. pipiens* mosquitos can be found in the twilight zone in the cold period of January, mainly on the side opposite to the entrance of the cave. They found that the zone maxima in the distribution of the mosquitos coincide with the decreasing light intensity in the twilight zone. The twilight zone is characterized by minor temperature fluctuations in conjunction with weather changes of the ambient environment, minimal plant life (mainly green algae and cyanobacteria) and less light.

Objective. It was to study the diversity, seasonal abundance, gender ratio and the vector status of mosquito imagos collected in 19 caves of the Bakony-Balaton Region, Hungary.

Hypothesis. It was hypothesized (based on the results of the international literature in the topic) that a relatively few mosquito species can overwinter in such natural shelters as caves. The presence of *Anopheles* and *Culex* species were expected in general.

2.2. MATERIALS AND METHODS

2.2.1. Study area

The Bakony Mountains and the Balaton Uplands are the parts of the Transdanubian Mountain Range situating on the ALCAPA megaunit, which has African origin

(Csontos and Nagymarosy, 1998; Márton and Fodor, 2003). These mountain ranges are built up mainly of Mesozoic carbonates, although Tertiary volcanites and non-volcanic Miocene sediments also can be found in the area (Németh and Martin, 1999). Several types of opened and covered karst structures occur in the Transdanubian Range including paleokarst structures that were mainly formed on Mesozoic carbonates (Bolner-Takács, 1999; Veress, 2009). Basalt covered karst is also known in the Bakony Mountains (Móga and Németh, 2005).

2.2.2. *Mosquito data*

The mosquito data were gained from the monography of Tóth (2006), which is the most detailed collection of the mosquito occurrence of the region. Mosquito imagos were collected in period from 1973 to 1999 by several authors. In some caves trappings were performed more than once. The number of the collected individuals were sorted by 1) species, 2) the time of collection and 3) the gender of the collected individuals. The definition of the term of 'cave' in Hungary is the following: 'a natural cavity whose longitudinal axis exceeds the 2 meters' length allowing the penetration of a man and it was formed in the firm rock of the Earth's crust.' The troglophile mosquito fauna of 19 caves were studied: Alba Regia Cave (Isztimér; 1), Bújó lik Cave (Ajka; 2), Forrás Cave=Forrás Cave of Tihany (Tihany; 3), Hajszaabarnai Cave=Hajszaabarnai Pénz lik Cave (Bakonyjókó; 4), Kecse lyuk Cave=Cseszneki sziklaodú Cave (Csesznek; 5), Kőpince Cave=Cuha valley No. 2. Cave (Bakonyszentlászló=Bakonyszentkirály; 6), Kőmosó Cave=Csesznek Cave (Csesznek; 7), Lóczy Cave (Balatonfüred; 8), Macska lik Cave (Nagyvázsony; 9), Magos hegy Cave (Dudar; 10), Nagy Pénz lik Cave (Bakonybél; 11), Odvas Kő Cave (Bakonyszücs; 12), Ördög lik Cave=Ördög lik Cave of Kőrös Mt. (Bakonyszücs; 13), Pokol lik Cave (Ajka; 14), Pörgöl Cave=Száraz Gerence Cave (Bakonyszücs; 15), Pula Basalt Cave (Pula; 16), Lake Cave of Tapolca (Tapolca; 17), Tilos erdő Cave (Pénzesgyőr; 18) and Tűzköves hegy Cave (Szentgál; 19). The synonym names used in the monograph and the official names were also indicated. The numbers after the settlement names are the sequence numbers of the caves used in the study. Hereinafter, the recently used officinal names of the caves were used. *Fig.10* shows the localization of the caves in the Bakony-Balaton Region).

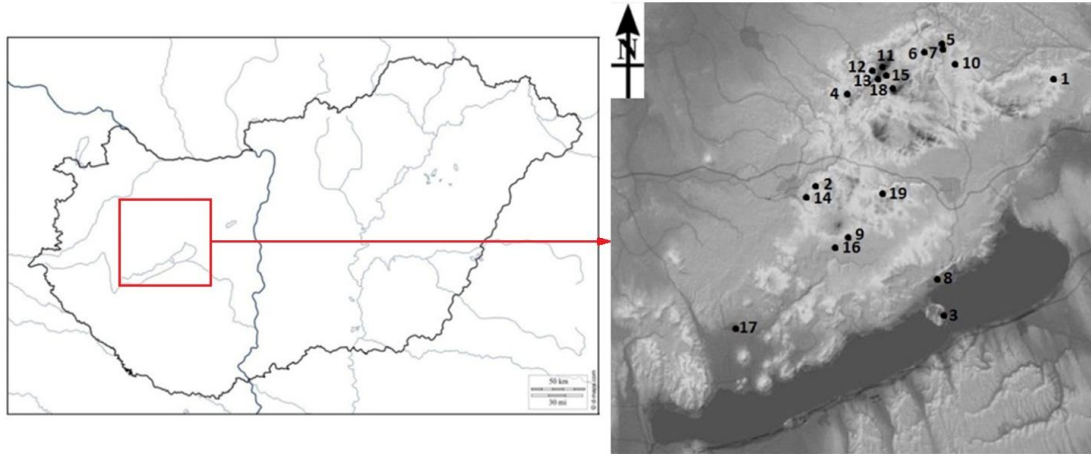


Figure 10. The geographical setting of the area in Hungary and of the studied caves in the Bakony-Balaton Region. (for location and name of the caves, see the text above).

2.2.3. Climate data

Mean monthly ambient temperature and precipitation values of the period 1973-1999 were gained from the 0.25° resolution E-OBS climate model (Haylock et al., 2008) according to the covering grid of 17.25° to 18.25° and 46.75° to 47.50°. Mean monthly values were averaged.

2.2.4. West Nile fever data

The countrywide case number data of WNF were gained from the periodicals of the Hungarian National Epidemiological and Surveillance System (Epinfo 1-2). The monthly sums of West Nile fever case numbers were converted into percentage values based on the total case number of the period.

2.2.5. Aridity index

Aridity has negative effect on the reproduction and activity of mosquito species. For the characterization of the level of aridity, which is correspondent to both the air and soil aridity level the Thornthwaite agrometeorological index (TAI) was employed (Sábitz et al., 2014; Eq.4).

$$TAI = 1.65 \cdot \left(\frac{P}{T+12.2} \right)^{\frac{10}{9}} \quad (4)$$

P = monthly precipitation sum

T = monthly mean temperature

2.3. RESULTS

2.3.1. Species composition of the cave-dwelling mosquito fauna

A total of 751 mosquito individuals of seven species were collected in the caves of the Bakony-Balaton Region in the period 1973-1999. It means that the 15.2% of the mosquito fauna of the region (46) were found in the studied caves. In average, 2.3 species were found per cave (minimum: 1, maximum: 4, median: 2.0, SD: 0.88). *Culex pipiens pipiens* specimens were found at 18 sites (94.7% of the caves), *Culiseta annulata* SCHRANK, 1776 at 15 sites (78.9%) and *Anopheles messeae* at 4 sites (21.1%). The other species were found in the following number of caves: *Anopheles maculipennis* MEIGEN, 1818 at 3 sites (15.8%), *Culex hortensis* FICALBI, 1890 at 2 sites (10.5%) and *Culex pipiens molestus* FORSKAL, 1775 and *Culex territans* WALKER, 1856 are known from only 1-1 sites (5.3-5.3%). None of the species of the genera *Aedes*, *Ochlerotatus*, *Coquillettidia*, *Orthopodomyia* or *Uranotaenia* were found in the caves of the region. *Culex pipiens pipiens* contributed 85.2% of the collected material and the further six species altogether reached only 14.8% of the mosquito material (Tab.1).

Table 1. The absolute and relative numbers of the collected mosquitos by species without the most frequent *Cx. pipiens pipiens*.

Species	Absolute numbers	Percentages of the total (%)
<i>An. maculipennis</i>	10	1.93
<i>An. messeae</i>	5	0.96
<i>Cx. hortensis</i>	2	0.39
<i>Cx. pipiens molestus</i>	4	0.77
<i>Cx. territans</i>	1	0.19
<i>Cs. annulata</i>	59	11.37

Culiseta annulata was the second most frequent troglophile mosquito species of the Bakony-Balaton Region (11.2%). The other six collected species accounted for only 3.6% of the mosquito fauna. The frequency order of the further collected mosquito species is the following: *Anopheles maculipennis* (1.5%)>*An. messeae* (1.2%)>*Culex pipiens molestus* (0.5%)>*Cx. hortensis* (0.3%)>*Cx. territans* (0.1%; Tab.2).

Table 2. The frequency of the mosquito species in the different cave groups (A: 6, 8 and 14; B1: 2; B2: 5, 11; C: 1, 9 and 17; D: 4, 18; E: 3, 7, 10, 12, 13, 15, 16 and 19).

Group	<i>An. maculipennis</i>	<i>An. messeae</i>	<i>Cs. annulata</i>	<i>Cx. hortensis</i>	<i>Cx. pipiens pipiens</i>	<i>Cx. pipiens molestus</i>	<i>Cx. territans</i>
A	1	0	0.33	0	0.66	0	0
B1	0	1	0	0	0	0	0
B2	0	0	0	0	1	0	0
C	0	1	1	0	1	0.33	0
D	0	0	1	1	1	0	0.5
E	0	0	1	0	1	0	0

The malaria mosquito *Anopheles maculipennis* was the common fauna element of Cuha valley No. 2. Cave, Lóczy and Pokol lik Caves. Only one mosquito species was collected in Bújó lik Cave, Cseszneki sziklaodú Cave and Nagy Pénz lik Cave. In Bújó lik Cave, only *An. messeae* in the Cseszneki sziklaodú and Nagy Pénz lik Caves solely *Culex pipiens pipiens* formed the resident mosquito fauna. In Alba Regia, Macska lik and Lake Cave of Tapolca *Anopheles messeae*, *Culex pipiens pipiens* and *Culiseta annulata* were also trapped. The common character of Hajszabarnai Pénz lik and Tilos erdő Caves was that *Culex hortensis*, *Cx. pipiens* and *Culiseta annulata* were the common mosquito fauna elements. Exclusively *Cs. annulata* and *Culex pipiens pipiens* formed the resident mosquito fauna of the Forrás Cave of Tihany, Csesznek, Magos hegy, Odvas Kő, Ördög lik, Száraz Gerence, Pula Basalt and Tüzköves hegy Caves.

2.3.2. Seasonal abundance of mosquitos in caves by genders

Female imagos formed the major part of the collected mosquitos. The gender ratio was 0.056 (♂/♀). Only the 5.62% of the mosquitos were males. In case of *Culex hortensis*, *Cx. pipiens molestus* and *Cx. territans*, only female individuals were collected. In case of *Anopheles maculipennis* (GR: 0.1), *An. messeae* (GR: 0.125), *Culiseta annulata* (GR: 0.037) and *Culex pipiens pipiens* (GR: 0.058) both male and female individuals were trapped. Male mosquitos were collected only in the second half of the year, while female individuals were collected both in the first and the second half of the year. Both the relative abundance values of males and females exhibited an increasing trend between August and November (Fig.11).

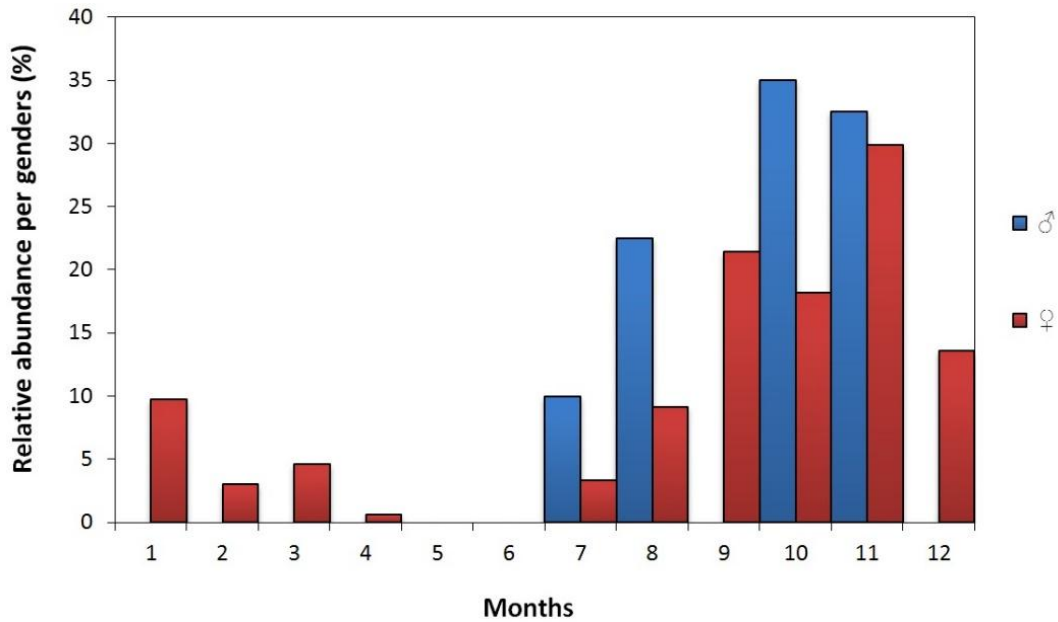


Figure 11. The relative monthly abundance values (%) of the mosquitos by genders in the period 1973–1999, based on the summarized data of the studied 19 caves.

In case of *Cx. pipiens pipiens*, the relative number of males started to increase in July, reached its maximum in November and males were not found later. From July to November the abundance of female mosquitos showed a similar pattern, but female mosquitos were continuously collected from July to April (Fig.12A). In case of *Culiseta annulata*, the relative number of males started to increase in October and reached a maximum in the same month. Less number of males was collected also in November. The abundance of females started to increase from August and reached its maximum in November. Female mosquitos were continuously collected from July to April (Fig.12B).

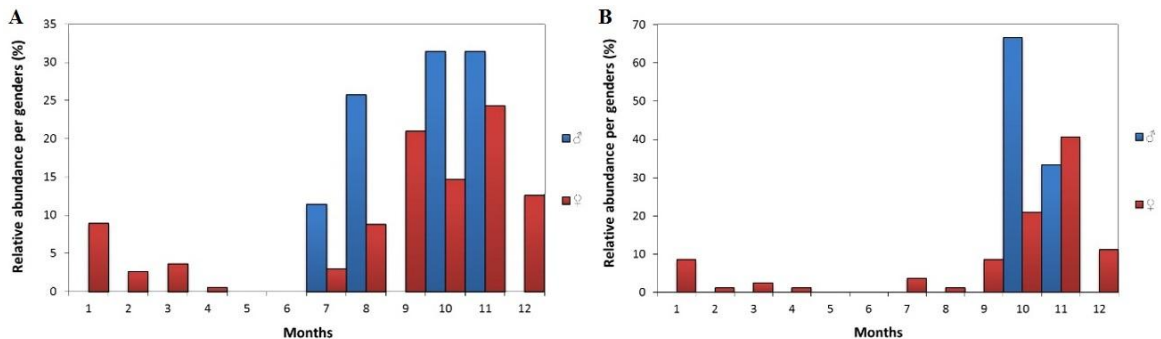


Figure 12. The relative monthly abundance values (%) of *Culex pipiens pipiens* (A) and *Culiseta annulata* (B) mosquitos by genders in the period 1973–1999, based on the summarized data of the studied 19 caves.

2.3.3. Seasonal distribution of the mosquitos

Troglophile mosquitos were collected from July to April. The total mosquito number showed an approximately continuous increasing trend from July to November and a decreasing trend from December to April. Most of the mosquito specimens were collected in autumn (61.5%) while in winter 22%, in spring the 4% and in summer only the 12%. The highest monthly abundance of *Culex pipiens pipiens* (25%), *Culiseta annulata* (40%) and *Anopheles messeae* (88.9%) individuals were observed in November. *Culex pipiens pipiens* had the highest relative monthly abundance values during the entire year. The highest species number of mosquitos was collected in October (5 species) and March (4 species). At average, 2.4 mosquito species were collected per month and 2.9 species in those months when mosquitos were present in the caves. The minimum number of mosquito species was collected in May and June (0-0), the maximum was collected in October (5 species). Four-four species were collected in February and March. The relative abundance of *Cx. pipiens pipiens* continuously decreased from December to April. The relative abundance of *Culiseta annulata* was the highest in April (*Fig.13*).

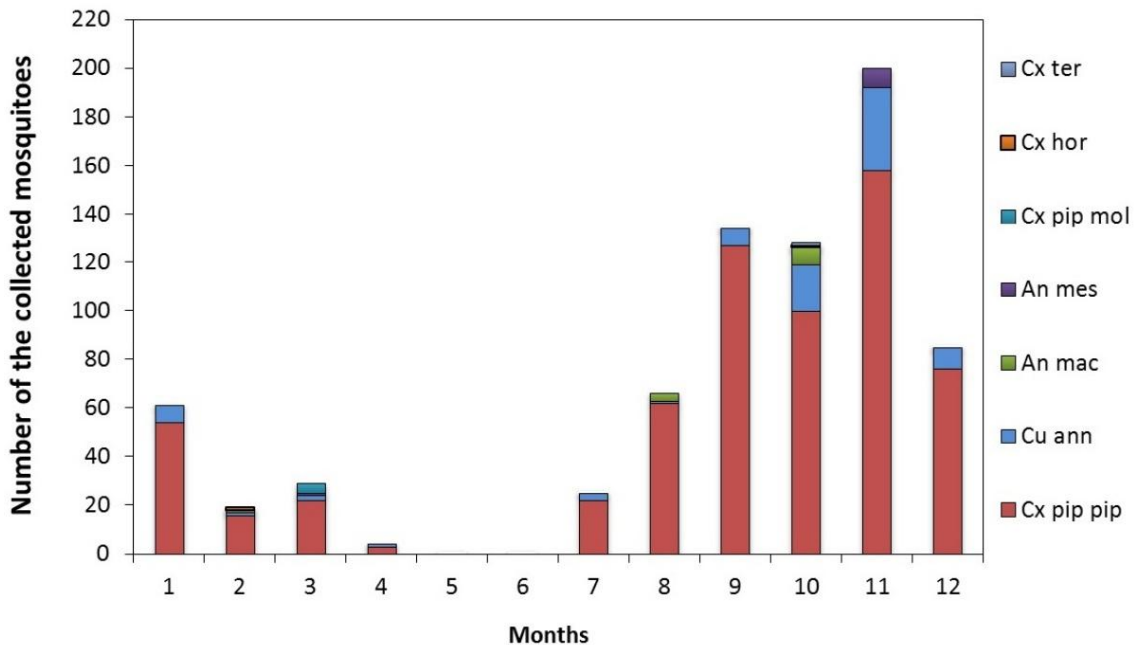


Figure 13. The absolute number of the collected mosquitos by months in the period 1973–1999, based on the summarized data of the studied 19 caves.

2.3.4. Comparison of cave-dwelling and regional fauna

The relative abundance of species of the troglophile mosquito fauna differs from the same species' frequency in the Bakony-Balaton Region. In both cases, *Culex pipiens pipiens* was the most abundant mosquito, but the dominance of this mosquito in the collected material of the region is less (84 vs. 60%). The abundance of *Culiseta annulata* is similar in the troglophile mosquito fauna and the fauna of the region (11 vs. 15%). In contrast, *Anopheles maculipennis* and *Culex territans* are more frequent in the region than in the troglophile mosquito fauna (12 vs. 16% and 0.2% vs. 6.3%). Both *Anopheles messeae* and *Culex pipiens molestus* contributed less to the troglophile and the regional abundance (1 vs. 2 and 1 vs. 0.1%; Fig.14).

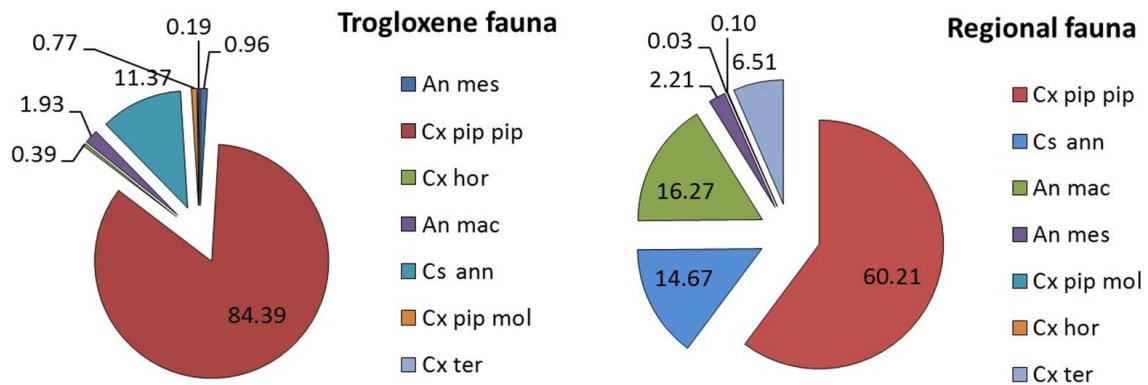


Figure 14. The relative abundance values of the studied mosquitos in the cave-dwelling and a regional mosquito fauna of the Bakony-Balaton Region according to the data of Tóth (2006) in the period 1973–1999, based on the summarized data of the studied 19 caves (An mac: *Anopheles maculipennis*, An mes: *An. messeae*, Cx hor: *Culex hortensis*, Cx pip pip: *Cx. pipiens pipiens*, Cx pip mol: *Cx. pipiens molestus*, Cx ter: *Cx. territans*, Cs ann: *Culiseta annulata*).

2.3.5. Climatic and solar factors

Mosquitos disappear from caves when the monthly mean temperature reaches the annual mean temperature of the region (about 10 °C). The summer re-appearance of *Culex pipiens pipiens* and *Culiseta annulata* in the caves occurred slightly before the summer thermal maximum (July and August). The relative abundance of the mosquitos in the caves starts to increase rapidly when the monthly mean temperature drops below the annual mean (Fig.15A). The Thornthwaite agrometeorological index (TAI) exhibited a roughly bimodal annual run with a greater late autumn-early winter and a smaller early summer peak. The relative abundance of *Culex pipiens pipiens* and *Culiseta annulata* started to increase in July, when the TAI showed its annual second minimum. During the summer precipitation and the consequent TAI maximum,

mosquitos were not collected in the studied caves. From July to November, the increase of the mosquito abundance coincided with the parallel increase of TAI. Mosquito abundance reached its maximum when TAI is almost the highest in November (Fig.15B).

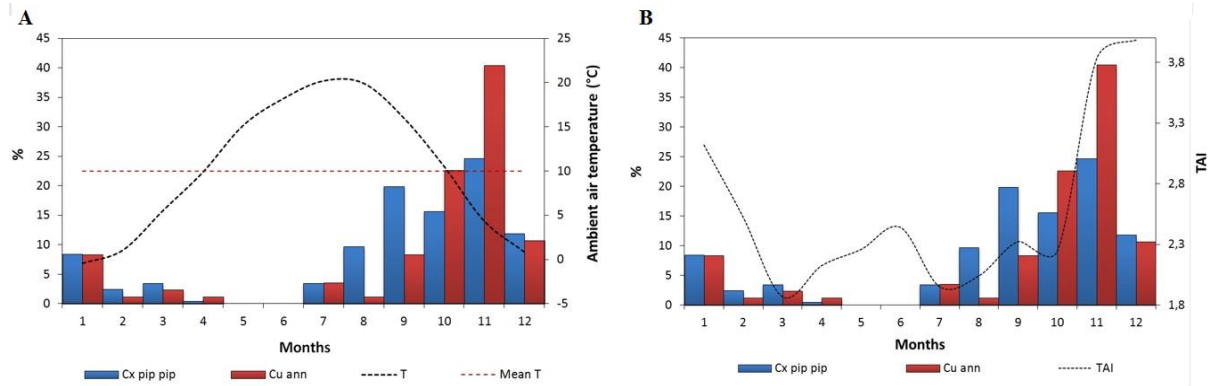


Figure 15. The annual relative abundance of *Cx. pipiens pipiens* and *Cs. annulata* in the period 1973–1999, based on the summarized data of the studied 19 caves; the monthly mean temperature (A) and the monthly mean TAI (B) values of 1973-1999.

2.3.6. Potential vector status of cave-dwelling mosquitos

Weighting the number of trapped troglophile mosquitos with their vector status (yes/no), the following results were found: potential vectors of the avian *Plasmodium* species - 96.9%; *Dirofilaria immitis* - 85.8%; Myxoma virus - 13.9%; non-avian *Plasmodium* species, *Francisella tularensis* MCCOY & CHAPIN, 1912; DOROFFE'EV 1947 and the pathogens of filariasis - 2.7-2.7-2.7%; Batai, Tahyna and West Nile - 3.2-3.2-3.2%, and Sindbis virus - 0.5% of the collected mosquito individuals, respectively (Tab.3).

Table 3. The potentially transmitted pathogens (Pla: non-avian *Plasmodium* species, BATV: Batai virus, TAHV: Tahyna virus, WNV: West Nile fever virus, Myx : Myxoma virus, Fil: other (non-*Dirofilaria*) parasitic nematodes, Fra: *Francisella tularensis*, avPla: avian *Plasmodium* species, Dir: *Dirofilaria immitis*, Sin: Sindbis virus (Joubert et al., 1967; Jöst et al., 2011; L’vov et al., 2004; Hubálek, 2008; Kenyeres and Tóth, 2008; Taylor et al., 1955; Zittra et al., 2015).

Species	Pla	BATV	TAHV	WNV	Myx	Fil	Fra	avPla	Dir	Sin
<i>An. maculipennis</i>	+	+	+	+	+	+	+	-	-	-
<i>An. messeae</i>	+	+	+	+	+	+	+	-	-	-
<i>Cx. hortensis</i>	-	-	-	-	-	-	-	-	-	-
<i>Cx. pipiens pipiens</i>	-	-	-	-	-	-	-	+	+	-
<i>Cx. pipiens molestus</i>	-	+	+	+	-	-	-	+	+	+
<i>Cx. territans</i>	-	-	-	-	-	-	-	-	-	-
<i>Cs. annulata</i>	-	-	-	-	+	-	-	+	-	-

The season of *Culex pipiens pipiens*, - the most important vector of WNF in Hungary, starts about one month later than the end of the winter diapause of the mosquito in the Bakony-Balaton Region. The annual maximum case number of human WNF was observed in September, one month later than the annual maximum abundance of *Cx. pipiens pipiens* at a county level. Although humans are only the dead-end-hosts of the virus, human cases indicate the main period when the mosquitos can transmit the virus. Those infected mosquitos, which start their diapause in the autumn months are can be the potential vectors of WNF in the next year (*Fig.16*).

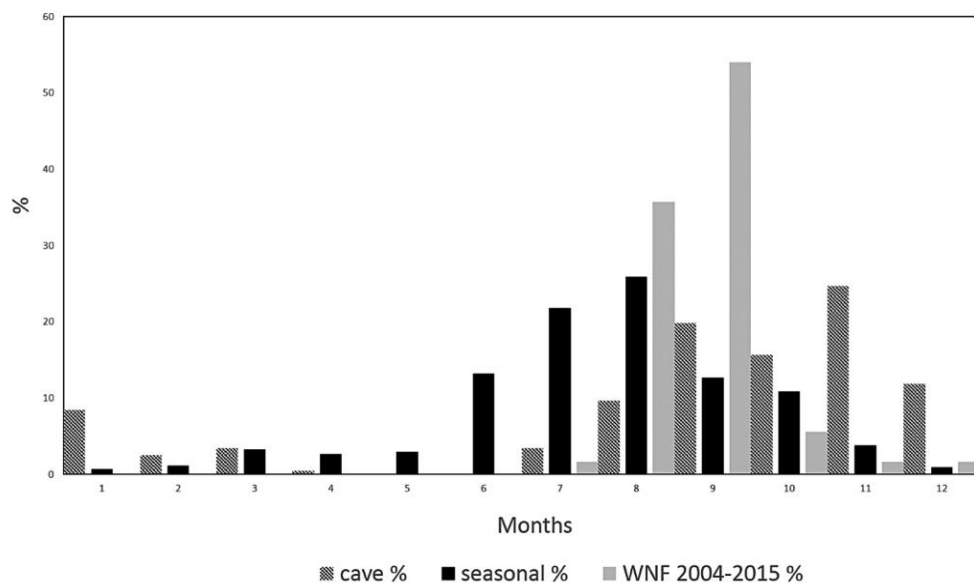


Figure 16. Comparison of the abundance of active (seasonal%) and diapausing(cave%) *Cx. pipiens pipiens* mosquitos in the Bakony-Balaton Region (in the period 1973–1999, based on the summarized data of the studied 19 caves) with the seasonal abundance of the species and the countrywide monthly percentage of observed WNF cases in Hungary in 2004-2015.

2.4. DISCUSSION

It is somewhat surprising that only seven mosquito species were collected from October to March in caves of the Bakony-Balaton Region since 19 mosquito species can overwinter in imago stage in Hungary: 9 *Culex*, 5 *Culiseta*, 4 *Anopheles* and 1 *Uranotaenia* species (Kenyeres and Tóth, 2008). All these 19 species were collected from epigean habitats in the Region. The four most abundant species were the following: *Culex pipiens pipiens*, *Culiseta annulata* and *Anopheles maculipennis* and *An. messeae*. Minár and Ryba (1971) found a similar troglophile mosquito composition in Moravia describing the presence of *Culex pipiens pipiens*, *Culiseta annulata* and *Anopheles messeae* from the investigated caves. They found *Culex pipiens pipiens* to be the most abundant species. *Cx. pipiens pipiens* and its close relatives are common troglophile fauna elements in the temperate areas of the world as it was observed in Japan (Shimogama and Takatsuki, 1967), in the Czech Republic (Minár and Hájková, 1966) and in the caves of South Korea (Whang, 1961). *Cx. pipiens pipiens* and *Culiseta annulata* often co-occur in caves (Minár and Hájková, 1966). None of the members of *Aedes* and the diverse *Ochlerotatus* genera occurring in the Bakony-Balaton Region were found in the studied caves. It can be explained by the different overwintering strategy of the various mosquito genera. In the temperate zone, most of the *Aedes* and *Ochlerotatus* species hibernate in the egg-stage (Becker et al., 2010) and start their development in spring after the eggs are flooded several times and hatching is induced. Only a few *Aedes* and *Ochlerotatus* species overwinter in the larva stage (Vinogradova, 1969). Based on the above-mentioned conditions, species of these two genera are not expected as adults in the caves.

A clear increasing trend of mosquito abundance was observed in October and November, which is the main period of entry (Gazave, 2001). Shimogama and Takatsuki (1967) described somewhat similar seasonal patterns about the troglophile *Culex pipiens pallens*, which is a close Asian relative of *Cx. pipiens pipiens* and *Cx. pipiens molestus*. They found that the number of females of *Cx. pipiens pallens* was scarce in summer and increased rapidly in November reaching its maximum in December in caves. In Japan, the abundance of this species decreased sharply in February. Theoretically, high predation pressure could be a potential reason of the low mosquito diversity in the late winter. In the caves of the Bakony-Balaton Region, 14

Chiroptera species can be found (Tóth, 2009). The most common bats are *Myotis myotis* BORKHAUSEN, 1797 and *Myotis oxygnathus* MONTICELLI, 1885. We found that the mosquito abundance started to decrease rapidly after December and reached its absolute minimum in May and June. In this period of the year, mosquitos were not collected in the caves. Most of the Chiroptera species in the temperate regions retreat to caves for winter and hibernate for several months (Fenton, 2001) imposing predation pressure during the peri-hibernation period in caves. In the other hand, arthropod predators, especially spiders also use caves as habitats. Still, it is unlikely that bat foraging activity could explain the observed annual abundance patterns of mosquitos in caves. Mosquitos form a minor (or even negligibly) part of the bat diet. A wide variety of nocturnal insects serve as food resources for bats, such as moths (Lepidoptera), beetles (Coleoptera), lacewings (Planipennia), caddisflies (Trichoptera), mayflies (Ephemeroptera), and midges (Chironomidae), with moths being the major part of the bats' diet (Becker et al., 2010; Gonsalves et al., 2013). The absence of the main mosquito species *Culex pipiens pipiens* is rather due to its life cycle than to predation. In all mosquito species, including *Cx. pipiens pipiens*, overwintering as hibernating females the imagos that manage to survive the winter abandon their shelters to lay eggs and die soon after.

During the spring period with lower temperatures, it takes about a month for the larvae to complete their development and the first generation of adults to emerge. For *Cx. pipiens pipiens* this happens approximately in the months observed. There is a coincidence between the disappearance of mosquitos from the caves and the rising temperature in spring. When mean monthly temperature reaches the annual mean temperature of the region (it is about 10 °C) in April, mosquitos leave caves and start to quest blood meal in the ambient environment. According to Minár and Ryba (1971) the emergence of mosquitos from overwintering sites can be observed when the temperature in the shelter is 8 °C for *Cx. pipiens* sensu lato and 8-12 °C for *Culiseta annulata*. They commonly occur both in the Czech Republic and Hungary in the turn of March and April. The wet and warm weather in May and June favors the activity and reproduction of mosquitos. As in mid-summer, after the summer solstice the aridity index drops below to a certain value (about 2.0 in TAI), mosquitos visit the caves again to avoid the summer atmospheric drought. Parallel to summer drought, the small-water

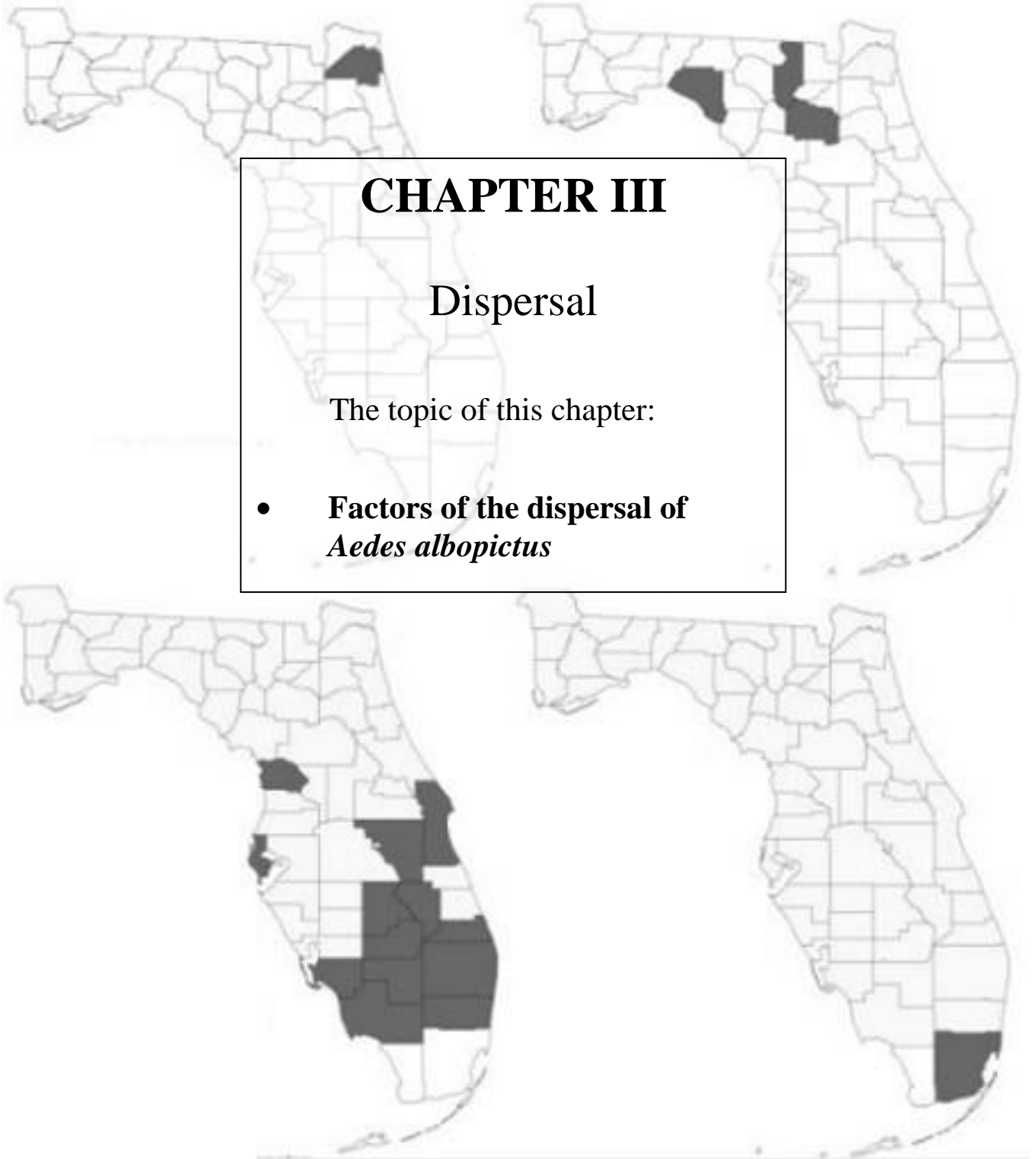
habitats (puddles, different natural- and technotelmata) being the most important breeding sites of mosquitos start to dry out. When ambient monthly mean temperature drops below the 10 °C, mosquito abundance increases rapidly in caves. It corresponds to the observations of Minár and Ryba (1971) who found that suitable overwintering sites for females of *Culex pipiens* sensu lato were cellars with temperatures of 0-8 °C. For *Culiseta annulata* the ideal air temperature during the winter diapause was between 7 to 8 °C in the Czech Republic (Minár and Ryba, 1971). It appears that male mosquitos do not survive the winter solstice. Male/female gender ratio was very low during the entire year. Male mosquitos were not found after December and were absent in the first half of the year. It means that there are no overwintering male mosquitos in the caves. This is a well-known fact for mosquitos that they overwinter in the adult stage. Male mosquitos do not suck blood and are unable to form enough fatty reserves to survive the winter. Moreover, the lifespan of males is usually shorter than that of the females of the same generation.

Shimogama and Takatsuki (1967) found that all the male *Culex pipiens pallens* mosquitos stayed close to the entrance in summer, and none of them penetrated beyond the middle section of the caves. They also described that while the total number of males was small during the entire year, the abundance of males was very low from February to April and began to rise only in May. In contrast, during the cold period, females penetrated the deeper zones of the caves. They concluded that this behavior can be the main cause of the very low survival rate of male mosquitos in winter. In another study (Ives, 1938) most individuals of *Culex* species were collected in the twilight zone in the caves, none having penetrated darker parts even in winter. *Anopheles maculipennis*, *An. messeae*, *Culiseta annulata* and *Culex pipiens molestus* mainly feed on mammals, while *Cx. hortensis* and *Cx. pipiens pipiens* rather prefer the blood of birds. *Cx. territans* prefers to feed mainly on blood of amphibians (Kenyeres and Tóth, 2008). Although *Anopheles maculipennis* and *An. messeae* are the front-line potential vectors of human *Plasmodium* species, infective malaria mosquitos that survive the winter are not infective in the spring anymore. Sporozoites in their salivary glands are not able to survive for more than 40 days at low temperatures, therefore the females are free of parasites by the time they abandon their winter shelters (WHO, 2010). The early onset of the malaria season in European countries formerly epidemiologically endemic

for malaria was due to cases with a long incubation period or relapses (Lysenko et al., 2003). The species of the *Anopheles maculipennis* complex including *An. maculipennis* and *An. messeae* can also transmit the WNV, but these mosquitos are not the chief vectors of the pathogen. Persistence in overwintering *Culex* mosquitos may be important in the maintenance of WNV virus because the virus was isolated from overwintering *Cx. pipiens* (Nasci et al., 2001). Farajollahi et al. (2005) detected WNV viral RNA from an overwintering pool of *Cx. pipiens pipiens* material concluding that the mode of infection of overwintering females may have been due to transgenerational transmission. Reisen et al. (2006) hypothesized that WNV can survive winters by continued enzootic transmission, vertical transmission by *Culex* mosquitos, or due to the chronic infection of birds. Goddard et al. (2003) concluded that mosquitos infected vertically during autumn, could potentially serve as a mechanism for WNV to overwinter and initiate horizontal transmission the following vegetation period.

Discussing the vector status of the mosquitos it can be concluded that mostly caves are the habitats of mosquitos that are vectors of non-human pathogens or pathogens that rarely cause human infections like *Dirofilaria immitis*. The winter transmission of infections to humans such as malaria is very unlikely. Mosquitos preparing for hibernation digest the blood to form fatty reserves for the winter without producing eggs at the same time, which is known as “gonotrophic dissociation”. Only females of some species within the *Anopheles maculipennis* complex that do not enter complete hibernation can take occasional blood-meals during winter to withstand the prolonged periods of starvation (Becker et al., 2010). For example, in Korea, Whang (1961) found that *Anopheles sinensis* WIEDEMANN, 1828 and *Anopheles sineroides* YAMADA, 1924 hibernate as adults in winter. Since these anophelines hibernating in cow stables were all fed, it was concluded that in caves they could feed in the cold period. A wide overlapping period was found in the second half of the vegetation season when *Culex pipiens pipiens* mosquitos are both active and start their diapause in caves in the Bakony-Balaton Region. Furthermore, from August to the end of fall they can transmit WNV to humans in Hungary. It is assumed that the observed monthly abundance of *Cx. pipiens pipiens*, the bridge vector of WNV, in caves can be used as the diapause model of the species in artificial, non-heated environments as cellars, mines, stacks and basements. Although the Bakony-Balaton Region is only a part of Hungary, due to the

relatively homogenous topographical and climatic circumstances the observed seasonal abundance patterns of the mosquito can be used in the modeling of the ecoregional seasonality of *Cx. pipiens pipiens*. In summer and fall, WNVs circulate in bird and *Culex* populations. Humans and other mammals are only the dead-end-hosts of the virus (Kilpatrick et al., 2007). The season of human WNF infections coincides with the re-appearance of diapausing mosquitos in caves. In case of WNV transmission, in addition to the exoanthropic cycle, a synanthropic cycle also exists (Savage et al. 1999; Tsai et al., 1998). In lowland areas (e.g. in major river basins) where large mosquito populations exist natural caves are missing due to the lack of rocks. In contrast, cellars, unheated rooms, garages and outbuildings could provide somewhat similar conditions in winter as the natural caves in the mountainous areas. Since surviving female mosquitos can be the hosts of WNF, the investigation of the seasonal coincidence of diapausing, host-seeker mosquitos and WNF cases can provide some information about the probability of the survival of the virus in winter even in the lowland areas.



CHAPTER III

Dispersal

The topic of this chapter:

- **Factors of the dispersal of *Aedes albopictus***

1. FACTORS OF THE DISPERSAL OF *Aedes albopictus*³

1.1. INTRODUCTION

In such aquatic insects as mosquitos like *Ae. albopictus*, the adult stage is the natural dispersive phase of the life cycle. Thorpe (1951) and Provost (1952) when studied the insect flights described two main categories: the appetential and nonappetential flying activities. Service (1997) distinguished an active and a passive dispersal of mosquitos. He referred to the appetential flight as active dispersal because such flights are selfpropelled and selfsteered. Characteristically, it is a non-unidirectional dispersal manner. Active flight serves the purpose of feeding or sheltering. It is a characteristic nature of active flight that usually extends only to short distances, such as a few hundred meters. In contrast, non-appetential flight or passive dispersal usually spans from few kilometres to larger distances, has unidirectional character and is assisted by environmental factors. Human-mediated transports also belong to the passive transport category. Service (1997) concluded that mosquito migration is often included in this way. In the last few decades, the area-expansion of the mosquitos confirmed this hypothesis (Kampen et al., 2013; Šebesta et al., 2012; Scholte and Schaffner, 2007; Scholte et al., 2007; Aranda et al., 2006).

Objective. It was aimed to estimate the total and passive dispersal per generation of *Ae. albopictus* based on the temperature-derived ontogeny rate of the species and the climate of the studied regions. Florida and Italy (the Apennine Peninsula and Sicily) were involved in the study due to the relatively recently observed invasions of the mosquito and the geographical similarities between the two peninsulas.

Hypothesis. It was hypothesized that based on the known active dispersal of the mosquito and the observed total dispersal distances; the average value of the passive dispersal component can be distinguished from the active dispersal capacity of the species.

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1.2. MATERIALS AND METHODS

1.2.1. Methodological outline

The employed method was based on the hypothesis that under different climate conditions there is a different speed in the dispersal of *Ae. albopictus* offering an opportunity to projections onto large scales. In this study, mean monthly temperatures was regarded as the explaining variable of the potential annual generation number of the Asian tiger mosquito, although the time lasting between the emergence and the oviposition of female mosquitos also was included in the calculations.

The following modeling steps were taken for the calculation of the dispersal distance of *Ae. albopictus* per a generation the:

- 1) The temperature-based ontogeny equation of the mosquito (based on two independent authors), the climate zonation of the United States Department of Agriculture (hence: USDA zonation) of the studied countries, the monthly mean temperature data of the reference cities of the climatic zones and the spatial colonization data of the mosquito were gained from different databases. Originally, USDA Plant Hardiness Zone Map is the standard by which plant breeders can determine which plants are most probable to survive at a location. The map is based on the average annual minimum winter temperature (USDA Agricultural Research Service, 2016). Due to the fact, that arthropod vectors are poikilotherm and consequently cold-sensitive organisms, the USDA zonation maps can be used in the robust climate classification of wider areas.

- 2) The monthly mean temperature values of the reference cities were matched to the USDA zones of the two countries. Temperature values were interpolated between the reference cities where it was necessary.

- 3) According to the monthly mean temperature values the potential monthly part of the annual generations were calculated based on the development rates of the immature mosquitos at specific temperatures. Counties/provinces were classified based on the extant USDA zones. The minimum time between the emergences from pupae of female mosquitos to the oviposition was added to the life cycle model.

- 4) The dispersal distance per generation was calculated based on the distance between established county/province colonization sites and the correspondent potential

number of generations. Spatial distances were calculated between the geographical centers of the neighboring administrative counties/provinces.

The expansion data of *Ae. albopictus* in Florida and Italy was based on the mapped data of Medlock et al. (2012), Moore and Mitchell (1997), O'Meara et al. (1995), Scholte and Schaffner (2007) and the VBORNET database (ECDC, 2017) in a county/province resolution. After the identification of the provinces/counties, these data were transformed into raster files. Depending on the sources, the temporal resolutions of the expansion were heterogeneous: for Florida, six maps were available each covering a 2-y period while for Italy four maps served as basis of analyses, each covering a 3-y period. Due to the data heterogeneity, in the descriptive analyses, the expansion in time was approximated by different (Boltzmann or polynomial) equations. Since the distribution maps' time frames were different in Italy and Florida, the dispersal values were normalized to the annual and then to generic values. The USDA zonation, which was developed by the Agricultural Research Service of the United States Department of Agriculture, a widely accepted and well-adaptable climate system, was applied in this study. An advantage of the use this climate zonation system that it can be well correlated to other biozonation systems since winter minimum values are the major limiting factors of the distribution of many cold-sensitive organisms including e.g. subtropical mosquitos. The area of Florida was divided into seven zones based on the existing main five USDA subzones between the latitude of cities Jacksonville (Duval County) and Miami (Miami-Dade County) since 8a and 11a subzones together cover only a negligible area of the state. The classification of the counties was also performed according to the USDA zone climate classification. The following main USDA subzones can be found in Florida: 8b, 9a, 9b, 10a and 10b (*Fig.17A1*). The Apennine Peninsula belongs to the USDA hardiness zones 5 to 10, but the lowland areas and the coastal regions of Italy to zones 8 to 10. The classification of the provinces was also performed according to the USDA zone climate classification (*Fig.17B1*). The Southern Alp region (strictly, this area is not the part of the Apennine Peninsula) belongs to zones 5 to 7. The monthly mean temperature of the ambient air mean temperature values was used in the study since the characteristic breeding habitats of *Ae. albopictus* in the human environment are mainly different standing waters (Lounibos et al., 2002), water-storage containers O'Meara et al. (1995), plastic tubs and boxes (Gratz, 2004; Alto and

Juliano, 2001). The monthly mean of daily ambient air temperature data according to the centre coordinates of Milan, Rome and Syracuse were obtained from the E-OBS gridded dataset (E-OBS, 2014) with 0.25° grid resolution. The monthly mean temperature climate data of the Florida cities (as e.g. Jacksonville, Daytona Beach, Naples, Orlando) were based on the data of the Florida Climate Center (Office of the State Climatologist)/Products and Services/Data, 1981-2010 Normals (Florida Climate Center). A climate normal was defined as the arithmetic mean of a climatological element computed over three consecutive decades (1981-2010). The 1981-2010 normals were provided by the National Climatic Data Center in Asheville, NC. *Figure 17A2 and B2* show the annual run of the monthly mean temperature values of different USDA zones in Florida and Italy.

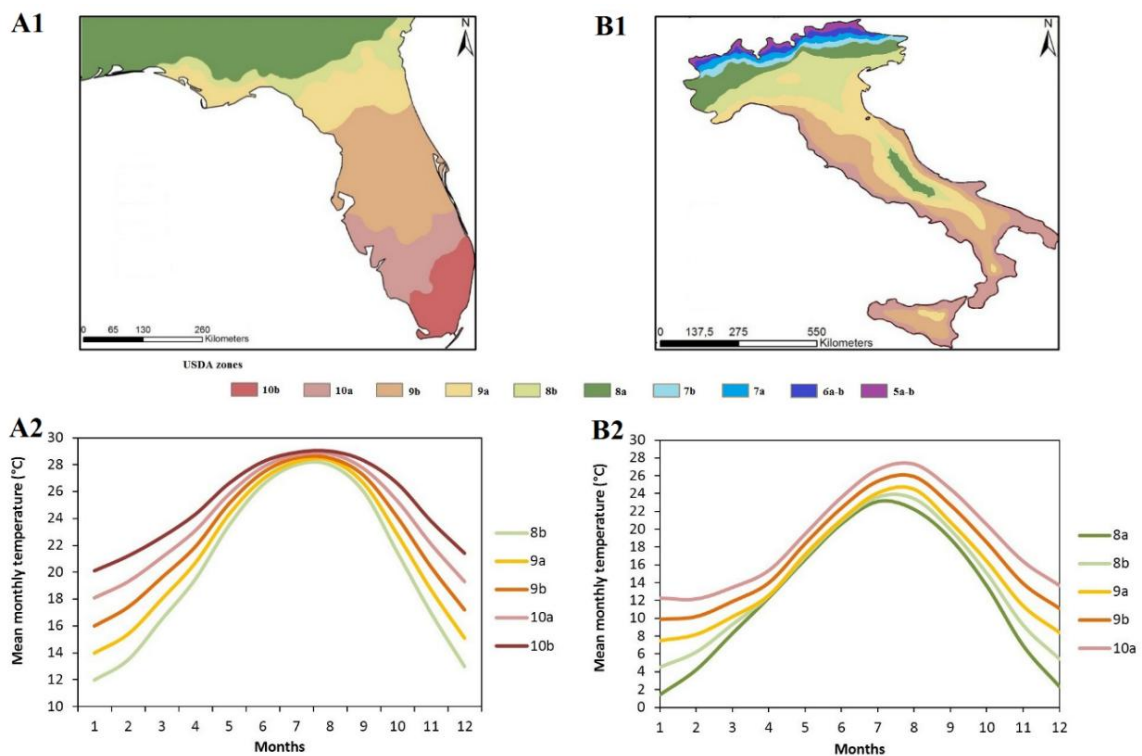


Figure 17. The USDA zones of Florida (1A); the USDA zones of the Apennine Peninsula (A1) and Sicily (B1). Note that color codes mark different USDA ranges in Florida and the Apennine Peninsula (Italy). The average monthly temperatures for a year for the two areas for each of the 5 USDA climate zones; Florida (A2) and the Apennine Peninsula (B2).

1.2.2. Calculation of the generic dispersal distances

The basic idea was that the minimum dispersal per generation can be calculated as the quotient of the mean of the maximum annual number of the potential generations per the traveled distance during a year between two adjacent areas (counties/provinces).

It is known that the life cycle of *Ae. albopictus* includes water-dependent stages and one aerial stage (Tran et al., 2013). Generation time was estimated as the time between oviposition to the next oviposition act. The minimum time between the oviposition of a female mosquito and the oviposition act of the next generation's female mosquitos (the time between generations; hence: *generation time*) include at least six main time factors: 1) the minimum time requirement of the development of the embryo from the oviposition to egg hatching, 2) the minimum cumulative time requirement of the four instar stadiums incl. the time of the larval moltings, 3) the time requirement of the pupal stage, 4) the minimum time between the emergence of females from pupae to the insemination, 5) the minimum time of the host seeking activity for blood-meal, 6) the time of blood digestion and ovarian development lasting to the oviposition (Eq.5).

$$\Sigma Gt = t_{ov-1^{\circ}} + t_{1^{\circ}-4^{\circ}} + t_{p-a} + t_{em-in} + t_{in-bm} + t_{bm-op} \quad (5)$$

where ΣGt is the total minimum time between the generations (between the oviposition and the oviposition act of the next generation's female), $t_{ov-1^{\circ}}$ is the minimum time requirement of the development of the embryo from the oviposition to egg hatching, $t_{1^{\circ}-4^{\circ}}$ is the minimum cumulative time requirement of the four instar stadiums incl. the time of the larval moltings and t_{p-a} is the mean time of the pupal stage, t_{em-in} is the minimum time between the emergence of females from pupae to the insemination, t_{in-bm} : the minimum time of host seeking activity for blood-meal and t_{bm-op} : the time of blood digestion and ovarian development lasting to the oviposition.

According to the topographical differences, the calculation of the spatial dispersal distance was based on the county or province areal level. Since only the county (in the USA) or province (in Italy) spatial occurrence data has been available, the distance between the quasi geometrical centra of the nearest counties or provinces were used in case of the adjacent periods to calculate the spatial dispersal. The geometrical centrum of the southeast colonized county was selected in the n^{th} period of the colonization and the geometrical centrum of the southeast colonized county of the $(n+1)^{th}$ period of the colonization between the nearest counties/provinces. The 'n' means the year of invasion from the start of the expansion of *Ae. albopictus* in Florida or in Italy (where the first year is $n=1$). The most likely, nearest colonization cases (meaning the area expansion of *Ae. albopictus* from the most adjacent country/province to another one) were considered in the study: 37 were involved for Florida and 31 for Italy.

The maximum means that the model neglects the time of flying. If the colonization occurred between two different climatic zones, the average of the monthly temperature values was used in the calculation of the generation number (Eq.6).

$$DisD_n = \frac{D}{G_n} \quad (6)$$

where: $DisD_n$: the spatial dispersal distance of the n^{th} sampled colonization case, D : the traveled distance per a year and G_n : the mean of the annual generation number between the two areas.

1.2.3. Calculation of annual generation numbers

To estimate the temperature based immature development model of *Ae. albopictus* mosquito we used the observations of Calado and Silva (2002) and Delatte et al. (2009) who experimentally established the development time of the species in each ontogeny stage at constant temperature conditions (15 °C to 35 °C in the study by Delatte et al. (2009). Though neither Calado and Silva (2002) nor Delatte et al. (2009) experimented with Asian tiger mosquito populations from Florida or Italy, in lack of other studies we used the equations provided by these authors. The similar outcomes of their studies suggest that the individuals of different introduced populations of Asian tiger mosquito inherited similar temperature requirements from their common Asian ancestors. On this basis, it was considered that both the results of Calado and Silva (2002) and Delatte et al. (2009) should be involved into the study. Since the minimal temperature-based developmental threshold of *Ae. albopictus* is 10.4 °C (Delatte et al., 2009), the number of the generations at less than 10 °C are only theoretical and were neglected in the model. Females of *Ae. albopictus* lay eggs on the edge of waters and not directly on water. The first three stages are aquatic. The lengths of the first three stages primarily depend on the species and the ambient (water) temperature. Exponential regression model was fit to the mean monthly temperature-period of development pairs to gain correlations between temperature and the average time of the steps of the metamorphosis according to the minimum time of the ovule-instar 1° metamorphosis (Eq.7-8), the minimum cumulative time of the instar 1° to the instar 4° metamorphosis (Eq.9-10) and the mean time of the pupa-adult metamorphosis (Eq.11-12) under different temperature conditions.

$$t_{ov-1^\circ} = 82.171e^{-0.101T} \quad (7)$$

$$t_{1^\circ-4^\circ} = 155.57e^{-0.114T} \quad (8)$$

$$t_{p-a} = 34.051e^{-0.098T} \quad (9)$$

where t_{ov-1° is the minimum time requirement of the development of the embryo from the oviposition to egg hatching, $t_{1^\circ-4^\circ}$ is the minimum cumulative time requirement of the four instar stadium incl. the time of the larval moltings and t_{p-a} is the mean time of the pupal stage.

$$t_{ov-1^\circ} = -0,0042T^3 + 0,337T^2 - 8,52T + 71,74 \quad (10)$$

$$t_{1^\circ-4^\circ} = -0,0057T^3 + 0,5483T^2 - 16,84T + 173,79 \quad (11)$$

$$t_{p-a} = -0,0019T^3 + 0,1659T^2 - 4,8295T + 49,723 \quad (12)$$

where t_{ov-1° is the minimum time requirement of the development of the embryo from the oviposition to egg hatching, $t_{1^\circ-4^\circ}$ is the minimum cumulative time requirement of the four instar stadium incl. the time of the larval moltings and t_{p-a} is the mean time of the pupal stage.

1.2.4. The time between the emergence and the oviposition

In case of *Ae. taeniorhynchus* it was found that most female were 30-40 hours old before they were inseminated (Edman et al., 1972). Multiple inseminations were observed in *Aedes aegypti* LINNAEUS, 1762 in semi-field conditions within 48 hours (Helinski et al., 2012). We calculated with 1.5-day minimum time between the emergence and the insemination of female *Ae. albopictus* mosquitos which can be a good estimate of the minimum time requirement of this part of the lifecycle of *Aedes* species. Del Rosario (1963) and Mori and Wada (1977) described that under natural conditions, 2–3 days after being inseminated *Ae. albopictus* females seek a host to blood-feed. Based on their results, 2 days were thought to be the minimum time requirement of host seeking after the insemination. De Lima-Camara et al. (2014, 2007) found that 3 days after blood-feed *Ae. albopictus* females are considered gravid and ready to oviposit. Summarizing the above described facts, we estimated a total minimum time requirement of the emergence to oviposition period of *Ae. albopictus* females about 5.5 days. The time of passive dispersal was neglected since it is known

that cargo and public transport played primarily role in the rapid expansion of the mosquito in both Florida and Italy. For example, traveling on an average speed of eighty kilometers per hour on a public road, 960 km distance can be reached by a car from the departure place in just half a day which is more than the observed annual linear spread of the mosquito both in Italy and Florida. Dividing the average of the length of the months (practically it is about 30-31 days) by time of the full metamorphosis time in a certain mean monthly ambient temperature we get the theoretical number of the generations per month (Eq.13, monthly part of the annual generation number: mGn). The total maximum theoretical number of the annual generations in an area can be calculated by the summarizing of the theoretical monthly part of the annual generation number (Eq.14).

$$mGn = \frac{30.5}{t_{ov-1^\circ} + t_{1^\circ-4^\circ} + t_{p-a} + t_{em-in} + t_{in-bm} + t_{bm-op}} \quad (13)$$

$$Gn = \sum_{k=1}^n \binom{1}{n} G_n \quad (14)$$

where T is the mean monthly temperature, t_{ov-1° is the minimum time requirement of the development of the embryo from the oviposition to egg hatching, $t_{1^\circ-4^\circ}$ is the minimum cumulative time requirement of the four instar stadiums incl. the time of the larval moltings and t_{p-a} is the mean time of the pupal stage, t_{em-in} is the minimum time between the emergence of females from pupae to the insemination, t_{in-bm} : the minimum time of host seeking activity for blood-meal and t_{bm-op} : the time of blood digestion and ovarian development lasting to the oviposition, mGn is the (theoretical) monthly part of the annual generation number and Gn is the total annual (theoretical) generation number.

1.2.5. Calculation of the passive dispersal distance component

Release and recapture studies showed that the maximum flying distance of *Ae. albopictus* females from the site of the release is about 500-800m (Rosen et al., 1976; Niebylski and Craig, 1994; Honório et al., 2003). It is important, that these results do not consider the effect of winds or anthropogenic transport (passive dispersal components) basically providing the maximum active dispersal value of the mosquito. This makes possible to estimate the average passive component of the dispersal of *Ae. albopictus* per a generation. Based on the calculation of the total annual generation

number and the observed distance of the spread of the Asian tiger mosquito between adjacent areas, the total dispersal distance of the species was calculated. The plausibly mainly anthropogenic passive dispersal distance component was calculated as the difference of the total dispersal and the active dispersal distance of the species (Eq.15).

$$DisD_P = DisD_T - DisD_A \quad (15)$$

where is $DisD_P$ the passive component of the dispersal distance, $DisD_T$ is the total observed dispersal distance and $DisD_A$ is the active dispersal distance of the species per a generation.

1.2.6. Statistics and software

Microsoft Excel 10.0 was used to fit exponential regression of the development time to temperature data of Calado and Silva (2002). The Boltzmann regression of the phenological model was made by the Kaleidagraph 4.5 software. Q-Q plot was generated to compare the dispersal data to the normal (Gaussian) distribution of the dispersal distance data. The climatic maps were re-plotted by ArcGis 10.1 software.

1.3. RESULTS

1.3.1. Comparison of the colonization characteristics in the countries

According to the linear model, the slope of the fitted curve on the areal expansion compared to the total expandable area was 2.17 higher in Florida than in Italy. As to the absolute colonized area (in km²), the slope of the fitted curve on the areal expansion was 1.47 times higher in Florida than in Italy up to the 90% of the expandable area. The increment of the colonized area in Florida showed a characteristic logistic growth pattern, the most important limiting factor being the available space. Essentially, the area of entire counties of the federal state Florida was colonized in less than 8 years. According to the fitted Boltzmann distribution model on the areal expansion of the mosquito, the start of the colonization approximately coincided with the first observations in Florida (Eq.16; Fig.18).

$$y = \frac{98.4127 + (-0.03658 - 98.4127)}{1 + \exp\left(\frac{(x-4.03847)}{0.69238}\right)} \quad (16)$$

In Italy, the growth of the inhabited territories was much more prolonged and the fitted polynomial model showed that the colonization of Italy might have happened

about 5 years earlier than the first observations and it might take at least 20 more years, although the model predicts that the growth is limited to the 91% for the country since about 9% of the area of Italy, mainly the Alpine regions, are not suitable for the colonization of the Asian tiger mosquito (Eq.17; Fig.18).

$$y = -0.0154x^3 + 0.2732x^2 + 4.2511x + 16.358 \quad (17)$$

where y is the colonized area in the percentages of the total, x is the number of years.

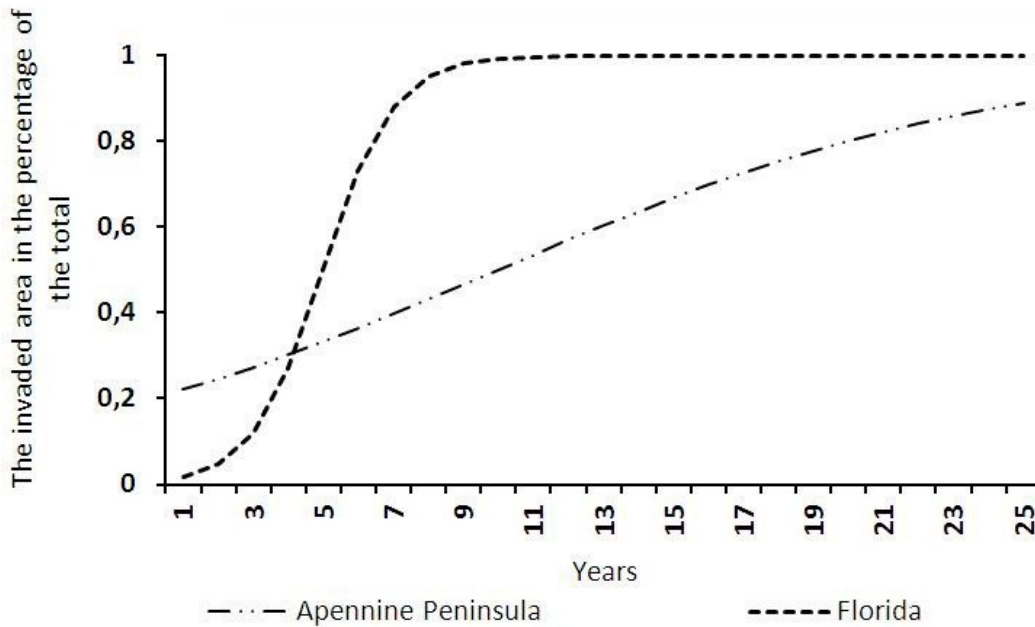


Figure 18. The phenological model of the territorial expansion of *Ae. albopictus* in the same resolution annual timescale in Italy and Florida according to the total expandable area.

Florida. The observed vector of the invasion route was almost north to south in Florida (Fig.19A). Colonization of *Ae. albopictus* in Florida emanated from one or two foci in the northeast part of the State which corresponds to an approximately unifocal starting area in view of the linear expansion model. The colonization speed reached its maximum by the third year of the total 6 years long period (Fig.19B) and the mosquito inhabited the entire Florida from its northernmost part to the southernmost part of the Eastern coast of Nassau and Jacksonville to the southernmost Monroe and Miami-Dade counties (Fig.19C). The calculated maximum number of the generations increased from 13-15 to 18-20 during the northsouth colonization of *Ae. albopictus* in Florida. The spatial dispersal distance was 45-100 km per year in most cases (Fig.19D). The normal Q-Q Plot of the spatial dispersal of the n^{th} sampled colonization case values show that

spatial dispersal of the n^{th} sampled colonization case values is close to normal distribution spatial dispersal of the n^{th} sampled colonization case values (Fig.19E).

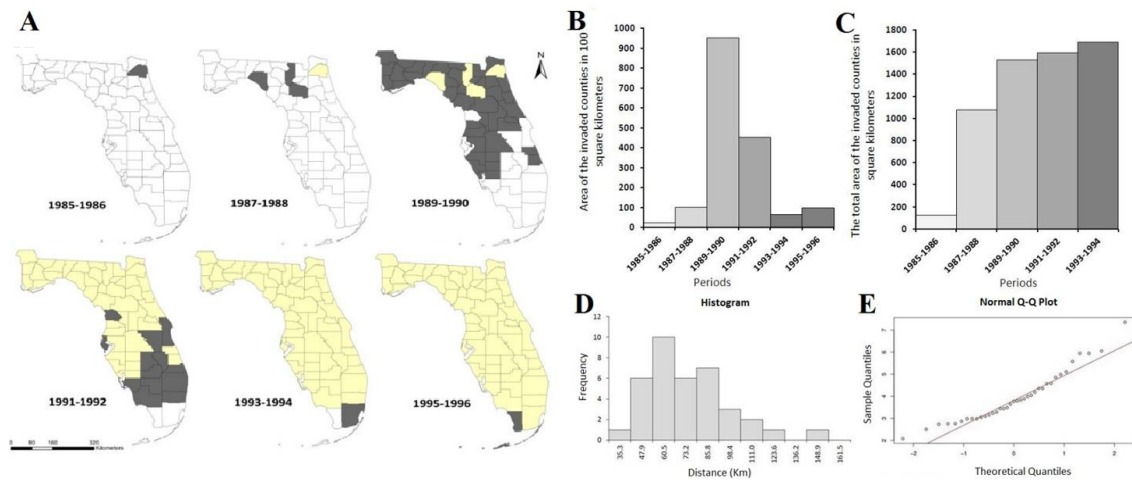


Figure 19. A: Expansion of *Ae. albopictus* in Florida in two years' temporal resolution (yellow: the already populated area, dark grey: the colonized area in the indicated period; B-C: Territorial expansion of *Ae. albopictus* in Florida Italy according to the size of the colonized area in 100 km² (left) and the total colonized area (right) by 2 years' periods; D: The histogram of the spatial dispersal of the n^{th} sampled colonization case values; E: the normal q-q plot of the spatial dispersal of the n^{th} sampled colonization case values in case of the spread of Florida by *Ae. albopictus*.

Apennine Peninsula. In contrast to Florida, the colonization start in the Apennine Peninsula was multifocal and only the major trend had a north to south profile (Fig.20A). The colonization speed reached its maximum in 2001-2003 (Fig.20B) but the species has may not colonized all the Italian provinces till the end of the studied period (Fig.20C). In most of the cases, the spatial dispersal was 45-100 km per year (Fig.20D). The normal Q-Q Plot of the spatial dispersal of the n^{th} sampled colonization case values shows a distribution close to normal distribution spatial dispersal at the low and exhibit dissimilar tail behavior at the high end of the distribution. The mean dispersal was 3.6 or 4.6 km per year (Fig.20E).

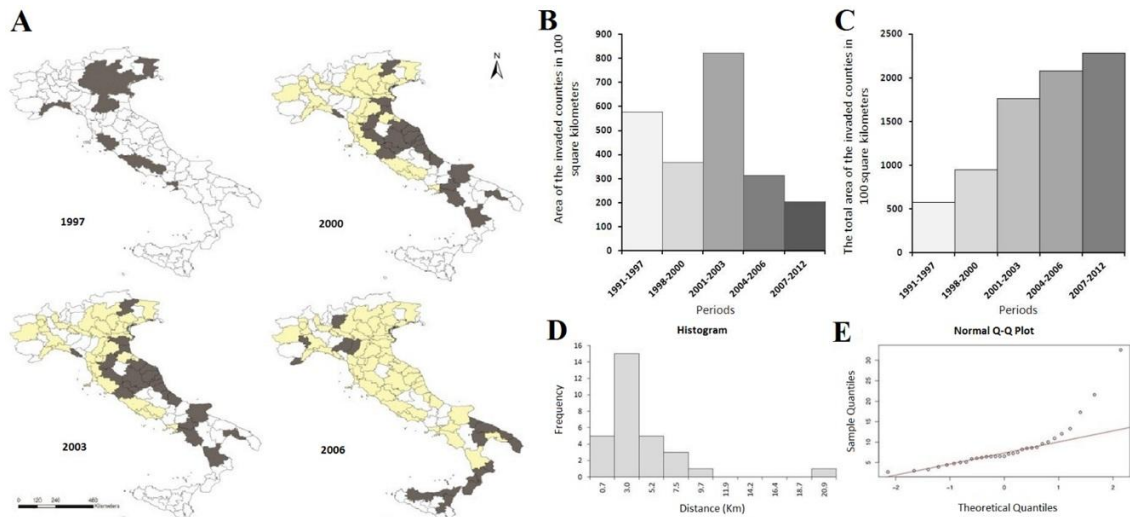


Figure 20. A: The expansion of *Ae. albopictus* in the Apennine Peninsula and Sicily in 1997, 2000, 2003 and 2006 (light gray: the already populated area, dark grey: the colonized area in the indicated years). B-C: The territorial expansion of *Ae. albopictus* in Italy according to the size of the colonized area in 100 km² and the total colonized area by 3-years periods except the first period of 1991-1997. D: the histogram of the annual expansion distance between the neighboring provinces, E: the normal Q-Q plot of the annual expansion distance between the neighboring provinces values in case of the spread of Italy by *Ae. albopictus*.

1.3.2. The average total active and passive dispersal distances

Based on the known maximum flying dispersal of female Asian tiger mosquitos (500-800m), the average total dispersal distance ($DisD_T$) of *Ae. albopictus* was 3.6-4.6 km year⁻¹ per generation in Italy and 4.6-5.3 km year⁻¹ per generation in Florida, while the average passive dispersal distances ($DisD_P$) of the mosquito were 2.8-4.1 km year⁻¹ per generation⁻¹ in in Italy and 3.8-4.8 km year⁻¹ per generation⁻¹ in Florida.

1.4. DISCUSSION

This study was based on a partly temperature-dependent generation number-based concept of the dispersal estimation of the Asian tiger mosquito. A central problem of each model to estimate the dispersal distance of the container-breeder was that models were based on the climate suitability of the species (Fischer et al., 2014; 2011; Trájer et al., 2014A; Rochlin et al., 2013; Caminade et al. 2014) that predicted the potential recent and future distributions of the mosquito. Release and recapture studies highlight another side of the issue, providing experimental data about the active dispersal of the individual mosquitos. It is difficult to estimate the passive factor. Another problem encountered when modeling dispersal is that localized expansions and long-distance movements can both explain the observed spread of the mosquito. Although we clearly

separated the localized expansions from the long-distance movements in the modeling, it must be recognized that this assumption can only be statistically true but not applicable to individual cases. The spatial dimension also can limit the usage of the model. Because *Ae. albopictus* can also “jump” over large distances, even migrating from continent to continent due to anthropogenic transport, or from a country to a non-neighboring country, the approach can be valid only when evaluating county/state or regional level invasions. This model was based on the well-known fact that the length of the developmental stages of arthropods is a function of the ambient temperature (Rueda et al., 1990; Bayoh and Lindsay, 2003, 2004; Teng and Apperson, 2000). Females of *Ae. albopictus* lay eggs on the edge of relatively small, warm water sources and not directly on water. The life cycle of *Ae. albopictus* includes three water-dependent stages and one aerial stage (Tran et al., 2013). The first three stages of mosquitos are aquatic, and their lengths also depend primarily on the species and on the ambient water temperature. Monthly mean temperature was used in the study because the characteristic habitats of *Ae. albopictus* in the human environment are mainly different standing waters (Lounibos et al., 2002), water-storage containers (O’Meara et al., 1995), plastic tubes and boxes (Gratz, 2004; Alto and Juliano, 2001). Since the Asian tiger mosquito originally adapted to the climate of warm temperate and subtropical areas, ambient temperature strongly influences its population dynamics (Alto and Juliano, 2001). The temperature-based population dynamics model of Alto and Juliano (2001) indicated that *Ae. albopictus* can expand in regions with high summer temperatures where the fast development of the individuals allows high rates of population growth and fast progress to maturity. This model can approximate the dynamics of the population but cannot provide appropriate information about the speed of the linear expansion. Since arthropods are temperature sensitive, climate zonation maps were used in the climate classification of wider areas. It was also assumed that due to the notable north to south geographical extension in the Florida and the Apennine peninsulas, the climate-based annual generation numbers of the mosquito cannot be described according to the monthly mean temperature values of one averaged climate zone.

The employed method paralleled the basic idea of the generic model of Cailly et al. (2012), who modelled all steps of the mosquito life cycle. Precipitation was not included in the model because it was proposed that precipitation determines the annual

abundance of the mosquitos rather than the annual number of generations. The effect of precipitation on mosquito populations is controversial since either drought or unusually high amounts of precipitation can induce the outbreak of mosquito populations depending on timing, climate and mosquito species (Chase and Knight, 2003; Rowley, 1995). Though neither Calado and Silva (2002) nor Delatte et al. (2009) experimented with Asian tiger mosquito populations from Florida or Italy, for the lack of other studies we used the equations provided by these authors. The similar outcomes of their studies suggest that the individuals of different introduced populations of Asian tiger mosquitos inherited similar temperature requirements from their common Asian ancestors. On this basis, it was decided that results of the above-mentioned authors should be involved into the study. Since the minimal temperature-based developmental threshold of *Ae. albopictus* is 10.4 °C (Delatte et al., 2009), the number of the generations at less than 10 °C are only theoretical and were neglected in the model. The phenology of the colonization showed that the time of the introduction coincided with the first observations in Florida. It is highly plausible that the real introduction of the Asian tiger mosquito preceded the first observations by about seven to eight years in Italy. This finding indicates that the phenological analysis of the dispersal can provide a more exact determination of the start of the colonization than the entomological observations themselves.

Another potential limitation of mosquito surveillance was that surveillance programs were not equal in the different municipalities. In Italy, the expansion was slower than in Florida and by the end year of the studied period of 2006, the mosquito colonized only part of the Apennine Peninsula, while in Florida the mosquito colonized the entire area of the state. In Florida, the north to south direction of the dispersal shows the continuous expansion of the mosquito. The observed difference between the speeds of the areal expansion of the Asian tiger mosquito in Florida and in Italy can be explained by the different annual generation numbers due to the cooler climate and the different topography of Italy. While the terrain of Florida is substantially a lowland, the Apennine Peninsula is bordered by the Alps from the north and the Apennine Mountains divide the eastern and western coastal lowlands of the area. The dry summer of the Apennine Peninsula and Sicily could also slow down the expansion of *Ae. albopictus*. We found that the total, linear dispersal distance of the Asian tiger mosquito

was 3.6-5.3 km/generation. This calculated passive dispersal is at least five to six times higher than the maximum flying dispersal as the active dispersal of the Asian tiger mosquito according to the release-recapture studies of the current literature (Honório et al., 2003: 800 m, Niebylski and Craig, 1994: 525 m).

Extracting the active dispersal component from the total dispersal distance per generation, surprisingly similar passive dispersal values (range: 2.8-4.8 km/generation) were found in the case of Florida and the Apennine peninsulas despite the different climate and topography of the areas. It can be concluded that the release-recapture studies can provide valuable information about the active dispersal distance of a species but are insufficient to predict the total dispersal distance and the real colonization capacity of *Ae. albopictus*. Another outcome is that climate can substantially influence the dispersal distance, and the potential number of generations may play a key role in the areal dispersal. It was found that passive dispersal distance of *Ae. albopictus* can be surprisingly similar, as was found in Italy and Florida. On a large spatial scale, the passive component can be well-estimated and parameterized. The investigation of the historical dispersal of *Ae. albopictus* can help health authorities tackle the problems caused by the mosquito as neither the technical background of transportation of goods nor the biology of the mosquito has changed significantly in the last thirty years.



CHAPTER IV

Urban environments

The topics of this chapter:

- **Dirofilariasis in urban environment**
- **The recent and future occurrence of *Phlebotomus* species in urban environment**

1. DIROFILARIASIS IN URBAN ENVIRONMENT⁴

1.1. INTRODUCTION

Many studies have analysed dirofilariasis caused by *Dirofilaria immitis* from the veterinary (Webber and Hawking, 1955; Newton and Wright, 1956), human medical (Ciferri, 1982; Muro et al., 1999; Pampiglione et al., 2009), parasitological and vector-epidemiological (Kartman, 1953; Ludlam et al., 1970; Labarthe et al., 1998; Cancrini et al., 2003), geographical (Bowman et al., 2009) and even climatic (Genchi et al., 2009, 2011) points of view. Even though in human *D. immitis* cases the parasites do not develop into adults in most cases, immature worms have been rarely found in humans (Muro et al., 1999). As regards geographical distribution, *D. immitis* occasionally causes human infections in the Mediterranean region of the European Union (Jelinek et al., 1996; Muro et al., 1999), and human dirofilariasis cases predominantly occur in the Americas, Japan, and Australia.

Several human medical aspects of dirofilariasis caused by *D. immitis* have been described in the literature (Moorhouse, 1978; Merrill et al., 1980; Ciferri, 1982; Theis et al., 2001; Simón et al., 2005). Human dirofilariasis cases are predominantly caused by *D. repens* in most countries of Eurasia (Simón et al., 2012). The treatment of infected dogs can lead to severe and potentially lethal complications such as thromboembolism after a massive chemical intervention (Rawlings et al., 1993). The preventive treatment of dogs could be an important element of the control of dirofilariasis as it was proposed for the dog populations of the Balkan Peninsula (Tasić-Otašević et al., 2015). Prevention relies on the characterisation of risk factors and the identification of vulnerable animal populations. The aim was to study the influence of urbanisation level and proximity to standing waters on the spatial distribution of dirofilariasis caused by the two *Dirofilaria* species in Szeged, Hungary.

⁴This chapter was published in Acta Veterinaria Hungarica:

Trájer, A.J., Rengei, A., Farkas-Iványi, K., Bede-Fazekas, Á. (2016). Impacts of urbanisation level and distance from potential natural mosquito breeding habitats on the abundance of canine dirofilariasis. Acta Veterinaria Hungarica, 64(3), 340-359.

Objective. It was aimed to investigate the effect of the distance from the potential mosquito habitats and the urbanisation intensity (hence: UI) on the prevalence patterns of *D. immitis* and *D. repens* caused dirofilariasis.

Hypothesis. It has been suggested that the spatial abundance patterns of domesticated hosts (dogs) and *Dirofilaria* vectors determine the abundance of dirofilariasis in an urbanised area.

1.2. MATERIALS AND METHODS

1.2.1. Methodological outline

A total of 56 canine dirofilariasis cases were investigated in the study; all examined between August 2013 and September 2014 at the Pet Ambulance in Szeged. Blood samples were tested by the following methods: modified Knott's method, *Dirofilaria* (Ag) ELISA tests (Witness[®] *Dirofilaria* Test, SNAP[®] 4Dx[®] Plus Test). In addition, in 35 cases PCR was used for the specific detection of *D. immitis* and *D. repens* as described by Casiraghi et al. (2006). In 11 cases PCR analysis was not performed. Adult helminth specimens were photographed during the dissection (see Fig.6, p.25). The basic concept of calculating the spatial abundance of canine dirofilariasis was that the spatial abundance of dirofilariasis cases in an urbanised area is determined primarily by the encounter of *Dirofilaria* vectors and the susceptible organisms, in this case the dogs. Equation 1 shows the general form of the compound probability of these components. The compound probability of an independent event is (Eq.18):

$$P(AB) = P(A) \times P(B) \quad (18)$$

where P(AB) is the compound probability, P(A) is the probability of the event A, and P(B) is the probability of the event B.

The compound probability of two independent events is the product of the probabilities of the distance from potential mosquito habitats and the abundance of dogs according to the UI of an area (Eq.19):

$$P_e = D_m \times A_{UI} \quad (19)$$

where is P_e the compound probability of the encounter with infected mosquitos, D_m is the distance from potential mosquito habitats, and A_{UI} is the abundance of dogs

according to the UI of an area. The maximum P_e value was expressed as 1. The other values were calculated as the ratio of the maximum encounter probability.

In the analysis the distance between the case site and the nearest point of the potential mosquito habitat was used. The simple two-sample *t*-test was performed using VassarStats: Website for Statistical Computation (Lowry, 2004). The graphs were constructed in Microsoft Office Excel 2010. The georeferencing of the Google Earth map source was performed by using the topographic maps of Hungary in the period of World War II (Tímár et al., 2008), which is a digital and georeferenced map publication in ArcGIS 10.0, using WGS-84 surface, UTM-34N co-ordinate system.

1.2.2. Stream classification

River stream types are often characterised by certain species of the fauna and the vegetation, and water catchment areas provide excellent habitats for mosquitos, such as e.g. *Aedes vexans* MEIGEN, 1830 (Kenyeres and Tóth, 2008). The habitat characteristics of fluvial ecosystems can be analysed by the different level of the spatiotemporal hierarchy. The qualities of macro-, meso- and micro-bedforms form a functional unit, which can be characterised by the qualities of bedform size, time-span of existence and superposition of bedforms in time (Jackson, 1975). The use of river system hierarchies in applied river research has been supported by several authors (Frissell et al., 1986; Amoros et al., 1987; Kern, 1994; Newbury, 1996; Petts and Amoros, 1996). The limnoecological characterisation of water bodies in this study was primarily based on the functional unit theory of Amoros et al. (1987). The identification of ephemeral (existing only for a short period) technotelma waters was not possible. As a working hypothesis, it was assumed that the spatial distribution of major water bodies and wetlands may have the most notable influence on the size of mosquito populations, and it has a relatively stable spatial pattern. The identified types of (major) aquatic habitats were extracted from the Google EarthTM satellite map of the studied area. To calculate the distance of the case sites from the potential mosquito habitats, first we defined and categorised the meaning of the 'potential mosquito habitat' according to the following categories: (1) floodplain, floodplain forest; (2) swamp, reeds, wetland; (3) oxbow, artificial lake. If a lake has a well-visible marsh, a shallow fringing marsh, fringing marsh swamp or swamp forest margin vegetation, the proximal margin of the wetland vegetation was used as the proximate of the potential mosquito habitat. The 'functional

sets' concept (Amoros et al., 1987) and the definitions are those used for the Austrian section of the Danube (Hohensinner et al., 2011) with minor modifications. The potential mosquito habitats are derived from the 'functional sets' concept of Amoros et al. (1987), except for one habitat, the 'artificial lake'; however, artificial waters provide the same conditions for mosquitos as the appropriate natural waters. The determined potamic (derived from the ancient Greek *potamos* [ποταμός] meaning river or stream) habitats of the studied area were as follow: eupotamon A (main stream), eupotamon B (permanently connected side channels, with permanent flow), parapotamon A (highly dynamic side arms, intact downstream connection, blocked upstream by bare gravel/sand deposits), parapotamon B (less dynamic side arms, intact downstream connections, blocked upstream by vegetated deposits), plesiopotamon (isolated water bodies, close to the main channel, often connected) and paleopotamon (not or seldom connected, isolated water bodies).

1.2.3. Urbanisation scoring

To quantify the degree of habitat urbanisation, the Urbanisation Score software (Czúni et al., 2012; Seress et al., 2014) was applied, which uses only publicly available satellite imagery from GoogleMaps, and the scoring approach introduced by Liker et al. (2008) was used. The Urbanisation Score software was developed in the Image Processing Laboratory at the University of Pannonia. The software generates semi-automated scores of habitat urbanisation. This application downloads an image of 1 km² area around a selected location, then divides it into 100×100 m cells, and scores the abundance of vegetation, buildings and paved surfaces in each cell. These scores are then used for calculating landscape-cover variables, which are then combined by Principal Component Analysis (PCA) into a score of urbanisations for each area. 'Urbanisation scores' are suitable for objectively expressing an area's level of habitat urbanisation, thereby ranking study sites along an urbanisation gradient.

1.2.4. Steps of the analysis

The applied methodological outline are as follows: (1) the software downloads the maps from GoogleMaps according to the given geographical co-ordinates; (2) the user selects 'training points' in each map which represent the different surface types (buildings, vegetations, roads, waters); (3) the software calculates the landscape

variables for each area, which is followed by PCA. The software uses the following landscape variables: number of cells with high building density and number of cells with high vegetation density (>50% cover; range: 0–100), number of cells with paved surfaces (range: 0–100), mean building density score and mean vegetation density score (range: 0–2). For each study area, the calculated scores for the abundance of the above-listed landscape variables are displayed for each 100×100 m cell. It is important to note that after the overview of the primary results the user can manually overwrite the software-generated cell scores in any image cell, changing the landscape category if it is necessary. After the manual correction of some image cell scores, urbanisation scores can be recalculated by re-running the PCA. The method was successfully used by some authors (Bókonyi et al., 2010, 2012A, 2012B; Zhang et al., 2011). In the present work, the centres of the streets of the case sites (hereinafter: ‘case sites’) were used as the location of the cases to protect the privacy rights of the dog owners. This compromise can cause some inaccuracy in the calculation, but for example the length of the streets of Szeged is negligible compared to the generally used 1-km² grid of the software. Urbanisation level was calculated at grids, which overlap the investigated dirofilariasis case sites in Szeged, Kiskundorozsma, Szatymaz and Algyő. The UI values were also calculated at two central downtown locations in Szeged (as the samples of the most urbanised areas) and two floodplain forests of the river Maros (as the samples of highly natural areas) close to the city. These four control sites were selected to gain comparable results in the PCA of the study (defining the most extreme points of the coordinate system).

1.3. RESULTS

1.3.1. Cases and riverbank characterization

PCR was performed in 35 out of the 56 cases. *Dirofilaria immitis* alone was detected in 18, while *D. repens* in 12 cases from the blood samples. In five cases the presence of co-infection with the two *Dirofilaria* species was detected. In 11 cases PCR analysis was not performed, but the presence of a *Dirofilaria* pathogen was confirmed in the blood samples. Dirofilariasis cases accumulate in the pericentre districts of Szeged. Surprisingly, some of the cases were reported from the downtown or panel block districts. Four main aquatic habitats can be found in the environment of Szeged, the

plesiopotamon, paleopotamon, parapotamon B and eupotamon A/B types according to the Amoros classification system (Fig.21 right). Riverbank characterisation showed that paleopotamon and plesiopotamon riverbed types dominate the aquatic habitats of the area, although a substantial number of channels are also notable. Minor lakes can be found almost only in the east district of the city and major sodic lakes can be found close to the northwestern districts. In total value, paleopotamonic waters are the most notable aquatic habitats within the studied grid (Fig.21 left).

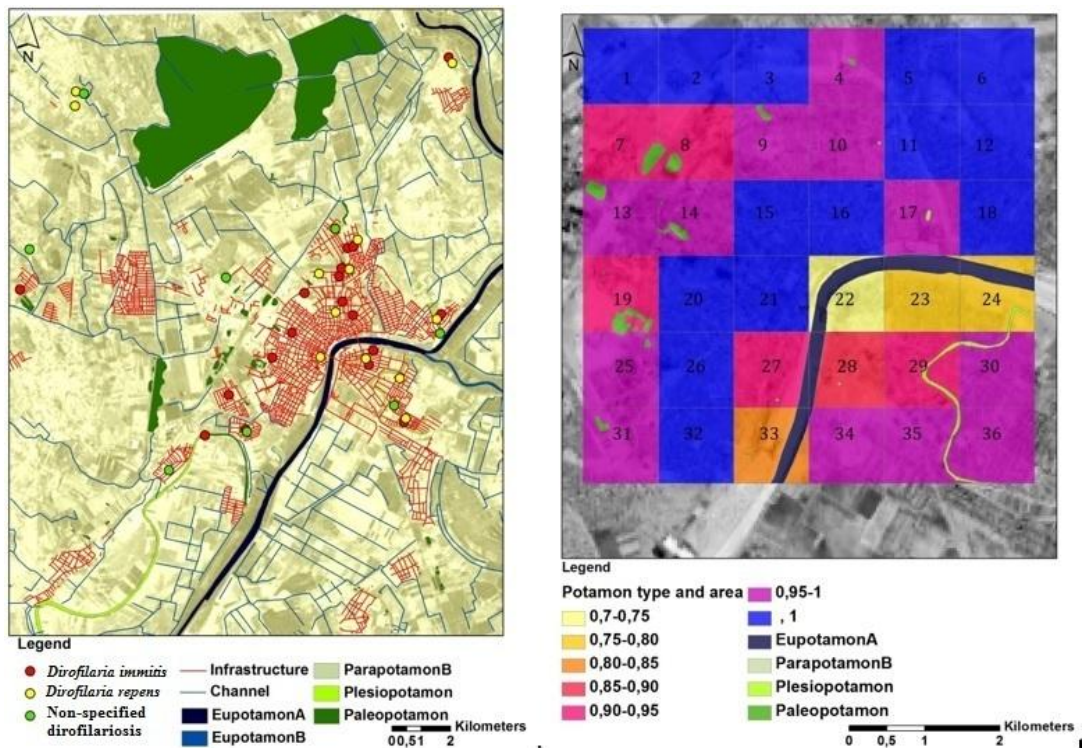


Figure 21. The waters of the wider area of Szeged with the location of the *D. immitis*, *D. repens* and non-specified dirofilariosis cases (left) and the residual area after subtraction of the area of the waters from the total area of the 1-km² grid of the downtown (right).

The results of the PCA analysis of Szeged show a typical one-centred city with a river passing through the centre and several minor suburban parts. The urbanisation level picture of the city is not symmetrical, since the old town was originally built in the right side of the city according to the direction of the river flow. The level of vegetation is between 1–50% in the downtown area, which corresponds to the parked landscape of the city. The left column of Fig.22 shows the spatial patterns of the factors (roads, vegetation and buildings) in Szeged, which are considered by the software in the estimation of UI level. The most urbanised areas are mainly restricted to this historical

part of Szeged (e.g. square 21 in the right-side picture of Fig.22). The extended block house zone surrounds the old town from the north and has a high to medium UI value.

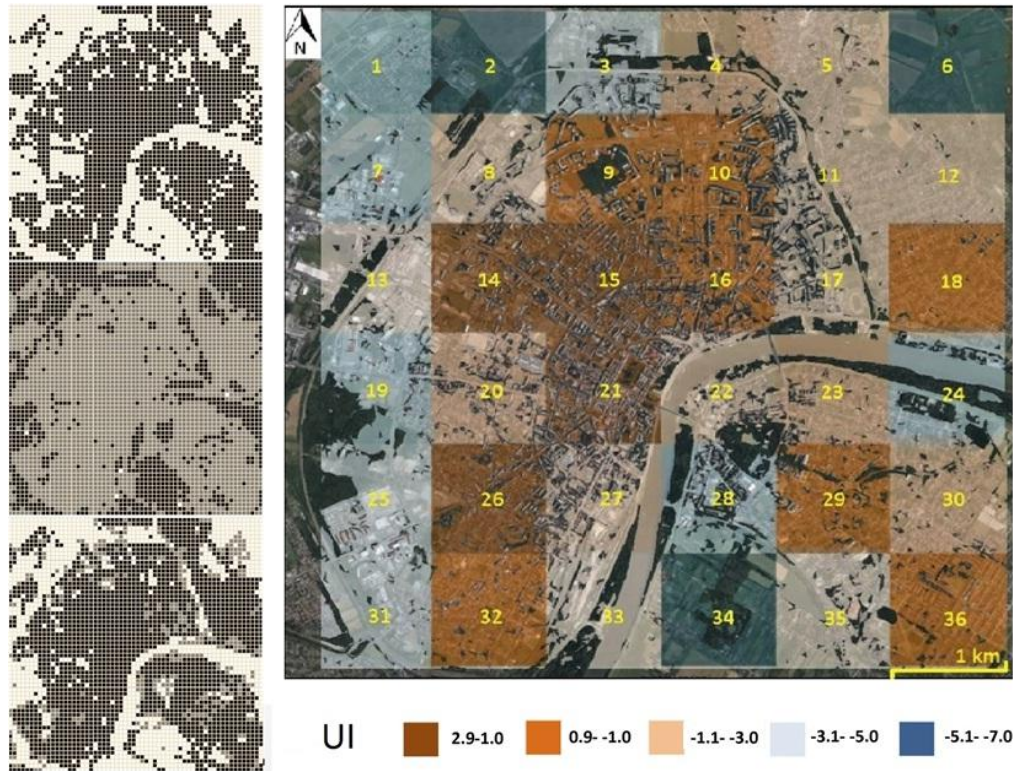


Figure 22. Left column: the coverage of the three measured parameters: upper: roads, medium: vegetation (and waters), lower: buildings. White square = none, grey square = <50%, black square = >50%. Right picture: the UI patterns in Szeged according to 1-km² areal resolution.

6.3.2. Distribution determining factors

All the dirofilariasis cases occurred within 1310 m from the nearest standing water, river or swamp of the inundation area. According to the distances from the potential mosquito habitat water bodies, the numbers of dirofilariasis cases were as follows: 0–262 m: 17 cases, 263–524 m: 31 cases, 525–786 m: 4 cases, 787–1048 m: 2 cases, 1049–1310 m: 2 cases. Overall, 30.4% of the infections occurred between 0 and 262 m from the case sites and 85.7% of the cases occurred within 524 m from the potential mosquito habitats. The different suburbs have a medium UI value in general. The river Tisza has a narrow floodplain within the city centre with the remnants of the former gallery forest (e.g. squares 24 and 33), which widens toward the edges of the city. According to the results of the two-sample *t*-test there is no significant difference ($P = 0.9210$) between the variances of the UI of the *D. immitis* and *D. repens* sites. The histographic patterns of the UI values related to the 1 km² area of the percentage of *D.*

immitis and *D. repens* case sites are somewhat similar to a unimodal frequency peak in case of the UI index interval of 1.45 ± 0.01 , which corresponds to the urbanised areas of the city. The UI values of the endemic sites except one case showed a transition (2.9 to -4.32) between the control vegetations (<-4.32). Some cases were observed also in the downtown areas (>2.8) of Szeged. According to the UI ranges the case numbers were as follow: 2.9 to 1.46: 5 cases, 1.45 to 0.01: 8 cases, 0.00 to -1.43 : 4 cases, -1.44 to -2.87 : 1 case, -2.88 to -4.32 : 1 case (*D. immitis*); 2.9 to 1.46: 2 cases, 1.45 to 0.01: 5 cases, 0.00 to -1.43 : 4 cases, -1.44 to -2.87 : 1 case, -2.88 to -4.32 : 0 case (*D. repens*). The compound probability of the UI and the proximity of the potential mosquito habitats showed the highest potential abundance of canine dirofilariasis cases in the peri-downtown areas where the distance from the closest natural mosquito breeding habitat is less than 800 m (Fig.23).

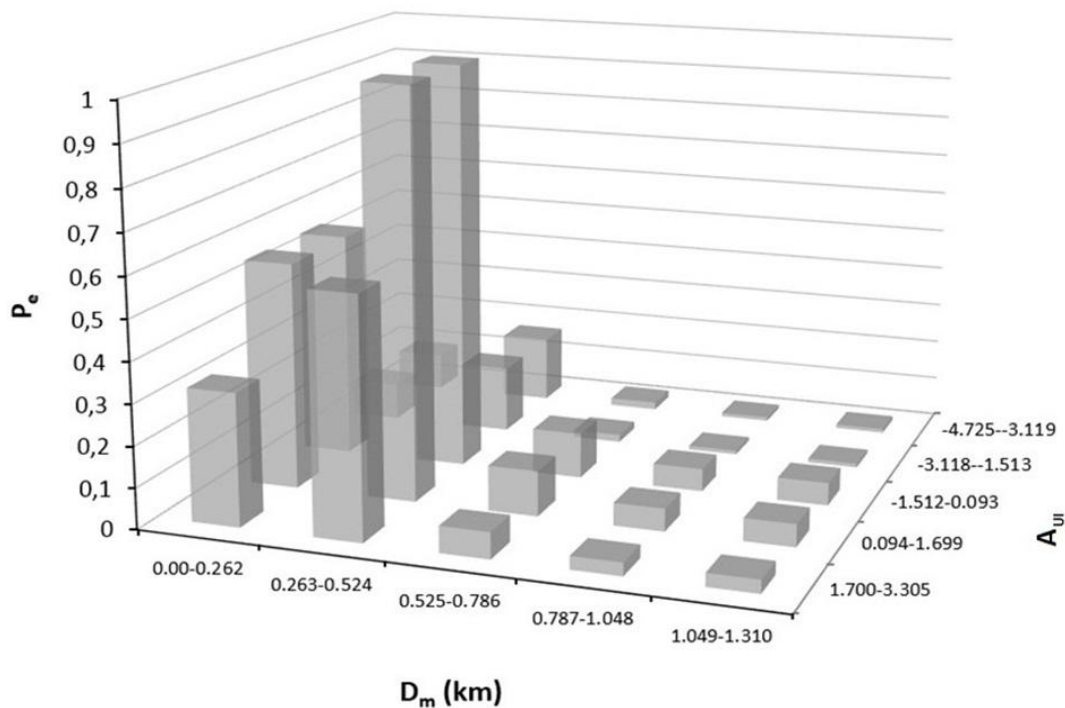


Figure 23. The matrix and bar chart diagram showing the compound probability of an encounter between the infected mosquito and the susceptible organism (P_e). A_{UI} : abundance of dogs according to the UI of an area, D_M : distance from the potential mosquito habitats in km, P_e : compound probability of the encounter of the infected mosquito and the susceptible organism.

1.4. DISCUSSION

This is the first study in Hungary which investigates the affinity of canine dirofilariasis to an urbanised region of temperate Europe. Since *D. immitis* and *D. repens* are present in the neighbouring Vojvodina, Serbia (Tasić et al., 2008) and the

infected dogs were local pets, it is highly plausible that the infections were autochthonous. It was found that *D. repens* is an almost as prevalent causative agent of canine dirofilariasis in Szeged as *D. immitis*. The rate of co-infection with *D. immitis* and *D. repens* was relatively low (5.7%), which cannot be explained by the spatial segregation of the abundance of these parasites within the studied area. It is plausible that in the first *D. immitis* infection cases dogs acquired the parasites in the garden due to the very close proximity of an oxbow, but this assumption cannot be generalised. On the other hand, the fact that almost 90% of the cases occurred within 524 m from the potential mosquito breeding sites may indicate that dogs were infected in the garden and mainly through bites by local mosquito specimens. The annual case number and the distribution of canine dirofilariasis can be the consequence of several other factors such as the type of the nearest potential mosquito breeding habitats and the presence/absence of wild carnivores (ferrets, foxes or even golden jackals - *Canis aureus* LINNAEUS, 1758) and probably domestic cats, because feline dirofilariasis also occur (Genchi et al., 2001). Different Culicidae species prefer various aquatic habitats and the composition and the total area of waters can change over time in a given area. Human-induced changes have a prolonged impact on habitats suitable for mosquitos, while the effect of artificial influences can be dissimilar for different mosquito species (Trájer et al., 2015B) that have a different vector value in the transmission of *Dirofilaria* species. The flight distance of potential mosquito vector(s) is likely to influence the spatial patterns found. In 2013 a mosquito trapping was performed at the case site of the first dirofilariasis cases in Szeged to detect the potential vectors of *D. immitis* (Zittra et al., 2015). The authors observed the presence of *D. immitis* in *Culex pipiens* s. l. and *Aedes caspius* PALLAS, 1771. In 2013, an independent trapping activity, which was performed at the first case site, confirmed the dominance order and composition of the mosquito fauna (Trájer et al., 2016B). An experimental parasitological study also showed that infection of the *Culex pipiens* complex has a notable host efficiency and infective potential for *Dirofilaria immitis* (Kartman, 1953). In addition, several other studies confirmed the *D. immitis* vector status of *Culex pipiens f. pipiens* by identification of the non-infective stage of *D. immitis* in the *Cx. pipiens* complex (Vezzani et al., 2011) and by detecting the filarioid DNA in the mosquito (Morchón et al., 2007; Yildirim et al., 2011). Members of the *Cx. pipiens* complex are very frequent in Hungary and they also

prefer several types of aquatic habitats (Kenyeres and Tóth, 2008). Aranda et al. (1998) emphasised the importance of *Cx. pipiens f. pipiens* in the transmission of filarioid specimens in canine cases. A mark–release–recapture study of *Cx. pipiens pallens*, the Far Eastern relative of the *Cx. pipiens* complex, conducted in an urban area of Japan estimated that the mean distance covered by the recaptured females was 287 to 517 m during 1–4 days (Tsuda et al., 2008). The maximum flight distance of *Cx. pipiens pallens* was estimated as 1,217 m. Since the lifespan of adult mosquitos is usually measured in days, the about 300–500 m flight distance of host-seeking mosquitos approximates their average maximum dispersal distance per generation. Naturally, other factors such as the wind and human transport can strongly influence the real dispersal rate (Bailey et al., 1965). Since most of the studied dirofilariasis cases occurred within a 524 m circle of mosquito breeding habitats, it can be concluded that this abundance pattern reflects the influence of the maximum flying distance of mosquitos. It is worth to note that the applicability of the method is somewhat limited by the fact that dogs and owners can move around their home e.g. by dog walking in parks, which may have a non-negligible impact on the observed abundance. Although it cannot be assumed, that dogs were stationary with no movement within the city; the model itself does not require or suggest that the observed spatial pattern of the cases depends solely on the flying capability of mosquitos. On the contrary, the encounter probability of dogs and mosquitos depends on the movement behavior of both the vectors and the dogs, and eventually on the behavior of dog owners. This somewhat contradicts the fact that several members of the above-mentioned *Cx. pipiens* complex use artificial waters as breeding sites. One reason may be that a large proportion of mosquitos occurring in the human environment originally developed in natural waters and not in domestic environments. Čabanová et al. (2018) much frequently found filarioid DNA in the mosquito samples of the floodplain area on the outskirts of Bratislava than in the residential zone of the city. Advanced Geographical Information Systems (GIS-) based geospatial tools exist for the visualisation, tracking and modeling of the complex, multi-factor-influenced epidemiological processes. Variables such as elevation, land-cover and land-use data, as well as meteorological variables emanating from earth-observing satellites allow the analysis of disease distribution and the changing incidence and prevalence in time and space. Climate-based forecast systems, based on the concept of

growing degree days, exist for several parasitic diseases including dirofilariasis (Bergquist and Rinaldi, 2010). The results of a GIS analysis-based model performed for the prediction of the territorial distribution of dirofilariasis caused by *Dirofilaria immitis* in Italy was highly concordant with the real territorial distribution of positive dogs (Mortarino et al., 2008). Rinaldi et al. (2011) proved that information derived from GIS-based descriptive maps provides a well-usable operational tool for planning, monitoring and managing control programmes for *Dirofilaria* infections. In this view, the study confirms the importance of two factors that can be used as basic inputs in GIS-based models.

2. THE RECENT AND FUTURE OCCURRENCE OF *PHLEBOTOMUS* SPECIES IN URBAN ENVIRONMENTS^{5,6}

2.1. INTRODUCTION

Based on the observations of Bettini and Mellis (1988), the pre-imaginal stages of the sandfly species are associated with a comparatively stable, humid, cool environment, protected from rain, direct solar radiation and wind and rich in clay and organic nitrogen. Organic matter has an important role in the evolution of sandflies, since pupae are attached to it by skin (Killick-Kendrick, 1987). According to Killick-Kendrick et al. (1986) the flight speed of the females is about 1 m s^{-1} , so they can disperse distances 2 km from breeding places. Thus, it can be stated, that sandflies are looking for nutrients in their proximity. Adults seek refuge in both anthropogenic and natural environments: e.g. inside buildings, barns, wall fissures, tree holes, animal nests (Maroli et al., 1994; Ascione et al., 1996; Maroli and Khoury, 1998). According to Moncaz et al. (2012), *Phlebotomus sergenti* PARROT, 1917 rests and breeds inside caves and in three nests of several rodent species.

^{5,6}This chapter was published in Applied Ecology and Environmental Research and Journal of Vector Borne Diseases: Trájer, A.J., Mlinárik, L., Juhász, P., Bede-Fazekas, Á. (2014). The combined impact of urban heat island, thermal bridge effect of buildings and future climate change on the potential overwintering of *Phlebotomus* species in a Central European metropolis. Applied Ecology and Environmental Research, 12(4), 887-908. and Bede-Fazekas, Á., Trájer, A.J. (2015). Potential urban distribution of *Phlebotomus mascittii* Grassi and *Phlebotomus neglectus* Tonn. (Diptera: Psychodidae) in 2021–50 in Budapest, Hungary. Journal of Vector Borne Diseases, 52(3), 213-218.

Females lay eggs in batches, tree holes, animal shelters, and inartificial crevices, as well as cracks of weathering construction materials, which are dark and rich in organic matter (Shortt, 1930; Tánczos 2012; Yuval, 1988). In the nature Hanson (1961) and Vanni (1940) found sandfly pupae on the surface of fallen dead leaves and forest floor and due to the fermentation heat of the compost, they can overwinter during cold conditions. Larvae need enough heat, humidity and organic matter to survive and develop (Naucke, 2002; Lindgren et al., 2006).

2.1.1. Heat island effect of Budapest

The urban heat intensity (hence: UHI) is an important additional climate-moderating effect, which has a similar importance attenuating the winter minimum temperatures as the heat bridges have. The UHI depends on the urban size (the spatial scale and the population size), the characteristics of the surface (e.g. the albedo of the surfaces, the amount of green space) and the natural and modified topography, the anthropogenic heat release (thermal pollution), and the prevailing wind direction (Kim et al., 2004). There is a positive correlation between maximum UHI and the order of magnitude of the population size of the settlements and in North America, Japan and Western Europe the steepness of correlations show differences (Oke, 1973; Heinrich et al., 2006). The ambient temperature is increasing from the border of the populated area to the geometrical center of the city. The maximum difference between the downtown of the city and the Plain of Pest, which is surrounding Pest (the east part of Budapest) can be - 6 °C to -7 °C in winter nights (Pongrácz et al., 2006; Bartholy et al., 2009; Lelovics et al., 2012).

2.1.2. The role of thermal bridges and weather conditions

Since fissures of walls, joint gaps, foot separations interrupt the continuity of the walls and the isolations they form thermal bridges (hence: THBs). If protection from excessive sun radiation and the availability of organic matter are assured, THBs can provide such microenvironment on buildings. In heated buildings, temperature increases toward the interior of the architect. It means, that the deeper parts of the walls get more heat than the parts that closer to the surface. Thermal bridging is created when materials that are poor thermal insulators come into contact, allowing heat to flow through the path of least thermal resistance (R-value) or a material's effectiveness in resisting the

conduction of heat created. Although nearby layers of material separated by airspace allow little heat transfer (Binggeli, 2010). With other words, THB is a part of a building or structure, which is situated between two spaces with significantly different temperature (most often a heated internal environment and the external environment with atmospheric conditions) and shows a higher thermal conductivity value (λ -value), than the surrounding structures or elements (Binggeli, 2010). Thermal bridges are integral parts of a construction and can be generated by weathering processes. Weathering can also liberate minerals essential for microbial life, which will enhance of generation of organic materials. Furthermore, microbial activity itself accelerates the chemical weathering by producing organic acids (Banfield, 1999; Drever, 1997).

Objective 1. The first aim of this sub-chapter was to study the possibility of the overwintering of sandflies due to the anthropogenic urban heat pollution (THBs and UHI) of the outdoor environment in Budapest, the capital of Hungary.

Hypothesis 1. Since the known cold-resistance of sandfly species is low or low-moderate, it was hypothesized that sandflies in urban environment can only overwinter in heat-polluted shelters.

Objective 2. The second aim of this sub-chapter was to project the possible future overwintering areas of *Phlebotomus mascittii* GRASSI, 1908 and *Ph. neglectus* in Budapest, the capital of Hungary those species were collected near to the capital in Törökbálint (Farkas et al., 2011; Tánzos et al., 2012).

Hypothesis 2. It was hypothesized that climate change will broaden the range of the studied two *Phlebotomus* species in Budapest.

2.2. MATERIALS AND METHODS

2.2.1. *The approach of the study*

According to the above detailed literature, natural refuges as leaf piles as well as the artificial ones, such as cracks of the buildings may be adequate habitats for sandflies and can serve as winter shelters. It was aimed to study the additional heat surplus of THBs (microclimatic factor) and the UHI (mesoclimatic factor), as well as to synthesize these effects. It is clear, that THBs of the cracks and corners are not the only air polluted, outdoor environments where sandflies can overwinter, but due to the easy access of the wall surfaces they are useful to study the joint changes of a heat polluted

system as the function of the changes of the outdoor mean ambient temperature. According to the literature detailed above, not only natural refuges can serve as adequate habitats for sandflies but buildings in the urban context as well. It was also aimed to run CEM to study the potential distribution of *Ph. mascittii* and *Ph. neglectus* in the period of 2021-2050 in Pest County, Central Hungary. The model is based on the observation of these two sandfly species in 2006-2009 in Törökbálint, suburb of Budapest, the UHI of Budapest and its agglomeration calculated on the basis of satellite images, and on the predictions for the reference (1961-1990) and the future (2021-2050) period of RegCM3 regional climate model (Winter et al., 2009).

2.2.2. Abiotic factors of overwintering and activity

The overwintering potentials of six *Phlebotomus* species: *Phlebotomus ariasi* TONNOIR, 1921, *Phlebotomus perniciosus* NEWSTEAD, 1911, *Phlebotomus perfiliewi* PARROT, 1930, *Ph. neglectus* and of *Ph. mascitti* were studied. According to Killick-Kendrick (1987), *Phlebotomus* species in the temperate areas of Europe can overwinter as the ontogenetic stage of 4th instar larvae. The different *Phlebotomus* species have different minimum temperature tolerances: -4 °C of *Ph. perfiliewi*, *Ph. neglectus*, *Phlebotomus papatasi* SCOPOLI, 1786, *Ph. mascitti*; 0 °C of *Ph. perniciosus*, and 5 °C of *Ph. ariasi* (Killick-Kendrick et al., 1984; Killick-Kendrick, 1999; Singh, 1999; Naucke and Schmitt, 2004). According to Lindgren et al. (2006) the preferred humidity for adults of *Ph. neglectus* and *Ph. perfiliewi* is between 60-80%, and for *Ph. papatasi* and *Ph. sergenti* is below 45%. While the number of the days with suitable temperature for the reproduction and for the growing of the larvae and the moisture index have a strong correlation with the ontogeny and growth of *Phlebotomus* larvae (Killick-Kendrick, 1987; Oshaghi et al., 2009), low temperatures and precipitation are expected to limit the *Phlebotomus* distributions.

2.2.3. Thermal imaging

A Testo thermometer was used. The camera has 845 measure points as close as 0.635 cm. It displays temperature with minimum and maximum values within the same thermal image. It was aimed to measure not only the ambient air temperature, but also the temperature of the wall surfaces. The temperature of the wall surfaces was measured within and outside of the THBs. Since the temperature of the warm THB and the

surrounding cold wall surfaces were recorded within one thermal image, the surface temperature of the wall was characterized with the minimum temperature value of the whole image. The temperature of THB was characterized by the measured maximum temperature of the image. Temperature values obtained with the Testo thermal imager may differ from the actual temperature values, thus they were calibrated with the temperature values measured on the spot with help of a GANN Elektronik-Feuchtemesser [Nr.: 6483 Hydromette RTU 600 (sensor) IR 40 (head)] electronic thermometer. Environmental temperatures in two periods were measured, one was a colder period (six measurements in six days between the 23rd-30th of January), and the other was relatively warmer (six measurements in six days from 25th of February to 13rd of March). Surfaces in the mornings were measured around AM 7:30 and AM 8:00, since in general the morning temperatures are the lowest during the day. This time the spots were shaded. During the period of measurements, the sun rose between AM 7:21 (23rd of January – first day) and AM 6:54 (25th February - last day).

2.2.4. Site of the study

Both buildings are situated along the riverside of the Danube and in the proximity of the Gellért Hill. One of the two spots is in a vertical and full-height nook on the south facade (marked with S1), the other one in a negative building edge facing southeast (marked with S2). Spot S1 is situated on a brick wall facade inside a nook with varying depth between 13 and 3 cm and protected by a plastic gutter pipe (d=90 mm) against the sunshine. Moreover, due to the capillary adsorption of water from the soil and wetting due to the broken gutter-pipe, spot S1 is almost always wet. This is further proved by the presence of moss colonies on the surface. Negative edge S1 has an ooidic, porous limestone cover, and partly shaded by a plastic gutter pipe with a diameter of 15 cm. A wall rue was found with *Asplenium ruta-muraria* LINNAEUS, 1753, fern, *Bryum argenteum* HEDWIG, 1801 mosses and green algae math on the Spot S2. *Asplenium ruta-muraria* is typical lithophyte, which originally lives on dry to moist, shaded limestone outcroppings, calcareous rocks. The presence of this fern and the non-vascular plants indicate moisture and shading. *Bryum argenteum* is a common moss which can tolerate dry and sunny environments and prefers the neutral or alkalic soils. Appearance and location of the two spots can be seen in Fig.24.

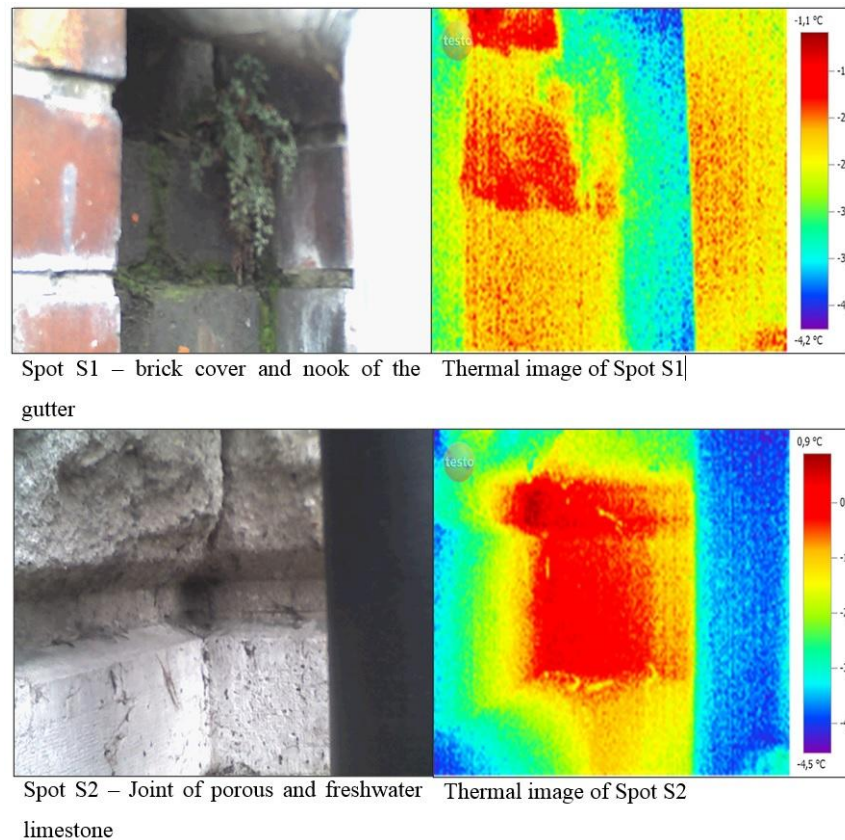


Figure 24. Appearance (left column) and thermal images (right column) of the two spots.

Not only the surface materials, but the structural elements of the two spots are also different. Both are outer walls, separating heated internal spaces and environmental conditions outdoor. Spot S1 is in a wall, whose structure is the following from inside to outside: 2 cm of color plaster on lime plaster, 44 cm large size brick and 12 cm small-size covering brick. The structure of the wall involving spot S2 is the following from inside to outside: 2 cm lime plaster, 48 cm large-size brick and 25-20 cm porous and freshwater limestone covering. These two spots are partly protected from weather conditions. The gutter pipes serve as a shader from solar radiation, as a wind-stopper, as well as a source of water in the S1 spot. The shading of the solar radiation is important, because solar radiation is one of the most important conditions that determine the habitat selection of sandfly species (Trájer et al., 2018).

Due to their orientation and location both spots are protected from the relevant direction of the wind, which is northwest to southeast, since the Gellért Hill develops a wind-tunnel. From the north side both spots are protected by the buildings itself, and due to the height of the buildings the effect of airflow is minimal. From the south direction S1 is partly protected by trees and bushes growing nearby and the body of the

gutter. S2 is protected from this direction by the south wing of the U-shaped building, and by the gutter-pipe. As for protection against excessive rain-wash, both the pipes and drips of the buildings are effective.

2.2.5. Climatic data

The ground temperature data of Budapest and its surroundings were obtained from MODIS (Moderate Resolution Imaging Spectroradiometer; Pagano and Durham, 1993) sensor of the Aqua satellite of NASA (Gutro et al., 2002). The satellite has a quasi-polar orbit and makes images between 02-03 UTC and between 12-13 UTC (Wan, 2004). Since the colder temperatures had importance in this research, images taken at night were obtained. A grid with 4900 point was selected between latitude 47.2208N-47.7958N and longitude 18.6073E-19.6740E. Between 2003-01-01 and 2008-12-31 those 643 images were taken, which had less than 20% data absence. The differences of urban and rural temperatures were calculated by Lelovics et al. (2012). The selected images were taken in 2007-11-29, 2007-01-27, 2005-01-24, 2003-01-16, 2008-11-23, 2003-12-07, 2007-02-04, 2004-12-07, 2006-12-11, 2005-11-03, 2005-04-05, and 2003-10-14 with urban mean temperatures -6.0, -5.9, -4.0, -3.9, -2.0, -1.9, 0.2, 0.3, 2.0, 2.1, 3.9, and 4.2 °C, respectively (Fig.25).

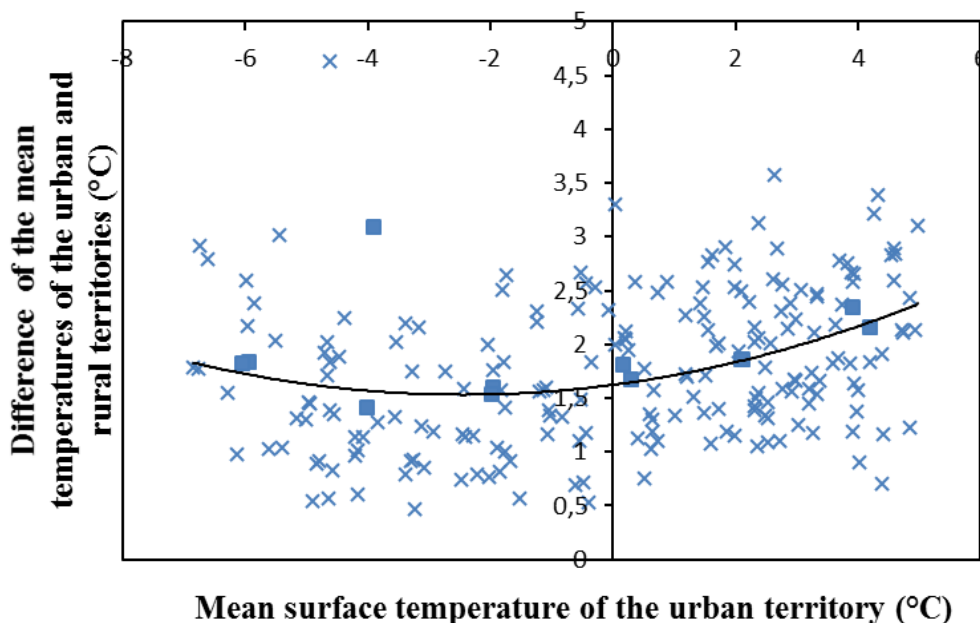


Figure 25. The difference of the mean temperatures of the urban and rural territories with a second order regression line. Only the days with less than 20% data absence and with urban mean temperature between -7 – 5 °C are displayed. The selected 12 days are marked with square symbols.

The effect of climate change was derived from the downscaled RegCM3 regional climate model (Winter et al., 2009) with the domain. The model was based on the IPCC SRES scenario A1B. The most important limiting factor of the distribution of *Phlebotomus* species in the region is the annual minimum temperature (Trájer et al., 2013), therefore the horizontal average of the minimum of daily minimum ground temperatures in January was used from the reference period 1961-1990 and the prediction period 2025-2050. The horizontal resolution of the grid was 10 km, and 48 points were found between latitude 47.2208N-47.7958N and longitude 18.6073E-19.6740E (the domain of the 4900-satellite data).

2.2.6. Impact of urban heat emission on sandfly distribution

It was supposed that the impact of UHI, the shelter of the THBs and future climate change encourage that sandfly species can overwinter in open space. Three different methods were employed to study whether Budapest and its surroundings provide suitable environments in climatic terms for the six sandfly species. The studied species were assorted by their cold tolerance in three groups as follow: group 1: *Ph. ariasi*, group 2: *Ph. perniciosus*, and group 3: *Ph. mascitti*, *Ph. neglectus*, *Ph. papatasi*, and *Ph. perfiliewi*. While only the UHI was considered by Method 1. (Eq.20), Method 2. supposes that, besides the effect of the UHI, the shelters provided by the THBs benefit the overwintering of sandflies (Eq.21). Method 3. calculates with the effect of UHI and THBs (measured nowadays) plus the predicted increase of the mean ground temperature by 2025-50 (Eq.22).

$$T_1 = T_0 - \Delta T_{UHI} + \Delta T_{air} \quad (20)$$

$$T_2 = f_{TB}(T_0 - \Delta T_{UHI}) + \Delta T_{air} \quad (21)$$

$$T_3 = f_{TB}(T_0 - \Delta T_{UHI}) - \Delta T_{FP} + \Delta T_{air}, \text{ where} \quad (22)$$

ΔT_{air} : difference of air and ground temperature

ΔT_{UHI} : temperature difference caused by UHI

$f_{TB}(T)$: sheltering effect of the THBs

ΔT_{FP} : temperature difference of the reference period and the future prediction

Conversion from ground temperature to air temperature (at 2 m height) was applied in all the three methods based on averaged differences in six observation points in the studied domain (Lelovics et al., 2012). The observations were made in winter at night. The calculated difference (1.8 °C) has the opposite sign than the three temperature altering effects (the air temperature is greater than the ground temperature). The effect of UHI was calculated by a script written in R for all the 4900 studied points. Previous studies showed that both second order polynomial regression and linear regression with major axis method are highly unstable for calculating the base temperature dependence of the volume of the UHI. Therefore, simple averaging was done based on the 12 selected images. The maximum of the UHI was +4.1 °C. The sheltering effect of the THBs was calculated based on the measures made in spot S2. Linear regression was made since the volume of the temperature difference showed correlation with the base temperature. The warming effect of the predicted climate change was approximated by averaging the warming in the 48 points of the domain. The value occurred to be -14.4 °C in the reference period; -10.3 °C in the prediction period, therefore 4.1 °C was subsequently used as difference. The result of the three methods in the case of the three groups was displayed by ESRI ArcGIS 10 software. The grid was interpolated by inverse distance weighted (IDW) method with power 2 and 12 neighboring points. The results were clustered between isotherms of the even integer numbers in the Celsius scale. Digital NUTS3 polygon borders were displayed to help orientation (GISCO 2013).

It was supposed that both the impact of UHI and future climate change encourage that sandfly species can overwinter in open space. *Eq.23* (reference period) and *Eq.24* (prediction period) show the calculations made to study whether Budapest and its surroundings provide suitable environments in climatic terms for the sandfly species.

$$f = \begin{cases} \textit{climatically suitable}, & \textit{if } T_{min,jan}^{1961-1990} > T_{min,jan}^{1961-1990,observed} \\ \neg(\textit{climatically suitable}), & \textit{if } T_{min,jan}^{1961-1990} \leq T_{min,jan}^{1961-1990,observed} \end{cases} \quad (23)$$

$$f = \begin{cases} \textit{climatically suitable}, & \textit{if } T_{min,jan}^{2025-2050} > T_{min,jan}^{1961-1990,observed} \\ \neg(\textit{climatically suitable}), & \textit{if } T_{min,jan}^{2025-2050} \leq T_{min,jan}^{1961-1990,observed} \end{cases} \quad (24)$$

The ground temperature of a certain location was calculated based on the ground temperature data of RegCM3 climate model and the temperature difference caused by UHI (Eq.25).

$$T_{min,jan} = mean(T_{min,jan}^{ground}) + mean(\Delta T_{UHI}) \quad (25)$$

The effect of UHI was calculated by a script written in R for all the 4900 studied points. Previous studies showed that both second order polynomial regression and linear regression with major axis method are highly unstable for calculating the base temperature dependence of the volume of the UHI. Therefore, simple averaging was done based on the 7 selected images. The maximum and the minimum of the UHI effect were +4.5 °C and +2.3 °C, respectively. After data exportation from Microsoft Excel 2010, the result was displayed by ESRI ArcGIS 10 software. The temperature grids were interpolated by inverse distance weighted (IDW) method with power 2 and 12 neighboring points. The isotherms were displayed by Contour method of Spatial Analyst extension and projected onto one map. Digital NUTS3 polygon borders (Torma et al., 2011) and the river Danube were displayed to help orientation.

2.2.7. Software and statistics

For processing the thermal images, Testo's own software, IRSoft Testo program was used. For linear regression analysis Microsoft Excel 2010 and Statistica 11 toolpack were used. R statistic analyzer and Microsoft Excel 2010 were used as data preprocessors. GIS modeling was achieved by ESRI ArcGIS 10 software, and the output layouts were edited by Adobe Photoshop.

2.3. RESULTS

2.3.1. Differences in thermal behavior of the two spots

Strong correlations were found (S1: $R^2=0.9785$, Eq.26 and S2: $R^2=0.946$, Eq.27) between the minimum and the maximum temperatures of the THBs. Temperatures of the limestone surface were found to be higher in most of the cases: in 67% of the measured minimum temperatures and in 75% of the measured maximum temperatures. Different gradients and intersections of trend lines fitted on the measured values showed that the two THBs behave differently due to the changes of the environmental

circumstances. Moreover, regarding both the minimum and maximum temperature values, relative differences are higher in the colder period (rel. difference of minimum values: 1.5 ± 1.3 °C and 3.0 ± 1.1 °C for the maximum values) than in the milder period with higher temperature values (rel. difference of minimum values: 0.7 ± 0.9 °C and 1.2 ± 1.6 °C for the maximum values). According to the fitted linear trend, this means a 3.9-3.6 °C permanent difference in the -10 to 15 °C interval for S1 and a 3.0-7.4 °C difference in the 10 to -15 °C interval for the S2 - see the two trend lines moving away from each other in *Fig.26*.

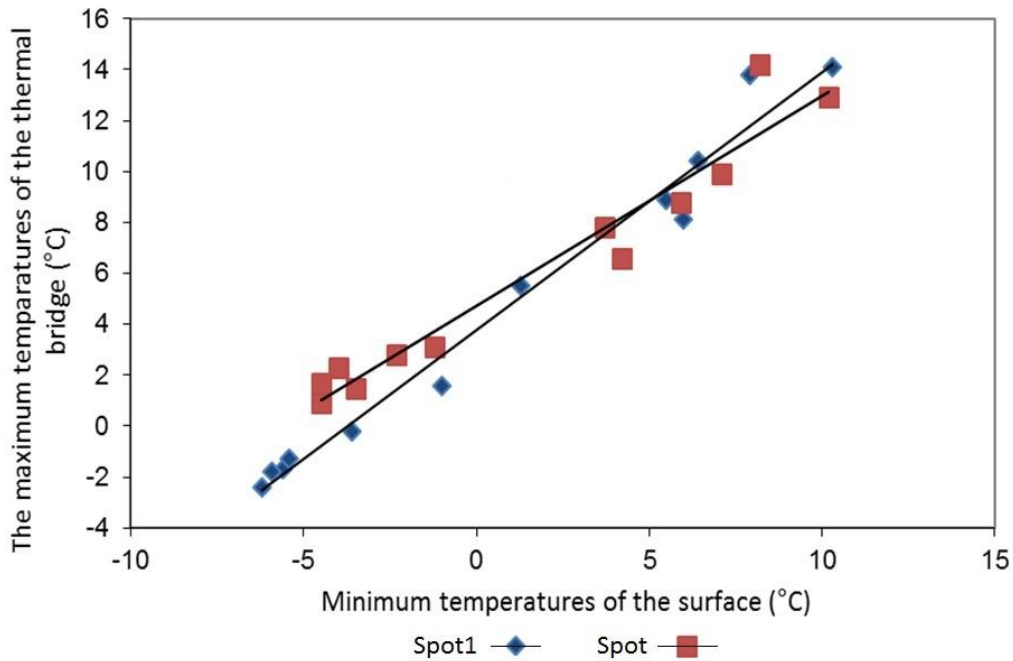


Figure 26. Correlation between the minimum and maximum surface temperatures measured on the two spots.

S1 spot:

$$T_{max\ TB} = 1.011 \times T_{min\ S} + 3.765 \quad (26)$$

S2 spot:

$$T_{max\ TB} = 0.824 \times T_{min\ S} + 4.715 \quad (27)$$

where

T_{max_TB} : the maximum temperature of the thermal bridge

T_{min_S} : the minimum temperature of the surface

2.3.2. Correlation between surfaces and ambient temperatures

Using the linear trends, we calculated the expected maximum temperature of the THBs according to the (ambient) minimum temperatures (of the surfaces). Intersection point of the two trend lines was calculated to be P (5.1 °C; 8.9 °C), which shows, that for the minimum temperatures lower than $x=5.1$ °C the differences between the maximum and minimum temperatures measured on the spots will be higher for the limestone cover. Temperatures of the environment (air temperature) at the time of the measurement (T_{en}) were both compared with the minimum and the maximum temperatures measured on the surface. It was found, that minimum surface temperatures correlate better to the air temperature, then local maxima well presenting the heating effect of the THBs - see Fig.27. Fitted trend-lines of the maximum possible surface temperatures were compared with the limits of tolerance of the different species.

By calculating the first coordinates of the intersection points of the trend lines and the horizontal limits belonging to the tolerated minimum temperatures of the species, the critical minimum environmental temperature of survival of the species can be determined (see Eq.26-27). It is noticeable, that due to the calculated heat surplus of the THBs, different sandfly species can tolerate environmental temperatures ranging from +1.6 to -12.6 °C, (outdoor environment).

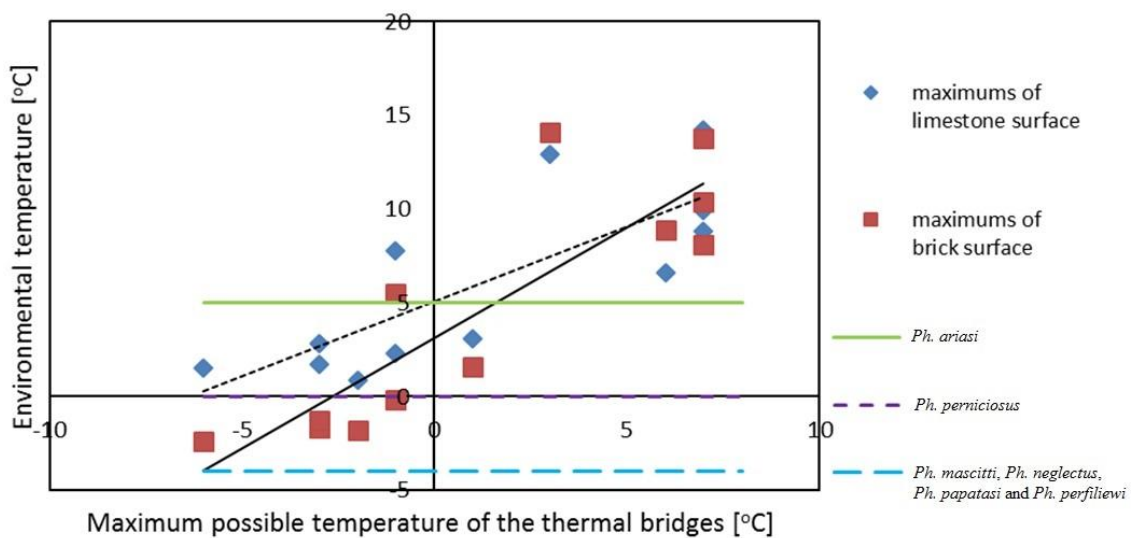


Figure 27. Correlation between the minimum and maximum surface temperatures measured on the two spots with the minimum temperature tolerance of the sandfly species groups.

S1 spot:

$$T_{en} = 0.797 \times T_{max\ TB} + 5.046 \quad (28)$$

S2 spot:

$$T_{en} = 1.180 \times T_{max\ TB} + 3.1087 \quad (29)$$

where

T_{en} : environmental temperature

$T_{max\ TB}$: the possible maximum temperature of the thermal bridge

The result of the linear regression based on the measures at spot S2 is shown in Eq.30.

$$T_{min} = 0.1481 * T_{max} - 5.3280 \text{ } ^\circ\text{C} \quad (30)$$

The descriptive statistics of the three methods in case of the three studied groups was summarized in Tab.4.

Table 4. Descriptive statistics of the three groups (1: *Ph. ariasi*, 2: *Ph. perniciosus*, 3: *Ph. mascitti*, *Ph. neglectus*, *Ph. papatasi*, *Ph. perfiliewi* and the three methods (specified in the text).

(°C)	Minimum	Maximum	Mean (all)	Mean (rural only)	Mean (urban only)
Method 1. (Group 1.)	2.7250	9.4451	6.5981	6.8295	4.9017
Method 1. (Group 2.)	-2.2749	4.4451	1.5981	1.8295	-0.0982
Method 1. (Group 3.)	-6.2749	0.4451	-2.4018	-2.1704	-4.0982
Method 2. (Group 1.)	-2.4718	5.2433	1.9747	2.2404	0.0271
Method 2. (Group 2.)	-8.2122	-0.4970	-3.7656	-3.4999	-5.7132
Method 2. (Group 3.)	-12.8046	-5.0893	-8.3579	-8.0922	-10.3055
Method 3. (Group 1.)	-6.5545	1.1606	-2.1079	-1.8422	-4.0555
Method 3. (Group 2.)	-12.295	-4.5797	-7.8483	-7.5826	-9.7959
Method 3. (Group 3.)	-16.8873	-9.1720	-12.4407	-12.1750	-14.3882

2.3.3. Impacts of thermal factors on sandfly habitats by species

The result of the GIS modeling can be seen in Fig.28A-C. The displayed temperature values mean the average air temperature of the region, which can be tolerated by the species in a certain location in case of the three methods.

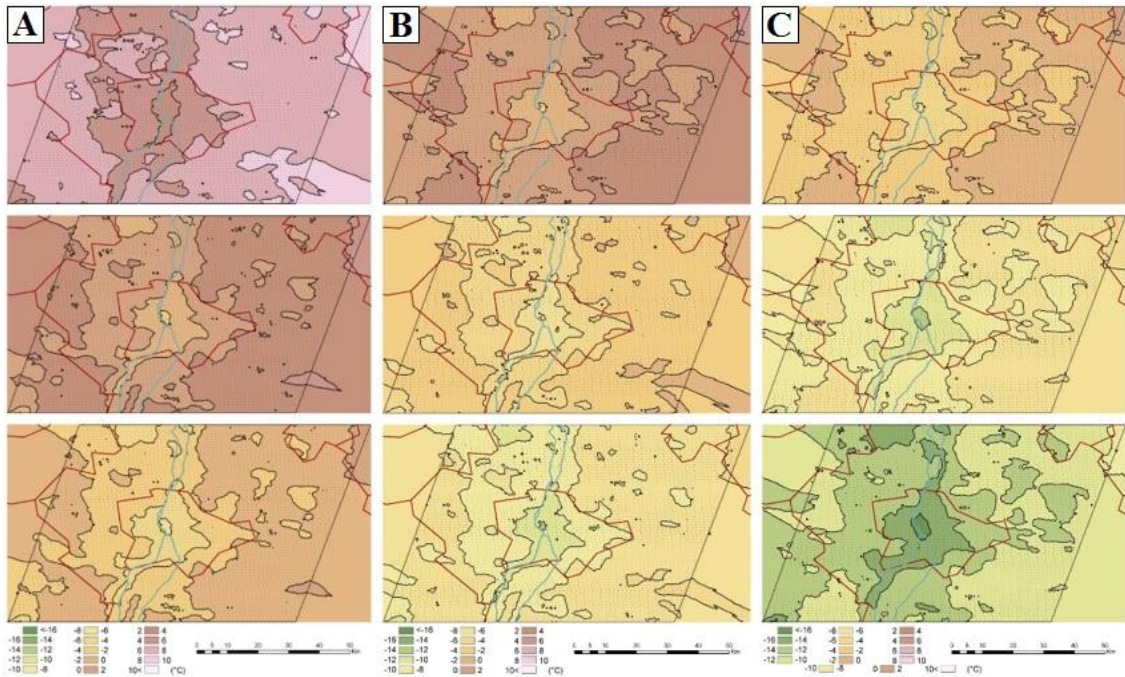


Figure 28. The average air temperature of the region which can be tolerated by *Ph. ariasi* (A column), *Ph. perniciosus* (B column) and by *Ph. mascitti*, *Ph. neglectus*, *Ph. papatasi* and *Ph. perfiliewi* (C column) in a certain location with UHI (Method 1., upper image), with UHI and the sheltering effect of the THBs (Method 2., middle image), and with UHI and the sheltering effect of the THBs in the period of 2025-2050 (Method 3., lower image).

2.3.4. Future ranges of two sandfly species in Budapest

In the location of the recent observation of the two studied species (Törökbálint, 47.436N, 18.916E), the warming effect of UHI was found to be 2.7 °C. According to the RegCM3 climate model the minimum ground temperature of January is -15.9 °C in the reference period and -14 °C in the prediction period. Since the studied sandflies can tolerate -4 °C, the sheltering effect of the built environment was about 12 °C. *Figure 29* shows the resulted border of the potential urban distribution of the studied species in case of both the periods 1961-1990 and 2025-2050. The modelled distribution also displays the data points of the satellite image and the calculated effect of the UHI with a blue-red colour ramp. The observation of the two sandfly species, which gives the base of this research, was marked with white cross in *Figure 29*.

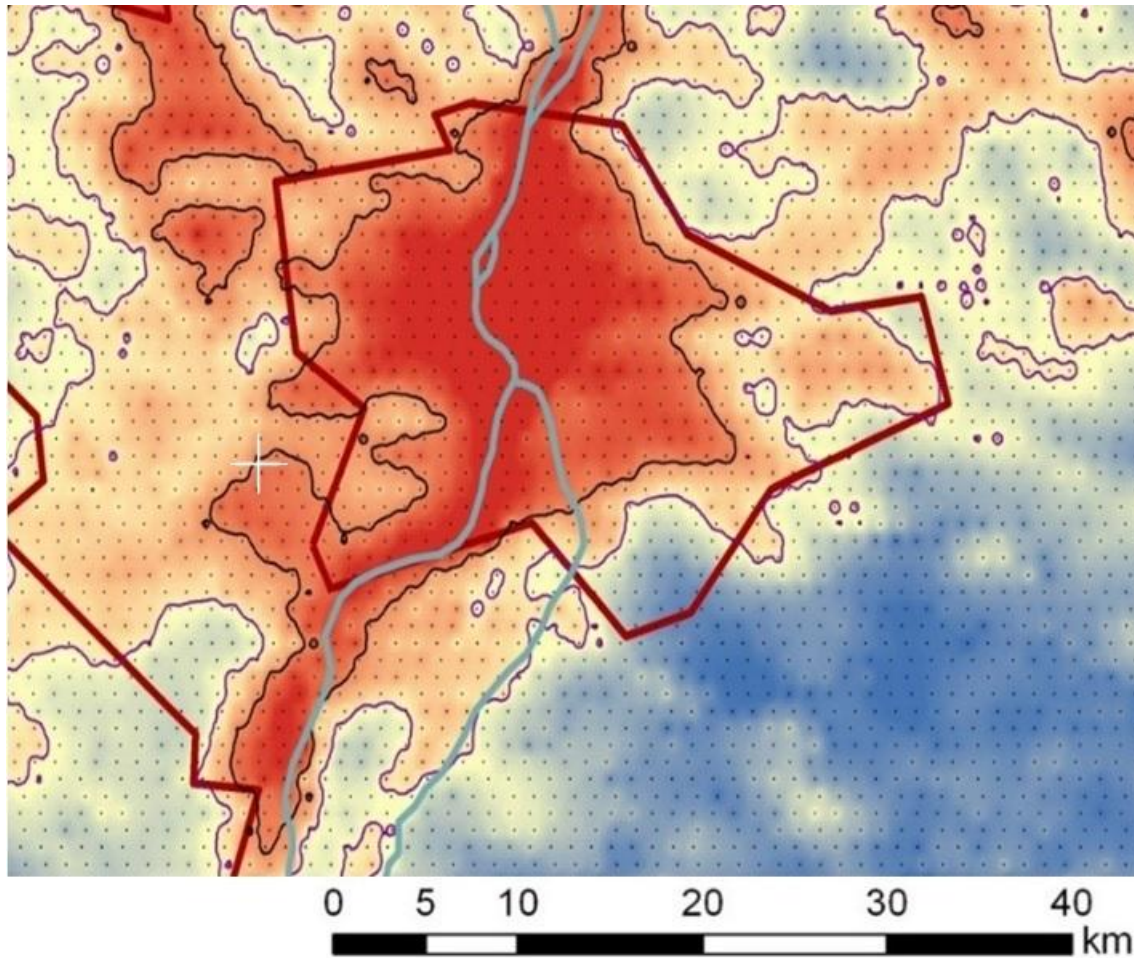


Figure 29. The average effect of UHI (blue-red), observation of Farkas et al. (2011) (white cross), and the potential urban distribution of *Ph. mascittii* and *Ph. neglectus* in the reference period (black contour) and in the period of 2025-2050 (purple contour) in the simplified base map of Pest County, Hungary.

In the reference period 57.8% of Budapest was modeled to be climatically suitable for the species, while in 2025-2050 89.4% of the town may become suitable. *Figure 30A-B* shows statistics and frequency distribution of the minimum ground temperature of January found within the modeled urban distributions of the species in the reference period and the projection period. 915 points (348 points - 38% in Budapest) were modeled to be suitable in the reference period and 2386 point (538 points - 22.6% in Budapest) in the projection period. The enlargement of the potentially suitable territories is 161% (between 1961-1990 and 2025-2050).

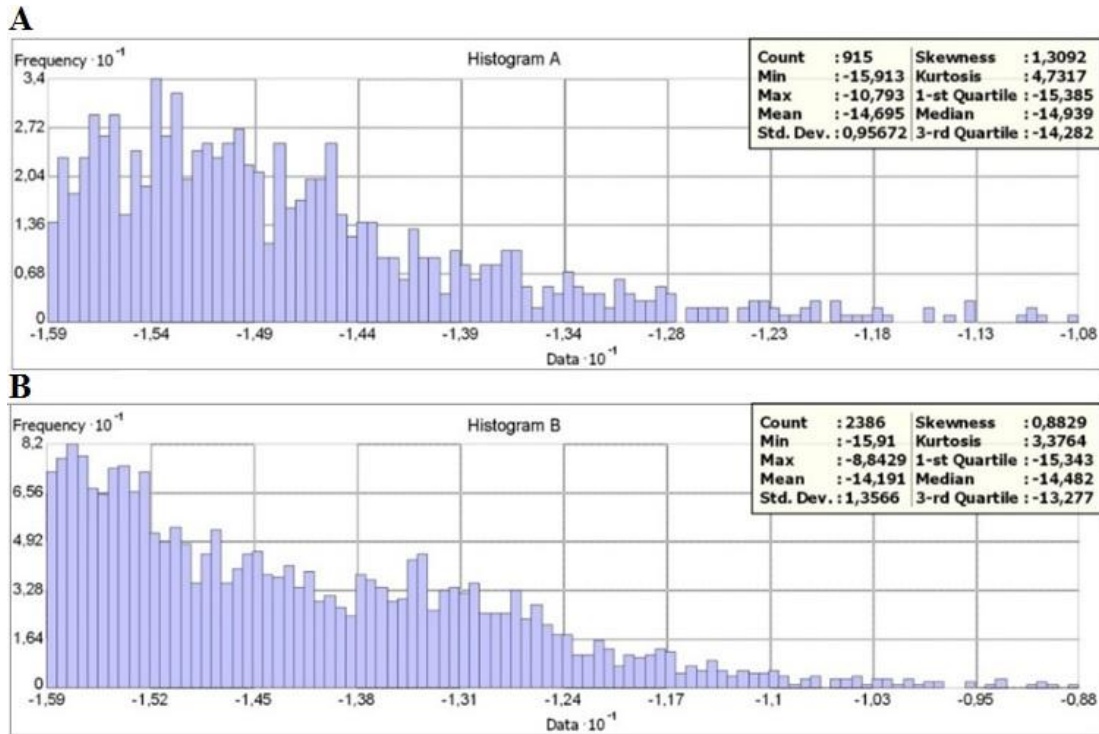


Figure 30. A: Frequency distribution and statistics of the minimum ground temperature of January (scale: 10 °C) within the modelled urban distribution of the studied species in the reference period (1961-1990, histogram A) and the period of 2025-2050 (histogram B).

2.4. DISCUSSION

The UHI is the principal driver of warming at urban scale (Stone et al., 2012). Some researchers consider the problem of the UHI that may become similarly or even more important issue than that of global warming since the rate of urban warming may be greater (Saitoh et al., 1996). Due to the UHI, the studied sandfly species have isolated occurrence in the urban area. The findings indicate that this distribution fragment may become the source of rapid future expansion of the sandfly species and consequently cause that leishmaniasis may become epidemic in the highly populated urban area. In agreement with Rosenzweig et al. (2005) who state that UHI-related hazard potential is likely to increase in a warmer climate, it should be highlighted that climate change can increase the risk of leishmaniasis in Budapest and in some other highly populated areas as well. According to the VBORNET database (VBORNET, 2017) in the case of the insulated distribution of *Ph. ariasi* in Paris the situation is very similar to the studied two species in Hungary, as the French capital is also the most northern occurrence of the sandfly species. According to the sandfly observations in Budapest and in the agglomeration (Tánczos, 2012; Tánczos et al., 2012), the presence of the *Ph. neglectus*,

Ph. mascittii and *Ph. perfiliewi* cannot be achieved without protected shelters, probably the anthropogenic heat emission. Regarding the facts that in the Carpathian Basin Budapest and its agglomeration is the most northern and isolated occurrences of the above mentioned three species and in the heated interiors the air moisture is low in the heating season (sandflies prefer the high air vapour content) it is plausible that sandflies can overwinter in heat polluted refuges, but not in the heated rooms. Wet rooms can be an exception. These refuges can be garages, unheated outbuildings, major cracks in the wall, and protected surfaces of THBs. To study the potential of the overwintering in the outdoor environment, two common THBs were selected with a moderate-low heat intensity, which can be found in many places in Budapest. It should be noted, that there are even warmer THBs, too, but the aim was to study general spots of general buildings. It was found that the morning temperatures of the spots change together with the surface temperature of the walls that are not affected by the THB effect (and respectively with the ambient temperature). In the studied points the temperatures of the THBs were 3-7 °C higher than their environment. It means that a usual THB and the UHI of the Capital can explain the observed outdoor occurrences according to the known biological hardiness of the three resident sandfly species.

At the first inspection, studying the indoor environment would be as much obvious as studying the external environment, since the heated rooms of buildings (e.g. showers, bathrooms), cellars, and caves may theoretically satisfy the minimum temperature and moisture requirements of sandfly species to overwinter and breed in many parts of the world. The material and many other factors can modify the intensity of the THBs. It was found that the drier limestone surface in lower temperatures was warmer than the wetter brick wall. The flora and the microbial math of the studied wet brick THB (S1) showed that due to the gutter, organic matter accumulation is observable in the cracks and in the joint gaps, which is essential for the potential colonization of sandfly larvae. First reason of the higher surface temperatures of the limestone surface compared to the brick covering in colder weather is that the latter one is a wetted surface. Since specific heat of the water is very high (4.2 kJ kg⁻¹ °C⁻¹), a wetted material cannot adapt to the changes of the environmental temperature as fast as the dry material. Moreover, higher surface temperature of the limestone surface can also contribute to the lower thermal conductivity value of the limestone (3.467 W m⁻² °C⁻¹) compared to the brick (7.750 W

$\text{m}^{-2} \text{ } ^\circ\text{C}^{-1}$), and the overall better thermal insulance value of the limestone-covered wall. Lower thermal conductivity means higher specific heat, thus higher heat capacity. Therefore, and because of the higher heat capacity of the limestone covered wall limestone adapts to changes of the environmental temperature much slower than the brick.

Moreover, with decrease of the environmental temperature, the limestone cover has a larger amount of heat support from the backing wall due to its higher heat capacity, which slows down the fall of temperature of the covering material. Thus, geometrical THB intensities in a wall structure with high heat capacity, thus high thermal insulation property, covered with well-insulating materials (for example porous stone materials: tuffs, sandstone and limestone) can provide high and permanent heat surplus even in case of sudden falls of temperature. The magnitude of climate moderating (sheltering) effect of the built environment (about $12 \text{ } ^\circ\text{C}$) was more than expected. In case the known cold tolerance limit of the *Phlebotomus* larvae, the study indicates that *Ph. mascittii* and *Ph. neglectus* can tolerate harder winters by utilizing the human built environments more than was previously thought. The authors suppose that the species could overwinter inside sheds, garages, cellars and other unheated ancillary buildings. Note that the model was based on the field study of Farkas et al. (2011) who found the *Phlebotomus* species in a territory that had suburban characteristics within 2 km radius, which is the known dispersal limit of the species (Killick-Kendrick, 1999). In that place there were no haystacks, livestock, piles of manure, gopher holes and other non-anthropogenic shelters, which could facilitate the overwintering of sandfly larvae. The recently developed UHI simulation approaches are still not able to cover all the phenomena that simultaneously contribute to the formation of UHI (Trájer et al., 2014B).

Although the model assumes constant UHI similarly to some other researches (Mirzaei and Haghghat, 2010), it should be mentioned that the UHI of Budapest may increase in the future. Climate change has the potential to alter the intensity, temporal pattern, and spatial extent of the UHI in metropolitan regions: meteorological conditions – including high temperature, low cloud cover, and low average wind speed – tend to intensify the UHI. If the UHI effect is playing a role not only in the present-day spatial temperature difference, but the rate of increase in urban temperatures over time, then

projections for climate change may underestimate the true extent of warming experienced in urban areas (Lindgren et al., 2006; Kolokotroni et al., 2012; Kershaw et al., 2010). The developed model has the chance of underestimating the expansion of the future potential urban distribution of the studied species. It is known that the magnitude of UHI depends on the city size and the number of inhabitants (Grimmond et al., 2010). Although the population of Budapest has been decreasing since some decades, the city-suburb complex has not been shrinking. Moreover, the research of Emmanuel and Krüger (Oke, 1973) shows that the UHI itself does not decrease, even in shrinking cities. Even though the population of Budapest has not shown increasing trend, the energy consumption – and very likely the heat pollution - of its inhabitants has been mounted up in the last decades (Emmanuel and Krüger, 2012), and may increase in the future as well.

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THE MOST SIGNIFICANT RESULTS

Seasonal patterns. The monthly relative abundance values of the larvae of *Anopheles maculipennis* were modeled for the reference period 1961-1990 and the periods 2011-2040 and 2041-2070 based on the REMO climate model for Central and East Europe and the North Balkan region. Strong, significant correlation ($r^2=0.94$, $p<0.0001$) was found between the monthly relative abundances of larvae and monthly mean air temperature values in Hungary between March and November. The threshold of the larval activity of *Anopheles maculipennis* was found to be about 4 °C. Comparing the modeled relative abundances for 1961-1990, 2011-2040, and 2041-2070, April and October months showed the most notable changes. **The model predicts that in Southeast Hungary, East Croatia, North Serbia, South Romania, and North Bulgaria, the main mosquito season will increase by 1-2 months to the period of 2041-2070 comparing to the reference period.** The model also indicates that **the complete main *Anopheles maculipennis* larva season of the mosquito will increase by two months in Southeast Hungary and at least 1 month in the other parts of the south Pannonian Ecoregion,** in the North Balkan region including South Romania and North Bulgaria for 2041-2070. *Culex pipiens pipiens* and *Culiseta annulata* were the most abundant troglophile mosquitoes; *Anopheles maculipennis*, *Anopheles messeae*, *Culex hortensis*, *Culex pipiens molestus* and *Culex territans* were also collected in caves from July to April. The total mosquito number showed an approximately continuous increasing trend from July to November and a decreasing trend from December to April. Most of the mosquito specimens were collected in autumn and winter. *Culex pipiens pipiens* individuals were present in the caves from August to April. **Male mosquitoes were collected only in the second half of the year, while female individuals during the entire year.** Both the relative abundance of males and females increased between August and November. **The infected *Culex pipiens pipiens* mosquitoes, which start their diapause in the autumn, can be the potential vectors of the West Nile virus during the next year. It can be concluded that caves are important habitats of mosquitoes that are vectors of nonhuman pathogens in Hungary.**

The factors of dispersal. The estimated total dispersals of female *Aedes albopictus* mosquitoes are 3.6-4.6 km year⁻¹ generation⁻¹ in Italy and 4.6-5.3 km year⁻¹ generation⁻¹ in Florida, values that are at least five to six times higher than those derived from release and recapture studies and from the previously measured flying distances of female Asian tiger mosquitoes. Subtracting the calculated dispersal distances with the known active dispersal of female *Ae. albopictus*, the passive dispersal component of the total dispersal distances was found to be 2.8-4.1 km year⁻¹ generation⁻¹ in Italy and 3.8-4.8 km year⁻¹ generation⁻¹ in Florida. **The results confirm that the active dispersal of female mosquitoes plays a secondary role in determining the rate of areal expansion and, in contrast, passive factors may play a primary role. It was concluded, based on similar average values of the passive dispersal distances of the mosquito in Florida and Italy, that at large spatial scales the anthropogenic component can be well estimated.**

Urban environments. According to the results of the two-sample t-test there is no significant difference ($p=0.9210$) between the variances of the UI of the *D. immitis* and *D. repens* sites. The histogrammic patterns of the UI values related to the 1 km² area of the percentage of *D. immitis* and *D. repens* case sites are somewhat similar to a unimodal frequency peak in case of the UI index interval of 1.45 ± 0.01 , which corresponds to the urbanised areas of the city. The UI values of the endemic sites except one case showed a transition (2.9 to -4.32) between the control vegetation (< -4.32). Some cases were observed also in the downtown areas (> 2.8) of Szeged. Overall, 56.5% of the infections occurred between 263 and 524 m from the case sites and 87.5% of the cases occurred within 524 m from the potential mosquito habitats. All the dirofilariasis cases occurred within 1.31 km from the nearest standing water, river or swamp of the inundation area. It was concluded that **most of the dirofilariasis cases were related to locations with a medium to high urbanisation index, although the proximity of mosquito-bearing waters also played an important role in the observed spatial infection patterns. The distance from potential mosquito habitats and the UI determine the abundance of dirofilariasis in urban environments.** It was found that the studied species can better tolerate hard winters by utilizing the human built environments more than was previously thought. **The recent occurrence of the species in Central**

Hungary indicates that *Phlebotomus* species can overwinter in non-heated shelters in the built environment. Jointly urban heat island effect and future climate change seem to be able to provide suitable environments for the studied species in urban areas. It was also presented that the recently observed northern most occurrence of *Ph. mascittii* and *Ph. neglectus* in the agglomeration of the Hungarian capital, Budapest would be the consequent of the UHI of the city. It is also very likely that because of climate change the recent insulated occurrence of this sandfly species will expand towards the rural areas. The results indicate that the present-day relatively small, extrazonal urban populations of the sandfly species may become the source of their more rapid expansion than we might expect based on the recent zonal distribution of this species.

THESIS POINTS

1. I have developed a model to determine the length of the larva season of *Anopheles maculipennis* malaria mosquito in the mid-21st century. I found that it can be extended by 1-2 months in Hungary depending on the regions.
2. Based on literature data, I examined the species and gender composition in monthly resolution, as well as the potential vector status of the troglophile mosquitos of the Bakony-Balaton Region. I found that only the female mosquitos can survive the winters in caves. One of the most significant vectors of West Nile fever, *Culex pipiens pipiens* is the most abundant species, but two potential malaria vector mosquitos also can overwinter in caves in notable numbers.
3. Based on mosquito data from Italy and Florida, I examined the patterns of the spread of *Aedes albopictus*. I found that not the active dispersal of the female mosquitos plays the most important role in the spread of the species, but the passive factors. Based on similar average values of the passive dispersal distances of the mosquito in Florida and Italy, that at large spatial scales this dispersal component can be well estimated.
4. The distance between the potential mosquito breeding site aquatic habitats and urbanization intensity determine together the distribution patterns of canine dirofilariasis in an urban environment.
5. I have examined the potential effects of the anthropogenic heat emission and climate change on the overwintering chance of sandfly species in urban environments. I found that man-made heat emissions in cities allow the survival of sandflies, and climate change will positively alter the survival chance of sandflies in the urban areas.

TÉZISPONTOK

1. Modellt dolgoztam ki az *Anopheles maculipennis* maláriaszúnyog XXI. század közepén várható lárvaszezon-hosszána előrejelzése céljából. Eredményeim alapján a lárvaszezon Magyarországon várhatóan 1-2 hónappal fog meghosszabodni, területtől függően.
2. Irodalmi adatok alapján havi felbontásban vizsgáltam a bakonyi és balatonfelvidéki barlangokban telelő szúnyogfauna faji és ivari összetételét, valamint lehetséges vektor szerepét. Azt találtam, hogy kizárólag nőivarú szúnyogok telelnek át a barlangokban. A legnagyobb számban előforduló *Culex pipiens pipiens* a Nyugat-nílusi láz egyik legjelentősebb vektora, de két potenciális maláriavektor szúnyogfaj szintén jelentős számban telel át barlangokban.
3. Olaszországi és floridai adatok alapján megvizsgáltam az *Aedes albopictus* terjedésének mintázatát. Megállapítottam, hogy nem a nőtény szúnyogok aktív terjedése játssza a fő szerepet a faj terjedésében, hanem a passzív faktorok. A hasonló floridai és olaszországi passzív terjedési távolságok alapján ez a komponens nagy távolságok esetén jól becsülhető.
4. Az urbanizációs intenzitás és a lehetséges legközelebbi szúnyogélőhelyek távolsága a kutyák lakhelyétől együtt determinálja a kutya dirofilariózis térbeli eloszlását.
5. Vizsgáltam az antropogén hőkibocsátás és a klímaváltozás lehetséges jövőbeli hatásait a lepkeszúnyogok áttelelési esélyére városi környezetben. Az ember által okozott hőkibocsátás lehetővé teszi a lepkeszúnyogok fennmaradását és a klímaváltozás előnyösen fogja alakítani a lepkeszúnyogok túlési esélyeit városi környezetben.

List of publications

*Cumulative**

Number of the international conference with oral presentation: 4

Number of the international conference with poster presentation: 5

Number of the national conference with oral presentation: 10

Number of the national conference with poster presentation: 4

Number of the international publication: 17

Number of the national publication in English: 13

Number of the national publication in Hungarian: 8

Cumulative impact factors: 19.751

Independent citations: 36

Dependent citations: 39

**without the in-press papers*

Papers directly related to the dissertation

Trájer, A.J., Padisák, J. (2019) Exploration of the main types of biome-scale culicid entomofauna (Diptera: Culicidae) in Europe. *Acta Zoologica Academiae Scientiarum Hungaricae. In-press paper.*

Trájer, A.J. (2018) Az *Aedes albopictus* Skuse (Diptera: Culicidae) Kárpát-medencei terjedését befolyásoló klimatikus tényezők és a klímaváltozás hatása a faj jövőbeli elterjedésére a térségben. *Légekör*, 63(2), 75-83.

Trájer, A.J. (2018) A klímaváltozás várható hatásai a szúnyog vektorok szaporodási körülményeire: előny vagy hátrány? Modellkísérlet (The potential effects of climate change on the breeding habitats of mosquito vectors: benefit or disadvantage?). *Egészségtudomány*, 2018(1-2), 85-107.

Trájer, A.J., Hammer T., Padisák J. (2018) Reflection of the Neogene-Quaternary phylogeography in the recent distribution limiting climatic factors of eight Mediterranean (Diptera: Psychodidae) *Phlebotomus* species. *Journal of Natural History*, 52(27-28), 1763-1784. **IF:** 0.875, **SJR:** 0.419, **Quartiles:** Q3 (ecology, evolution, behavior and systematics).

Trájer, A.J. (2018). Which mosquitoes (Diptera: Culicidae) are candidates for DNA extraction in forensic practice? *Journal of Forensic and Legal Medicine*, 58(2018), 183-191. **IF:** 1.103, **SJR:** 0.622, **Quartiles:** Q1 (law), Q2 (medicine), Q2 (pathology and forensic medicine).

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- Trájer, A.**, Tánzos, B., Hammer, T., Padisák, J. (2018). Solar radiation and temperature conditions as the determinants of occurrence of *Phlebotomus neglectus* Tonnoir (Diptera: Psychodidae). *Journal of the Entomological Research Society*, 20(2), 13-27. **IF**: 0.293, **SJR**: 0.163, **Quartiles**: Q4 (evolution, behavior and systematics; insect science).
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- Trájer, A.J.,** Padisák, J. (2013) A klímaváltozás várható hatása a szúnyogok és a lepkeszúnyogok, valamint az általuk terjesztett betegségek jövőbeli elterjedésére. *Iskolakultúra: pedagógusok szakmai-tudományos folyóirata*, 2013(12), 73-85.
- Bede-Fazekas, Á., **Trájer, A.J.** (2013). Ornamental plants as climatic indicators of arthropod vectors. *Acta Universitatis Sapientiae, Agriculture and Environment*, 5(1), 19-39.
- Trájer, A.J.,** Bede-Fazekas, Á. (2013). Új vektoriális betegségek megjelenésének lehetősége, és a már őshonos betegségek jelentőségének növekedése a klímaváltozás következtében. A XXI. század egészségügyi és hadászati biztonságát fenyegető hazardok. *Hadtudomány: A Magyar Hadtudományi Társaság folyóirata*, 23(Suppl.1), 255-270.
- Trájer, A.J.,** Bede-Fazekas, Á., Hufnagel, L., Horváth, L., Bobvos, J. (2013). The effect of climate change on the potential distribution of the European *Phlebotomus* species. *Applied Ecology and Environmental Research*, 11(2), 189-208. **IF:** 0.456, **SJR:** 0.301, **Quartiles:** Q3 (ecology, evolution, behaviour and systematics; agronomy and crop science).
- Trájer, A.J.** (2008) Klímaváltozás egészségi hatásai, különös tekintettel az extrém hőmérsékletre. Szakdolgozat. Semmelweis Egyetem, Közegészségügyi Intézet & Országos Környezetegészségügyi Intézet.

Congress attendances directly related to the dissertation

- Trájer, A.J.,** Bobvos, J., Páldy, A., Padisák, J. (2018). A leishmaniasis vektorainak jövőbeli előfordulása Európában és az elterjedést limitáló éghajlati tényezők egymáshoz viszonyított jelentősége. Hogyan tovább a klímatudatos jövő felé? – Tudományos konferencia. Konferencia helye, ideje: Budapest, Magyarország. 2018. november 28. Innovációs és Technológia Minisztérium, Magyarország, **poster presentation.**
- Trájer, A.J.** (2017). Diversity, seasonal abundance and vector status of the cave-dwelling mosquito (Diptera: Culicidae) fauna of the Bakony-Balaton Region, Hungary 10th Symposium for European Freshwater Sciences 2017 (10 SEFS 2017) Konferencia helye, ideje: Olomouc, Czech Republic. 2017.07.02-07.07. European Federation for Freshwater Sciences, **poster presentation.**

- Trájer, A.J.** (2017). Az *Aedes albopictus* (Diptera: Culicidae) kárpát-medencei terjedését befolyásoló klimatikus tényezők és a klímaváltozás hatása a faj jövőbeli elterjedésére a térségben. In: Németh, Á. (szerk.) Orvosmeteorológiai Konferencia-2017 Konferenciakötet. Konferencia helye, ideje: Budapest, Magyarország, 2017.03.02-2013.03.03. Budapest: Magyar Meteorológiai Társaság (MMT), 2017, *oral presentation*.
- Trájer, A.J.** (2015). Az antropogén klímaváltozás várható hatása a lepkeszúnyog és szúnyog vektorok elterjedésére és szezonálisára. In: Németh, Á. (szerk.) Orvosmeteorológiai Konferencia-2015 Konferenciakötet. Konferencia helye, ideje: Budapest, Magyarország, 2015.05.28-2013.05.29. Budapest: Magyar Meteorológiai Társaság (MMT), 2015, *oral presentation*.
- Trájer, A.J., Padisák, J.** (2014). A csallóközi-szigetközi Duna-ágak mederfejlődésének hatása a szúnyogok számára potenciálisan alkalmas élőhelyek alakulására. In: Bíró, P., Reskóné Nagy, M., Kiss Keve, T. (szerk.) LVI. Hidrobiológus Napok: A hidrobiológiai kutatások eredményei és gyakorlati hasznuk: Szóbeli előadások kivonatai. 36 p., *oral presentation*.
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- Bede-Fazekas, Á. **Trájer, A.J.** (2013). Modeling the climate envelope of some European vector species. In: Gergely, R. (szerk.) Workshop on Modeling in Life Sciences. 14 p. konferencia helye, ideje: Szeged, Magyarország, 2013.11.30 Szeged: Szegedi Tudományegyetem Bolyai Intézet, 2013., p. 2, *oral presentation*.
- Bede-Fazekas, Á. **Trájer, A.J.** (2013). Európai lepkeszúnyog fajok potenciális elterjedése a 21. században. In: Koncz, I., Nagy, E. (szerk.) Tudományos Próbatálya: PEME VI. Ph.D. konferencia. Konferencia helye, ideje: Budapest, Magyarország, 2013.03.12 Budapest: Professzorok az Európai Magyarországiért Egyesület, 2013., pp. 243-250, *oral presentation*.

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Other papers related to arthropod vectors and vector-borne diseases

- Nah, K., Magpantay, F.M.G., Bede-Fazekas, Á., Röst, G., **Trájer, A.J.**, Wu, X., Zhang, X., Wu, J. (2019) Assessing systemic and non-systemic transmission risk of Tick-borne Encephalitis Virus in Hungary. PLOS ONE. *Accepted paper*.
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- Trájer, A.J.**, Hammer, T., & Szigeti, Z. (2019). Influence of physical factors of apartments, educational attainment, nationality and unemployment on the number of *Cimex lectularius* inquiries. Central European Journal of Public Health, 27(1), 32-36. **IF**: 0.800, **SJR**: 0.372, **Quartiles**: Q3 (medicine; public health, environmental and occupational health).
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- Trájer, A.J.** (2011) Szúnyogok és a klímaváltozás. Természettudományi Közlöny, 142(5), 219-221.

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- Trájer, A.J.**, Bede-Fazekas, Á. (2013). Modeling the temperature-related averaged annual run of relative LB incidence in the period of 1998-2012 in Hungary. In: Semmelweis Egyetem PhD Tudományos Napok 2013. 208 p. Konferencia helye, ideje: Budapest, Magyarország, 2013.04.11-2013.04.12. 2013., p. 76, ***oral presentation***.
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