MAGYAR AGRÁR- ÉS
ÉLETTUDOMÁNYI EGYETEM

Hungarian University of Agriculture and Life Sciences

Biology, Seasonal Dynamics and Egg Parasitoids of Brown Marmorated Stink Bug, *Halyomorpha halys* (Hemiptera) in Hungary

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JOHNSON WAHENGBAM

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The PhD School

Name: Doctoral School of Agricultural and Food Sciences

Discipline: Crop Production and Horticultural Sciences
Department of Entomology
Institute of Plant Protection

Head of the Doctoral School
Prof. Dr. Melinda Kovács
University Professor,
Full Member of the Hungarian Academy of Sciences

Supervisors:
Katalin Radácsiné Hári, PhD
Assistant Professor
MATE Department of Entomology, Institute of Plant Protection
Péter Radácsi, PhD
Associate professor
MATE Department of Medicinal and Aromatic Plants, Institute of Horticultural Sciences

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Approval of the Head of Doctoral School **Approval of the Supervisor(s)**

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ABBREVIATIONS

DD	Degree Days
BMSB	Brown Marmorated Stink Bugs
DMS	Daily mean temperature
EPPO	European and Mediterranean Plant Protection Organization
CABI	Centre for Agriculture and Bioscience International
FWER	Familywise Error Rate

1.0. INTRODUCTION

Globalization has been threatening native biodiversity, and the spread of invasive pests leads to outcompeting native species, altering ecosystem processes and causing biodiversity loss (KOLLMANN 2007). Non-native pests are introduced either accidentally or with the increases in international trade. In fact, biological invasion is the second most significant factor contributing to biodiversity loss, following habitat destruction (KEANE & CRAWLEY 2002; DADHWAL et al. 2025). Slowing down the rate of invasion necessitates the identification of native habitats, preferred environmental conditions, bio-ecology, and potential bioagents of invasive species.

The Brown Marmorated Stink Bug (BMSB), *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae) is originated from South and North Korea, Japan, Taiwan and China (ZHU et al. 2012). The species invaded North America and Europe then spread rapidly. In America, BMSB was believed to be introduced accidentally and was first collected from Allentown, Pennsylvania in September 1998 (HOEBEKE & CARTER 2003) then subsequently the species expanded its range dramatically in East America (JONES & LAMBDIN 2009, ZHU et al. 2012). Now, it has been reported that the species has presence in 47 states and 4 Canadian provinces (NORTHEASTERN IPM CENTER 2023). In Europe, BMSB was first reported in Switzerland in 2008 (WERMELINGER et al. 2008) and in the following years it has been reported from several regions of Europe such as Italy, France, Germany, Greece, Hungary, Serbia, and Romania (HECKMANN 2012, RICE et al. 2014, MILONAS & PARTSINEVELOS 2014, VÉTEK et al. 2014, MACAVEI et al. 2015, GAPON 2016), and also detected in Bulgaria, Russia, Georgia, the Autonomous Region of Abkhazia (GAPON 2016, SIMOV 2016) and Turkey (ÇERÇİ et al. 2021).

BMSB is a polyphagous pest, active in the field at temperatures not lower than 15 °C, even with wind speeds as high as 0.75 m/s. Both nymphs and adults are capable of traveling long distances by walking, with adults able to cover up to 5 km in 24 hours through flight (LEE & LESKEY 2015). This ability contributes to their dispersion from crops to wild habitats, vice versa, and from one landscape to another. BMSB is considered one of the most serious nuisance pests due to its overwintering aggregation behavior in urban areas such as buildings, abandoned houses, etc. (LESKEY et al. 2015, BARISELLI et al. 2016,). Feeding by BMSB occurs in multiple growth stages of plants and has a detrimental impact on the quality and yield of crops. BMSB infestation is low in its native habitat and is considered an occasional pest in fruit orchards and soybean fields (LEE et al. 2013), however, outside its native range in the USA and Europe, BMSB causes serious economic losses in some regions such as $37 million (USD) in apples in the mid-Atlantic region of USA in 2010 (UNITED STATES APPLE ASSOCIATION 2010, LESKEY & NIELSEN 2018, REGMI et al. 2024), in Italy, the government disbursed €500 million financial support for fruit farmers following the damage caused by the BMSB in 2019 (COMMISSION IMPLEMENTING REGULATION (EU), 2020/465). It is estimated that the establishment of BMSB in New Zealand could potentially decrease the country's GDP and the horticultural export value by billions of NZ$ by the year 2038 (CLOUGH 2017).

In Hungary, BMSB was first recorded in 2013 in Budapest, the route of entry was unknown as the pest was not reported from the neighboring countries at that time (VÉTEK et al. 2014). In 2016, following an official survey on its distribution in Hungary, it turned up in various parts of the country, with a mass occurrence in Pécs (South Hungary). BMSB has caused damage to vegetable and fruit crops, and ornamental trees, and one survey confirmed that it poses a serious threat to crop production in Hungary. In late 2016, the pest was reported by growers infesting vegetables. Investigation revealed that 94% of seeds in dry bean pods, and 100% of the sampled green hot pepper fruits were damaged (VÉTEK & KORÁNYI 2017). Hungary's media took notice of the growing nuisance problems caused by BMSB in 2017 (VÉTEK et al. 2018).

Several studies have been conducted since the invasion and spread of BMSB in the USA and Europe with the aim of constructing a life table for different developmental stages, phenology, photoperiodic and temperature requirements of development, or identify their potential natural enemies (NIELSEN et al. 2008, HAYE et al. 2014, COSTI et al. 2017, ROT et al. 2022). Multiple studies in North America and Europe have focused on identifying potential parasitoids of BMSB, since its invasion, contributing to the development of sustainable long-term management practices against this invasive pest species. These comprehensive analyses indicate that three main families of hymenopteran parasitoids are capable of successfully parasitize the eggs of BMSB in regions where it have been introduced: Scelionidae, which includes the genera *Telenomus, Trissolcus*, and *Hadronotus* (reported as *Gryon*), Eupelmidae (genus *Anastatus*) and Encyrtidae (genus *Ooencyrtus*) (JONES et al. 2014, HAYE et al. 2015, DIECKHOFF et al. 2017, COSTI et al. 2019, MORAGLIO et al. 2020, ZAPPONI et al. 2020, ROT et al. 2021, ANDREADIS et al. 2021). In addition to the detection of potential native parasitoid species, the discovery of non-native parasitoids such as *Trissolcus. japonicus* (Ashmead) in Switzerland in 2017 (STAHL et al. 2019b) and in Northern Italy in 2018 (SABBATINI PEVERIERI et al. 2018), as well as *Trissolcus mitsukurii* (Ashmead) in Northeastern Italy in 2016 (SCACCINI et al. 2020), Western Slovenia in 2020 (ROT et al. 2021), Germany in 2021 (DIECKHOFF et al. 2021), Southwestern France in 2024 (MARTEL et al. 2024) and Serbia in 2024 (KONJEVIĆ et al. 2024) has opened new avenues for biological control of BMSB in Europe.

1.1. Objectives

The invasion of BMSB in Hungary threatens horticultural crops and creates nuisance through aggregations of overwintering populations in buildings (VÉTEK & KORÁNYI 2017, VÉTEK et al. 2018). Hungary's climate characterized by warm summers (average high 23–28 °C, with peaks above 35 °C) and cold winters (average low –3 to –7 °C, occasional minimum below –10 °C) (ANONYMOUS, 2025). Such a continental climate appears compatible with the establishment and overwintering of BMSB (CIANCIO et al. 2021) However, in Hungary, comprehensive studies on its biology and life history are lacking, underscoring the need to investigate its life phenology and voltinism. Furthermore, no studies on potential parasitoids of BMSB have been conducted since its invasion in Hungary. Therefore, this study aims to analyze the biological characteristics and the potential parasitoids of BMSB in Hungary to improve pest management strategies. In these views the objectives of the present work are as follows:

- To assess overwintering mortality of locally collected brown marmorated stink bug (*Halyomorpha halys*) individuals under semi-natural conditions in Budapest, Central Hungary.
- To investigate the phenology of Hungarian *H. halys* populations by monitoring seasonal life stages and activity patterns.
- To construct life tables for *H. halys* populations under semi-natural conditions in Hungary.
- To determine degree-day requirements for key developmental and phenological stages of *H. halys* under natural temperature conditions in Budapest, Central Hungary.
- To survey on eggs parasitoids *H. halys* in Hungary, aiming to identify the native parasitoid species, and assess their parasitism rates.

2.0. LITERATURE REVIEW

2.1. Nomenclature of BMSB

BMSB has had a complex nomenclatural history, previously known as *Halyomorpha mista* (Uhler) or *H. brevis* (Stål) (synonyms), and *H. picus* (Fabricius) (misidentification, *H. picus* is an Indian species often mistaken for BMSB (RIDER & ZHENG 2002, LEE et al. 2013). However, JOSIFOV & KERZHNER (1978) definitively determined that only one species of *Halyomorpha*, *H. halys*, exists in eastern China, Japan, and Korea. Consequently, any mentions of *Halyomorpha* spp. from these regions are considered synonymous with BMSB (RIDER & ZHENG 2002).

2.2. Invasion and spread of BMSB in Europe

BMSB was officially reported for the first time in 2008 from Zurich, Switzerland (WERMELINGER et al. 2008), with an earlier record dating back to 2004 from Lichtenstein (ARNOLD 2009). According to HAYE et al. (2013), there were two possible routes for the entry of BMSB into Europe, either through shipments from Asia or shipments from the US (with one case reported from Germany). The coincidence of a Chinese garden being built in Zurich Lake in 1993, where Chinese plants and materials were imported, and the replacement of roof tiles with original material from China in 1998, may have contributed to the introduction of BMSB. During 2012 to 2013, a significant population of BMSB was documented in Bern and Basel (HAYE et al. 2013), with a solitary observation from Germany (HECKMANN 2012) and the initial documentation of a breeding population outside Switzerland in Strasbourg, France (CALLOT & BRUA 2013). BMSB was initially documented in Italy between 2012 and 2013 (MAISTRELLO et al. 2014) within Emilia-Romagna, a significant fruit-producing area in Europe (FANFANI & PIERI 2016). In Italy, the origin of the introduction in Emilia-Romagna believed to have possibly been from the United States, although the lack of sufficient data makes it difficult to confirm while in Lombardy likely from Switzerland southward spread (CESARI et al. 2015). The pest has now been documented in various regions across Europe, as indicated in Table 1. and possesses the capability to spread extensively on a global scale. After appearing in 2008 in Europe, the spread of the BMSB has now reached 30 countries with widespread distribution in Switzerland, Italy, Hungary and Slovakia and also BMSB has been intercepted in four countries, including England, Sweden, Norway, and Iceland (CABI, 2020).

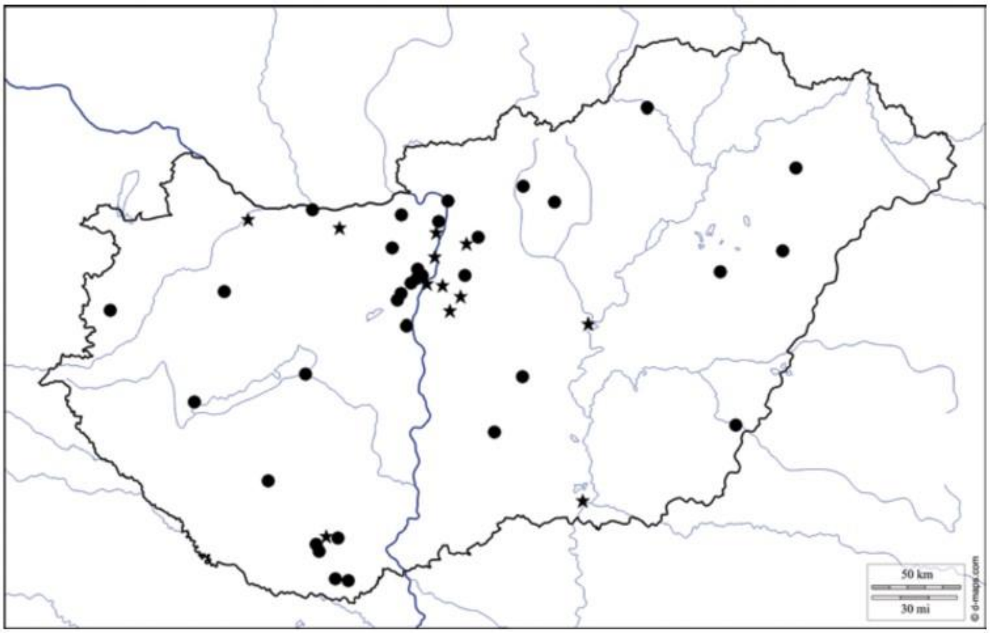
Table 1. The distribution of *Halyomorpha halys* in Europe

Sl. No.	**Country**	**Distribution**	**Reference**
1	Albania	Present, Few occurrences	EPPO (2025) CLAEREBOUT et al. (2018)
2	Austria	Present, Localized	EPPO (2025) YAN et al. (2021)
3	Belgium	Present, few occurrence	EPPO (2025) CLAEREBOUT et al. (2018)
4	Bosnia and Herzegovina	Present, Few occurrences	ZOVKO et al. (2019)
5	Bulgaria	Present	EPPO (2025) HRISTOZOVA & HARIZANOVA (2022)
6	Croatia	Present, Localized	EPPO (2025) ŠAPINA &JELASKA (2018) PAJAČ ŽIVKOVIĆ et al. (2021)
7	Czechia	Present, Localized	EPPO (2025)
8	France	Present, Localized	CALLOT & BRUA (2013) GARIEPY et al. (2015)
9	Germany	Present, Localized	HECKMANN (2012)
10	Greece	Present	MILONAS & PARTSINEVELOS (2014) GARIEPY et al. (2015)
11	Hungary	Widespread	PAPP et al. (2014) VÉTEK et al. (2014)
12	Iceland	Absent, intercepted	EPPO (2022)
13	Italy	Widespread	MAISTRELLO et al. (2014)
14	Sardinia	Present, localized	EPPO (2025) CIANFERONI et al. (2018)
15	Sicily	Present	EPPO (2025) CIANFERONI et al. (2018)
16	Liechtenstein	Present, Few occurrences	ARNOLD (2009)

Sl. No.	Country	Distribution	Reference
17	Malta	Present, localized	EPPO (2025) TASSINI & MIFSUD (2019)
18	Moldova	Present	EPPO 2025
19	North Macedonia	Present	KONJEVIĆ (2020) EPPO (2025)
20	Norway	Absent, Intercepted only	EPPO (2025)
21	Poland	Present, few occurrence	EPPO (2025) CLAEREBOUT et al. (2018)
22	Portugal	Present, localized	EPPO (2025) GROSSO-SILVA et al. (2020)
23	Romania	Present, localized	EPPO (2025) MACAVEI et al. (2015)
24	Russia	Present, localized	EPPO (2025) MITYUSHEV (2016)
25	Southern Russia	Present, localized	EPPO (2025) REZNIK et al. (2022)
26	Serbia	Present, localized	EPPO (2025) ŠEAT (2015)
27	Slovakia	Present, widespread	EPPO (2025) HEMALA & KMENT (2017)
28	Slovenia	Present, localized	EPPO (2025) ROT et al. (2018)
29	Spain	Present, localized	EPPO (2025)
30	Sweden	Absent, Intercepted only	EPPO (2025)
31	Switzerland	Present, widespread	WYNIGER & KMENT (2010) HAYE et al. (2013)
32	Ukraine	Present, localized	EPPO (2025) CLAEREBOUT et al. (2018)
33	United Kingdom	Present, few occurrence	POWELL et al. (2021) EPPO (2025)
34	England	Absent, Intercepted only	POWELL et al. (2021) EPPO (2025)

2.3. Distribution of BMSB in Hungary

The initial cases of BMSB in Hungary were identified in 2013 at two different locations in Budapest (VÉTEK et al. 2014). Subsequently, in 2014, additional cases were reported at various locations in Budapest (PAPP et al. 2014, VÉTEK et al. 2014). In the following year, 2015, BMSB was discovered in Budakalász and Martonvásár (VÉTEK 2016), and by 2016, after an official survey on its distribution in Hungary, it was detected in multiple regions of the country, with a significant presence in Pécs (South Hungary) (VÉTEK & KORANYI 2017). The Hungarian media began to take notice of the escalating nuisance issues caused by BMSB in 2017 (VÉTEK et al. 2018). This invasive species has led to substantial damage to vegetable and fruit crops, as well as ornamental trees, with one study confirming its severe threat to plant production in Hungary (VÉTEK et al. 2014, VÉTEK & KORÁNYI 2017). The capture of various haplotypes in bait traps (MORRISON et al. 2017) highlighted the urgent necessity for comprehensive research on population expansion, biology, and management strategies (VÉTEK et al. 2018). The distribution of BMSB and their intensity in different locations of Hungary were given below in Figure 1.



★ Mass occurrence ● BMSB recorded regardless of numbers

Figure 1. Distribution of *Halyomorpha halys* in different regions of Hungary (VÉTEK et al. 2018)

2.4. Genetic diversity of BMSB in invaded areas

The molecular analysis of the mitochondrial cytochrome c oxidase (CO) subunit II gene, COI, and 12S ribosomal RNA gene has provided valuable insights into the origin and genetic diversity of the BMSB, determined that the BMSB population in the USA originated from a single introduction from Beijing, China (XU et al. 2014). GARIEPY et al. (2014) investigated the invasion pathways and source populations of BMSB by analyzing genetic diversity in samples collected from Asia, North America, and Europe. The results showed that Asian populations possess substantially higher genetic diversity compared to those in Canada and Switzerland. In Canada, three haplotypes were identified, with evidence indicating that the population was introduced via the United States, likely originating from Hebei/Beijing, China. On the other hand, in Switzerland, two out of three haplotypes were frequently observed, but the origin of the native Swiss sample remains uncertain. However, the dominant haplotype in Switzerland showed similarities with samples from Hebei and Beijing, suggesting a potential connection. Interestingly, the remaining two haplotypes in Switzerland were unique and did not match any Asian samples. Additionally, the haplotypes in North America and Switzerland were not similar, indicating two distinct invasion pathways to the USA and Europe (GARIEPY et al. 2014). In Europe, a total of nine COI haplotypes were confirmed, with many of them not being recorded elsewhere. This suggests the occurrence of multiple invasions from Asia (GARIEPY et al. 2015).

2.5. Likelihood of introduction of different stages of BMSB

The winter aggregation behavior of the BMSB adults in various structures and materials has made them the most frequently intercepted stage during quarantine inspection and survey. This contrasts with the eggs and nymphal stages, which are typically intercepted along with transported fresh fruits, vegetables, and nursery stock. Several studies have highlighted the higher interception rate of adult BMSB due to their behavior (HOLTZ & KAMMINGA 2010, DUTHIE et al. 2012, GARIEPY et al. 2014, LESKEY et al. 2014). The second to fifth stages have higher risk of introduction with fresh materials compared to eggs and first instar nymphs. Eggs may not survive in lower temperatures due to their sensitivity, typically hatching within a few days. Transport has the potential to disturb the feeding behavior of first-instar nymphs on the egg mass following their emergence, resulting in elevated mortality rates (LESKEY et al. 2014). The introduction of nymphal instars is commonly associated with the transportation of nursery stock, however, stringent regulations overseeing the transport and treatment of nursery plants significantly diminish the likelihood of trans-oceanic, inter-state, or long-distance introductions (DUTHIE et al. 2012).

2.6. Pathway of BMSB Introductions

According to LESKEY et al. (2014), the pathway of introduction is caused by:

a. Crop production: During the exploration of host plant resources, intentional dispersal occurs. This deliberate movement takes place among various agricultural crops. This pathway can be a long distance or local (NIELSEN et al. 2013, WIMAN et al. 2014).

b. Disturbance: Associates with disrupted habitat and populations hot spot with the pathway being limited to a local scale.
c. Forestry: Deliberate scattering while seeking out the location for overwintering and this route of pathway can be long distance or local.
d. Hitchhikers: Often arises because of BMSB seeking sheltered overwintering sites and the pathway can be a long distance or local (HOEBEKE & CARTER 2003).
e. Self-propelled: Deliberate dispersal in seeking suitable host plants or overwintering sites which frequently take place over long distances or within a local area (WIMAN 2015a)

The primary factor behind the possible introduction of BMSB into California, Washington, and Idaho was due to transportation of aggregated population by people migrating from the eastern to the western USA (LESKEY et al. 2014). Adults exhibiting aggregation behavior are more likely to be involved in introduction pathways, particularly when it comes to non-plant material. The risk of establishment is significantly higher when dealing with aggregations of BMSB, which consist of multiple insects of both sexes, compared to individual interceptions. In exporting countries that can be considered as the major source of transporting BMSB population such as China, Korea, Japan, and the USA, the formation of aggregations usually begins in August and September (HOEBEKE & CARTER 2003, HAMILTON 2009). During this time, the occurrence of interceptions of BMSB tends to escalate during quarantine inspections, particularly when goods stored outside in the source country are being transported (DUTHIE et al. 2012). Individuals of BMSB are more prone to unintentionally hitchhike on personal items such as luggage etc. while larger cargos are more likely to occur in aggregations. The greatest risk of harboring aggregations of BMSB occurs with large items that have been stationary for prolonged periods during the onset of winter. It seems that ocean-bound cargo containers or packing crates are among the most common pathways for the introduction of BMSB, potentially being responsible for the initial introduction of this species into the USA in the mid-1990s (HOEBEKE & CARTER 2003, HAMILTON 2009). Nevertheless, BMSB has also been discovered on ship decks and other cargo, including transported machinery, furniture, and cars (HOLTZ & KAMMINGA 2010, DUTHIE et al. 2012).

The level of potential risk involved in introducing adults on produce or other plant material is generally regarded as being low to moderate. However, it is worth noting that this mechanism may have been responsible for the initial introduction of BMSB into Switzerland (WERMELINGER et al. 2008). Once BMSB becomes established, the dissemination across continents is likely to follow the paths of human activity, such as highways and railways. Various types of vehicles, including cars, tractor-trailers, recreational vehicles, and moving trucks, have all been identified as potential carriers capable of introducing this pest over land. However, deliberate introductions are highly unlikely due to the universally acknowledged status of BMSB as a pest and its absence of any known unintended uses (LESKEY et al. 2014).

In Hungary, BMSB route of entry is unknown though it was considered as it reached the country through natural dispersion from the west. However, the species were not reported from neighboring countries during that time, so the possibility was rather unlikely (VÉTEK et al. 2014).

2.7. Flight and dispersal behavior of BMSB

BMSB exhibit high mobility, and extensive research has been conducted to study their dispersal capacity and behavior in order to gain a better understanding of how they spread from one host to another and adapt to changing landscapes. Various methods, such as harmonic radar, laboratory flight mills, and ethological software, have been employed to monitor their movement (WIMAN et al. 2014, LEE et al. 2014, 2015). Field-based mark-recapture studies have utilized immunomarking and fluorescent dusts in conjunction with modified handheld lasers (LESKEY & NIELSEN 2018, KIRKPATRICK et al. 2019). Adult BMSB are capable of flying up to 5km within a 24-hour period, with some individuals capable of flying even greater distances. The longest flights occur during peak dispersal from overwintering sites, as opposed to foraging flights (LEE & LESKEY 2015, WIMAN et al. 2015a, LESKEY & NIELSEN 2018). In the field, flight initiation requires a temperature of at least 15°C and lower wind velocities. Flight rates decrease below 10% when wind speeds exceed 0.75m/s. BMSB flight is influenced by ambient temperature and light intensity, while factors such as sex and relative humidity do not affect flight behavior. Additionally, BMSB tends to fly in the opposite direction of the sun (LEE & LESKEY 2015). Laboratory and field monitoring studies have revealed that nymphs in the 3rd and 4th instar stages cover greater horizontal and vertical distances compared to adults in laboratory settings. However, under field conditions, surface temperature affects the movement of nymphs, with 5th instar nymphs covering longer distances than 3rd instar nymphs. Shorter movements occur at surface temperatures below 25°C, while higher temperatures result in individuals covering greater distances (LEE et al. 2014).

Stimuli such as plant phenology and nutritional requirements trigger the movement of BMSB. The use of modified handheld lasers with fluorescent markers and harmonic radar in studying adult dispersal behavior can aid in tracking the specific locations of BMSB adults over extensive distances (LEE et al. 2014). When BMSB tagged adults are released on various host and non-host plants, they show a clear preference for the known host plant over the non-host plant, where the

BMSB remains six times longer. BMSB demonstrates a strong ability to disperse within the host plant in response to attractive stimuli (LEE et al. 2014, RICE et al. 2015).

2.8. Economic importance

The invasion of BMSB in the United States led to a significant outbreak in the mid-Atlantic region in 2010, resulting in substantial crop damages. This included apples, peaches, nectarines, tomatoes, peppers, sweet corn, and soybeans which suffered estimated losses of approximately US$37 million, while certain stone fruit growers experienced devastating losses of up to 90% (LESKEY & NIELSEN 2018). In addition to causing damage to crop, the overwintering population of these insects also gives rise to pest issues for both homeowners and businesses across the BMSB range and thus considered as one of the most severe agricultural and nuisance pests due to its aggregation behavior during overwintering (BARISELLI et al. 2016, LESKEY et al. 2015). BMSB feeding occurs in multiple growth stages of plants and has a serious impact on quality and yield of crops. Infestation of BMSB in their native place is low and acknowledge as occasional pest in fruit orchards and soybean (LEE et al. 2013), although, outside their native range in USA and Europe they caused severe damage.

In Italy, BMSB was first reported in 2012 (COSTI et al. 2017) from Emilia Romagna, one of the most important fruit-producing regions of Europe (FANFANI & PIERI 2016). Despite it being just 2 years since its discovery in this area, fruit injuries were observed (MAISTRELLO et al. 2016). During summer 2015, a large outbreak with over 50% deformed fruits was reported from commercial pear orchards. (MAISTRELLO et al. 2017, COSTI et al. 2017). In the northern regions of Italy, there has been an increase in attacks on various crops such as apple, pear, kiwi, peach, apricot, cherry, hazelnut, soya, and corn. These attacks have resulted in substantial losses, with estimated damages reaching €250 million in 2019 (MALUMPHY et al. 2021). A serious threat is also posed by BMSB spreading rapidly across Europe.

Regardless of their establishment in Switzerland in 2004, Swiss farmers and horticulturists have observed minimal impact on their horticultural and agricultural crops. However, the overwintering population of pests is regarded as an annoyance and a household nuisance (HAYE et al. 2014), Nevertheless, it was not until 2017 that the occurrence of crop damage and the progressive rise in the population of BMSB, accompanied by a shift from one to two generations per year, were documented. This population growth can be linked to the increasing temperatures (SIBYLLE et al. 2020).

During the late summer of 2016, a survey was conducted in Hungary, uncovering the presence of BMSB infesting vegetables. The investigation revealed that 94% of dry bean pods contained damaged seeds, while 100% damage in green hot pepper fruits (VÉTEK & KORÁNYI 2017). By 2018, the species had become widespread in numerous parts of the country, mostly in almost all the districts of Budapest (VÉTEK et al. 2018) and now poses serious threat in crop production

2.9 Feeding behavior of BMSB

BMSB feeding involves secretion of saliva that contains various enzymes for extra intestinal digestion, followed by inserting styles and sucking up the sap from the plant. Maximal feeding occurs at 16°C and 17°C and feeding ceases at 3–6°C and above 26–29°C. These temperature thresholds were determined through the utilization of electronically monitored probing studies (WIMAN et al. 2014). Their feeding habits led to symptom like dry corky tissue near feeding sites (LESKEY et al. 2012, ACEBES-DORIA et al. 2016a), small size fruit, and vegetables (SMITH et al. 2014, WIMAN et al. 2015b, KUHAR et al. 2012, ZOBEL et al. 2016), discolor, depress and distort on fruit surface (ACEBES-DORIA et al. 2016a, ZOBEL et al. 2016), empty kernel in hazelnuts (HEDSTROM et al. 2014) etc. Though the symptoms and damage severity depend on life stages, numbers of individual, host phenology and host stages. Studies on blueberries showed BMSB fed more on healthy fruit than previously fed fruit due to biochemical changes (ZHOU et al. 2016).

2.10. Host range of BMSB

BMSB, a pest known for its ability to feed on a wide range of plant species, has been found to consume over 100 different plants from various families (LESKEY et al. 2013, LESKEY & NIELSEN 2018, MALUMPHY et al. 2021). Research conducted in the United States has revealed that BMSB demonstrates a stronger preference for non-Asian host plants compared to Asian host plants (MARTINSON et al. 2016). Specifically, female BMSB tend to lay their eggs on plants that have longer fruiting periods (LESKEY & NIELSEN 2018). In North America, there are more than 170 plant species that BMSB feeds on, belonging to a diverse range of families. Most of these species are found in trees, and BMSB commonly utilizes plant families such as Rosaceae and Sapindaceae, which include various wild hosts like *Acer negundo* Linnaeus, *Acer macrophyllum* Pursh, and *Crataegus monogyna* Jacq, as well as cultivated hosts like *Malus domestica* Borkh, *Prunus persica* (L.) Batsch, *Pyrus communis* L, and *Vitis vinifera* L. Additionally, BMSB shows a preference for laying eggs on specific fruit vegetables, sweet corn, and soybeans (SMITH et al. 2014, SARGENT et al. 2014, ZOBEL et al. 2016, LESKEY & NIELSEN 2018). The phenology and quality of the host plants play a crucial role in the growth, development, host selection, and survival of BMSB. Nymphs have shown inadequate development when exclusively reared on apples, but they can successfully complete their development on peaches (ACEBES-DORIA et al. 2016b). Moreover, BMSB may necessitate multiple hosts to ensure proper development. The ability of BMSB to be present on both wild and cultivated host plants suggests their capability to transition between diverse environments (NIELSEN & HAMILTON 2009a, 2009b BAKKEN et al. 2015, MARTINSON et al. 2016, ACEBES-DORIA et al. 2017, LESKEY & NIELSEN 2018). Research conducted on woody ornamentals and wild host trees in North America indicates that BMSB shows a higher preference for angiosperms over gymnosperms. Interestingly, this differs from its native range, where gymnosperm hosts have been utilized for population forecasting (LEE et al. 2013, FUNAYAMA 2015, BAKKEN et al. 2015, BERGMANN et al. 2016, LESKEY & NIELSEN 2018).

In native, BMSB outbreak occasionally occurred on tree fruit (FUNAYAMA 2002). In invaded region, the first instances of damage on apples and pears were observed in Allentown, Pennsylvania, and Pittstown, New Jersey in the United States (NIELSEN & HAMILTON 2009a). In American orchards where BMSB has established itself. It swiftly becomes the dominant stink bug species, unlike the native stink bugs. Moreover, it proves to be a persistent pest throughout the entire duration of the tree fruit's growth season (NIELSEN & HAMILTON 2009a, LESKEY et al. 2012).

The host plant inventory in Europe consists of 51 species from 32 families, encompassing a mix of non-native and indigenous plants. High numbers of nymphs and adults were observed on *Catalpa bignonioides* (Walter)*, Sorbus aucuparia* (Linnaeus)*, Cornus sanguinea* (Linnaeus)*, Fraxinus excelsior* (Linnaeus), and *Parthenocissus quinquefolia* (Linnaeus). BMSB can complete its life cycle using *Paulownia tomentosa* (Thunberg), *Ailanthus altissima* (Mill), *Ilex aquifolium* (Linnaeus), and *Prunus persica* (L.) Batsch as host. Fruiting vegetables like tomatoes and peppers are also susceptible to BMSB damage, however, it is more commonly observed later in the season. The feeding process can hinder the development of seeds in crops such as maize or soybean, leading to failure. (LESKEY et al. 2013).

2.11. Eco-biology of BMSB

Comprehensive studies on phenology and biological characteristics are essential for enhancing and adjusting pest control methods during critical life stages and in predicting pest outbreaks. The efficacy of pest management tactics greatly depends on aligning them with the distinct developmental phases of insects. It is imperative to deploy bioagents and chemicals at the precise moment for maximum impact.

2.11.1. Voltinism of BMSB

There have been documented instances of one or two generations of BMSB in its native areas, including China, Japan, and Korea (LEE et al. 2013). Nevertheless, HOFFMAN (1931) put forward the notion that Southern China could potentially witness a higher number of generations per year, ranging from four to six. In China, two generations of BMSB, with egg-laying beginning from mid-May to late July, and the emergence of second-generation adults occurring from late August to mid-September (WANG & WANG 1988, QIN 1990, ZHANG et al. 1993, QIU 2007, LEE et al. 2013). According to BAE et al. (2008, 2009), BMSB has the capacity to undergo up to two generations annually in the southern part of South Korea. In Japan, BMSB is widely distributed across country and is likely to be dominant species in cooler regions (ADACHI et al. 2007). Various sources including anecdotal evidence, laboratory and field studies in Japan, reported the existence of one or two generations per year (SAITO et al. 1964, WATANABE et al. 1979, ODA et al. 1980, YANAGI & HAGIHARA 1980, KAWADA & KITAMURA 1983, FUJIIE 1985, KATAYAMA et al. 1993, FUNAYAMA 2008). Moreover, it was suggested that BMSB exhibits a univoltine life cycle in northern Japan and a bivoltine life cycle in southern Japan; however, direct empirical evidence supporting this geographic pattern has not been clearly demonstrated (WATANABE 1980).

In the region of the United States that has been invaded, the BMSB typically goes through one to two generations per year (NIELSEN & HAMILTON 2009b, BAKKEN et al. 2015). A research study conducted in Northeastern USA focused on the life history of BMSB, supporting the notion that BMSB follows a univoltine pattern in Eastern Pennsylvania (NIELSEN & HAMILTON 2009b). The presence of BMSB was first noted in North Carolina in 2009, eventually establishing itself as a significant pest by 2015. The voltinism of BMSB in North Carolina displays a combination of univoltine and bivoltine patterns, influenced by temperature fluctuations (OGBURN et al. 2023). NIELSEN & HAMILTON (2009b) found that the degree days (DD) in Eastern Pennsylvania were sufficient for the completion of two generations of insects. However, there exists a delay between the emergence of adult insects in spring and their egg-laying behavior, possibly attributed to the maturation of female ovaries.

In Europe numerous research studies have been carried out regarding the biology of BMSB (HAYE et al. 2014, COSTI et al. 2017, REZNIK et al. 2022, ROT et al. 2022). In Zurich, Switzerland, it was previously understood that BMSB had a single generation per year (HAYE et al. 2014). However, in 2017, a transition from one generation to two generations per year was observed, which can be attributed to the increasing temperatures (SIBYLLE et al. 2020). On the other hand, in the South Alps of Italy, Sochi region of Russia, Western Slovenia, Greece and Turkey, BMSB has been found to complete two generations per year (COSTI et al. 2017, REZNIK et al. 2022, ROT et al. 2022, ÖZDEMIR et al. 2023, KOUTSOGEORGIOU et al. 2025).

2.11.2. Overwintering of BMSB

The flight of adult BMSB individuals to overwintering sites commences in the period spanning September to November, with the highest level of activity usually observed in mid-October (SAITO et al. 1964, KOBAYASHI & KIMURA 1969, KAWADA & KITAMURA 1992, QIN 1990, ZHANG et al. 1993). At temperatures below 9ºC BMSB become inactive (LEE et al. 2013). The gatherings observed during the winter months were initiated by mature individuals reacting to tactile or olfactory cues (TOYAMA et al. 2006) or may involve vibrational movement (BEDOYA et al. 2020) and are found in dark locations and once settled then unlikely to leave (TOYAMA et al. 2011) until the nutrients stored in fat bodies depleted (FUNAYAMA 2012). The overwintering flights mostly occurred to the west facing portion of building than other cardinal directions (QIN 1990). Overwintering insects are commonly found in man-made structures (KOBAYASHI & KIMURA 1969, YANAGI & HAGIHARA 1980, WATANABE et al. 1994, FUNAYAMA 2002, LEE et al. 2013, BEDOYA et al. 2020), as well as in natural environments such as litter and tree holes, crevices of dead tree, beneath tree barks, and in dry high elevation mountain ranges (WANG & WANG 1988, QIN 1990, LEE et al. 2014). The survival rates of BMSB during overwintering are typically low, with percentages ranging from 35 to 40% (ROT et al. 2022). According to SCACCINI et al. (2020) due to its cold-intolerant nature, exposure to low temperatures during the winter and extreme spring frost events can greatly contribute to a greater mortality rate for BMSB and survival rates decline at temperature below 5ºC. The low survival can also be attributed to an insufficient accumulation of nutritional reserves as the summer generation enters diapause earlier (FUNAYAMA et al. 2012). KIRITANI (2007) found that for BMSB, at 1ºC increase in temperature above 4ºC resulted in a 13.5% increase in survivorship. BMSB also demonstrated greater tolerance to low temperatures compared to *Nezara viridula* (Linnaeus), with 81% mortality for *N. viridula* and 31% for BMSB at a mean temperature of 4ºC. However, ODA et al. (1980) suggested that the mortality of overwintering BMSB due to low temperatures may not be directly correlated.

2.11.3. Sexual maturation and reproduction of BMSB

When it comes to egg production, BMSB accesses multiple host plants. However, it has been found that rearing on a single diet, such as snap bean (WATANABE 1979), mung bean (BAE et al. 2009), or pear (FUJIIE 1985), fails to result in egg production. After the emergence of adults, female individuals become sexually mature within a span of 2 weeks (WATANABE 1979, 1980, YANAGI & HAGIHARA 1980, KAWADA & KITAMURA 1983, QIU 2007, BAE et al. 2009). Nevertheless, the pre-oviposition period of BMSB is significantly influenced by temperature. In laboratory conditions, females displayed an average pre-oviposition period of 12 days (HAYE et al. 2014), 13 days (NIELSEN et al. 2008), and 18 days (MEDAL et al. 2013) when exposed to a temperature of 25 °C. Research conducted in Italy (COSTI et al. 2017) and Western Slovenia (ROT et al. 2022) identified the existence of two generations of BMSB annually, known as the overwintering generation and the summer generation. The pre-oviposition period for the overwintering generation, which refers to the duration between emergence from overwintering sites and the first egg laying, ranged from 35± 4.29 days in Italy to 39.43± 3.28 days in Slovenia. In contrast, for the summer generation, the period between adult emergence and the first oviposition was significantly shorter, averaging 12.31 ± 0.89 SE days in Italy and 16.63± 1.37 days in Slovenia.

Various research studies have extensively documented the oviposition and mating behavior of BMSB in both natural field conditions and controlled laboratory environments (KAWADA & KITAMURA 1983, WANG & WANG 1988, CHU et al. 1997, QIU 2007). It has been noted that copulation can occur repeatedly as highlighted by KAWADA & KITAMURA (1983). Mating behavior is not limited to specific times of the day, with copulation lasting anywhere from 5 to 14 minutes (SAITO et al. 1964, KAWADA & KITAMURA 1983, WANG & WANG 1988). However, MEDAL et al. (2013) found that the duration of mating sessions ranged from 8.43 to 11.00 minutes, with an average duration of 10.15 minutes.

The production of eggs in BMSB is influenced by various factors. Females that mate multiple times tend to produce more eggs, while egg production decreases with age. However, females could produce eggs throughout their lifespan if they have access to optimal abiotic conditions and high-quality food (KAWADA & KITAMURA 1983). BMSB produced a cluster of egg mass, females typically lay around 28 eggs (NIELSEN et al. 2008, MEDAL et al. 2013). NIELSEN et al. (2008) discovered that the mean duration between oviposition events was 4.3 days at 25 °C in laboratory conditions. MEDAL et al. (2013) observed that eggs were laid every 5–12 days at 25 °C. On the other hand, HAYE et al. (2014) noted that the average interval was 17 days at natural temperatures from June to September in Zurich-Wollishofen, Switzerland. Earlier research conducted in the native habitat of BMSB revealed varying durations for the egg-laying period. YANAGI & HAGIHARA (1980) documented a span of 44 days, whereas KAWADA & KITAMURA (1983) reported a longer duration of 104 days. The average number of eggs per female over a lifetime varied between 168 (MEDAL et al. 2013) and 212 eggs (NIELSEN et al.

2008) at a temperature of 25°C. Nonetheless, when the fecundity was measured under natural temperature conditions in Switzerland, Western Slovenia and northern Italy, the average realized lifetime fecundity of BMSB was found to be 46-79 eggs in Switzerland (HAYE et al. 2014). The number of eggs laid per female in Slovenia differed between the overwintering and summer generations, with averages of 174 and 76 eggs, respectively (ROT et al. 2021). Whereas, in Italy, the overwintering and summer generations laid 285 and 214 eggs per female (COSTI et al. 2017). In their native habitat, females can lay anywhere between 100 to 500 eggs, with an average of 240 eggs per female (YANAGI & HAGIHARA 1980). Comparatively, the total fecundity per female in North America and Europe was lower when compared to the native areas. The shorter egg-laying period in Slovenia in both generations can be attributed to the higher latitude and less favorable climatic conditions, especially the temperature (ROT et al. 2022). Additionally, there is an escalation in egg mortality rates from summer to autumn. Field observations show that the percentage of egg mortality varied from 6.6% towards the end of August to 100% towards the end of September, which coincided with temperatures falling below 15°C (HAYE et al. 2014).

2.11.4. Effects of photoperiod and temperature in the development of BMSB

Photoperiod, temperature, and diet are all factors that have a significant impact on reproductive development (LEE et al. 2013). Reproductive development can be influenced by exposure to different photoperiods, for adults it was studied by FUJIIE (1985) and for nymphs by WATANABE (1979) and NIVA & TAKEDA (2003). However, the exposure of eggs to photoperiod does not seem to have any effect (WATANABE 1979). NIVA & TAKEDA (2003) suggest that the reduction in photoperiod can suppress the reproductive activity of adult individuals, which are the ones that eventually migrate to overwintering sites. The induction of diapause in adult individuals is affected by shorter day conditions (WATANABE 1980, FUJIIE 1985, NIVA & TAKEDA 2003, TOYAMA et al. 2006, 2011) and lower temperatures (WATANABE 1980). The ovarian development of BMSB occurs when exposed to photoperiod of 14 hours or more (WATANABE et al. 1978, 1979, 1980, YANAGI & HAGIHARA 1980). Multiple investigations have indicated that reproductive diapause initiate during the early to mid-August period (SAITO et al. 1964, WATANABE 1980, YANAGI & HAGIHARA 1980, FUJIIE 1985, KATAYAMA et al. 1993, FUNAYAMA 2002). SAITO et al. (1964) noted that females obtained from *Paulownia* spp. at the end of July could lay eggs, while those collected on 20 August could not. The research carried out by REZNIK et al. (2022) in the Sochi region of Russia focused on the ovarian development of BMSB revealed that the proportion of females with fully developed ovaries sharply declined to zero when the critical day length decreased from 15 hours. Furthermore, in the natural environment, females exhibited fully or partially developed ovaries and fully or partially filled spermatheca from late May to early September, whereas during the rest of the year, almost all dissected females were in a nonreproductive (diapause) state. In Central Japan, the photoperiod from late April to mid-August is suitable for ovarian development, and a minimum temperature of 16.3ºC is required for this development (WATANABE 1980).

Numerous studies within BMSB's native range have shown that temperature is a key factor affecting its development (ODA et al. 1980, FUJIIE 1985, QIU 2007). Similarly, diet also has an impact on its growth (WATANABE 1979, ODA et al. 1980, FUNAYAMA 2002, 2005, 2007). The eggs usually reach maturity over a period of 5-6 days (WATANABE 1979, YANAGI & HAGIHARA 1980, ODA et al. 1980, KAWADA & KITAMURA 1983, CHU et al. 1997). Following the hatching of the initial instar congregate in clusters either around or near the eggs prior to scattering to forage for food (SAITO et al. 1964, WANG & WANG 1988, QIN 1990, CHU et al.1997). The nymphs' physical characteristics, such as body size, pigmentation, feeding behavior, and rate of development, were found to be influenced by the amount of daylight they were exposed to, as the photoperiod decreased, the nymphs exhibited faster development (NIVA & TAKEDA 2003). The eggs, on the other hand, took an average of 44 to 52 days to reach the fifth instar stage, as reported by several studies (SAITO et al. 1964, KOBAYASHI 1967, WATANABE et al. 1978, YANAGI & HAGIHARA 1980, ODA et al. 1980, FUJIIE 1985, CHU et al. 1997, QIU 2007).

Several studies have been conducted in the USA and Europe since the invasion, focusing on the impact of photoperiod and temperature. In the USA, NIELSEN et al. (2008) and OGBURN et al. (2023) conducted research in this area. In Europe, HAYE et al. (2014), COSTI et al. (2017), MURVANIDZE et al. (2018), and ROT et al. (2022) have contributed to the understanding of this topic. NIELSEN et al. (2008) and OGBURN et al. (2021) briefly elaborated the effect of photoperiod and temperatures in development and survival of BMSB. conducted a study to examine the effects of photoperiod on BMSB in North Carolina, USA, and compared their results with previous studies from Japan, Europe, and the USA. Their findings showed that even small changes in day length can significantly affect the fertility of adult female BMSB. Specifically, F1 nymphs exposed to day lengths of 14.0 to 14.3 hours in mid- to late-July in Mills River developed into non-reproductive adults, suggesting a potential diapause state. In contrast, F1 nymphs exposed to slightly longer day lengths of 14.3 to 14.5 hours during late June to early July in Goldsboro matured into reproductive adults. Notably, the diapause-inducing photoperiod range observed at Mills River (14.0–14.3 hours) is within the 13.5–15 hours range reported for Japanese populations (WATANABE 1979, YANAGI & HAGIHARA 1980, FUJIE 1985) located at similar latitudes with Mills River (35.5448°N for Mills River compared to approximately 36.6485°N to 36.6958°N for the study sites in Japan). Diapause induction in BMSB populations in northern latitudes, such as Modena, Italy (44.53°N) (COSTI et al. 2017) and Sochi, Russia (43.6°N) (MUSOLIN et al. 2019), requires day-lengths of 15 hours or less. The relationship between variations in photoperiod response among these populations and either inherited traits from their original habitats or adaptations to new environments remains unknown.

Besides photoperiod, temperature has the potential to influence the diapause reaction of insects as (TAUBER & TAUBER 1976, TAUBER et al.1986). The differences in temperature between Goldsboro and Mills River, North Carolina, USA, had a significant effect on the reproductive status of F1 adult BMSB. Temperature plays a critical role in diapause induction: nymphs raised under photoperiods longer than 16 hours and at temperatures ≥24°C developed into reproductive adults, whereas those reared at 20°C emerged as adults in a reproductive diapause state (NIVA & TAKEDA 2003, MUSOLIN et al. 2019). A decrease in the survival, egg hatch, and reproductive rates of BMSB has been documented when temperatures exceed 30 °C (NIELSEN et al. 2008, HAYE et al. 2014, SCACCINI et al. 2019, GOVINDAN & HUTCHISON, 2020). Additionally, even brief exposures of 35–38 °C lasting only 4 hours can result in lethality (AIGNER & KUHAR, 2016). The survival and reproductive success of BMSB are likely to be greatly influenced by temperature, which in turn plays a crucial role in the establishment of its population. OGBURN et al. (2021) reported that high temperatures in Goldsboro and Mills River, North Carolina, USA, negatively affected BMSB populations. Notably, second-generation (F2) egg hatch rates were very low in July, along with longer developmental times. In Goldsboro, F2 egg hatch averaged only 25.8 ± 8.6% during July and August, when daily temperatures reached 30.7 ± 0.1 °C, compared with 90.0 ± 4.9% for first-generation (F1) eggs in May at 26.5 ± 0.4 °C. This sharp decline in egg hatch reduces the reproductive potential of first-generation adults, thereby limiting the number of second-generation adults contributing to the overwintering population. Early emergence of overwintered adults also contributed to low population densities, with 30.4% in Goldsboro and 22.0% in Mills River failing to lay eggs. It has also been reported that elevated spring temperatures resulting in the premature emergence of overwintering BMSB, prior to the availability of food resources, have been linked to reduced population densities in the northern regions of Japan (FUNAYAMA 2012). The longevity and fecundity of post-diapause adults are positively influenced by prolonged exposure to below freezing temperatures throughout the overwintering period (SCACCINI et al. 2019, LOWENSTEIN AND WALTON 2018, OGBURN et al. 2021). Bivoltinism in Italy has facilitated the rapid increase of BMSB population in Northern Italy, resulting in greater severity in comparison to Switzerland (which was univoltine until 2017) (HAYE et al. 2014, COSTI et al. 2017). Nevertheless, it seems that heat stress could hinder the establishment of BMSB, as temperatures in eastern North Carolina were high enough to induce stress on population growth and counteract the benefits of bivoltinism (OGBURN et al. 2021).

2.11.5. Degree Days of BMSB

NIELSEN et al. (2008) estimated that a total of 537.63 degree-days (DD) are required for the complete development from egg to imaginal ecdysis. Furthermore, an additional 147.65 DD are necessary for the preoviposition period of the female. OGBURN et al. (2021) study provides valuable insights into the timing and patterns of adult emergence, oviposition, and eclosion of F1 adults. The study analyzed the season total degree-day (DD) accumulations generated from 1 January to 30 October were 1348-1336 DD, the peak numbers of overwintering adults, which occurred between 175 and 200 DD. Furthermore, the researchers noted that oviposition by overwintered adults extended from 200 to 250 DD, continuing until 1050 to 1200 DD. Regarding the eclosion of F1 adults, the study found that it commenced at approximately 700 DD. The emergence of F1 adults reached its peak between approximately 1000 and 1200 DD.

In Europe, the Swiss BMSB requires total degree day was briefly studied in Switzerland (HAYE et al. 2014), and Western Slovenia (ROT et al. 2022) under natural temperature conditions and the accumulation DD was calculated using the lower threshold of 12.2ºC. In Swiss population (univoltine), total degree day required for the egg-to-adult stage was 588.24 DD and the emergence from overwintering to first oviposition was 117.65 DD. However, in Western Slovenia the population in bivoltine namely overwintering generation and summer generation, total degree day required for the egg-to-adult stage in overwintering generation and summer generation were 530.87±12.40 (SD) and 545.17± 16.61 (SD) respectively, and the pre oviposition period for the overwintering generation (emergence from overwintering to first oviposition) and summer generation was 118.77±7.72 (SD) and 179.00±16.84 (SD) respectively (ROT et al. 2021).

In native region of BMSB, LEE et al. (2013) suggests the maximum temperature threshold is 30ºC and provides a comprehensive summary of the minimum temperature thresholds and the cumulative degree-day (DD) requirement in Asia, which are presented in Table 2.

Table 2. Comprehensive summary of the minimum temperature thresholds and the cumulative degree-day (DD) requirement of *Halyomorpha halys* from egg to adult in Asia (Japan) (LEE et al. 2013).

Minimum temperature threshold (°C)	Degree days egg to adult	Reference
11.0	630	FUJIIE 1985
11.7	580	KONO et al. (1979) cited by KIRTANI 2007
11.9	648	UCHIDA (1986)
12.1	649	KITA (1979) cited by KIRTANI 2007
12.9	625	WATANABE 1980
13.9	471	YANAGI & HAGIHARA 1980

2.11.6. Life table of BMSB

In Europe, life table studies under natural temperature conditions were undertaken in Switzerland, Italy, and Slovenia. The net reproductive rate (*Ro*) in the Swiss population exhibits a relatively lower value when compared to the net reproductive rate of BMSB population in Italy and Slovenia, alongside the occurrence of two generations in Italy and Western Slovenia (Table 3.) (HAYE et al. 2014, COSTI et al. 2017, ROT et al. 2021). The BMSB population discovered in Emilia Romagna, Italy, exhibits identical haplotypes to those found in most of the USA and the Beijing region (CESARI et al. 2015) and complete two generation per year with high reproductive rate. The total generational mortality was higher in summer generation compared to overwintering generation in Italy and Slovenia (COSTI et al. 2017, ROT et al. 2022). In the overwintering generation, the highest mortality in the total generational mortality was attributed to the eggs stage (COSTI et al. 2017) and 2nd nymphal stages (ROT et al. 2022). Conversely, in the summer generation, the diapausing adult mortality contributed the most to the overall generational mortality in Italy and Slovenia (COSTI et al. 2017, ROT et al. 2022). In Switzerland, the studies conducted by HAYE et al. (2014) revealed only one generation per year, with the highest mortality contribution to the total generational mortality coming from the eggs, 1st nymphal, and 5th nymphal stages. The high mortality observed in the 5th nymphal stages was attributed to the large number of eggs laid in August and the subsequent cold temperatures in the following month, as well as the overwintering mortality of adults. The total generational mortality recorded in Switzerland was 86.7%, (HAYE et al. 2014) while in Italy it was 56.46% in the overwintering generation and 97.47% in the summer generation (COSTI et al. 2017). In Slovenia, the total generational mortality was 60.94% in the overwintering generation and 89.86% in the summer generation (ROT et al. 2021).

Table 3. The net reproductive rate of increase (Ro) of *Halyomorpha halys* in Europe.

Location	**Overwintering generation (*Ro*)**	**Summer generation (*Ro*)**	**Reference**
Switzerland	5.69		HAYE et al. 2014
Northern Italy	24.04	5.44	COSTI et al. 2017
Western Slovenia	14.8	5.6	ROT et al. 2022

2.11.7. Phenology of BMSB

The initiation of the emergence process from overwintering sites commences between late March and mid-May in the native range (WATANABE et al. 1978, WANG & WANG 1988, QIN 1990, ZHANG et al. 1993, FUNAYAMA 2012) coinciding with ambient temperatures surpassing 10ºC (QIN 1990). The adults BMSB from overwintering sites emergence started from late April and May in US and Europe (NIELSEN & HAMILTON 2009b, HAYE et al. 2014, COSTI et al. 2017, ROT et al 2022, SCHOOF 2023). In Slovenia and Italy, the emergence from overwintering sites took place on two separate occasions. The first emergence happened either at the end of January or the beginning of February, but unfortunately, those adult insects were unable to survive. The second emergence occurred at the end of March, coinciding with average daily temperatures surpassing 12 ºC. This second emergence reached its peak at the end of April, with average daily temperatures exceeding 15 ºC (COSTI et al. 2017, ROT et al. 2022). Exit from overwintering sites is triggered by exhaustion of resources and lower nutritional levels in the body (LEE et al. 2013, FUNAYAMA 2012). After exiting from overwintering sites, BMSB used transitional host plant before colonizing on cultivated crops (LEE et al. 2013, FUNAYAMA 2012) and feeding starts when temperatures exceed 17ºC (NIELSEN et al. 2008, LEE et al. 2013).

In China, oviposition by overwintered females typically begins from mid to late May (WANG & WANG 1988, ZHANG et al. 1993, QIU 2007). In Japan, oviposition occurs from early June through July (SAITO et al. 1964, FUJIIE 1985, KAWADA & KITAMURA 1992, KATAYAMA et al. 1993, FUNAYAMA 2002, FUNAYAMA 2007). In the region that was invaded by BMSB and experienced two generations per year, the oviposition began either in mid-May or at the end of May continues until mid-August (COSTI et al. 2017, ROT et al. 2022, HOLTHOUSE & ALSTON 2020). Successful emergence from overwintering when the daily maximum temperature exceeds 14°C. The peak emergence and first mating of BMSB occur in May, when the daily maximum temperature exceeds 21°C (COSTI et al. 2017).

On the other hand, in Switzerland, where BMSB completed only one generation, the oviposition started after mid-June and continued until the end of September. The highest number of eggs being laid was observed towards the end of June, and the emergence of adult BMSB began in August. However, eggs laid in August and September did not hatch due to low autumn temperatures. The total duration from eggs to adults varied between 60 and 131 days under natural fluctuating temperatures. The first new generations appeared in mid-August when the photoperiod was below 15 hours, indicating the onset of diapause (HAYE et al. 2014). However, two generation was recorded during 2018–2019, possibly due to climate change (STÖCKLI et al. 2020).

In the region where BMSB completed two generations per year, the initial appearance of 1st generation adults was observed in July, and they commenced egg laying from mid-July to the beginning of September. However, the 1st instar nymphs that emerged at the end of August failed to reach adulthood due to the change in photoperiod from 14 to 13 hours. The peak period for oviposition in the overwintering generation was observed from mid-June to mid-July, while for the summer generation, it occurred during late July to mid-August, coinciding with a mean temperature of approximately 25.5ºC. The adults of the second generation began to appear from mid-September to mid-October, when the photoperiod had already dropped below 13 hours of light. Interestingly, these adults did not exhibit any reproductive behavior and immediately entered diapause (COSTI et al. 2017, ROT et al. 2022). HAYE et al. (2014) put forward the notion that the ability to generate the second generation lies solely with first-generation adults that have experienced prolonged daylight conditions (where the day length surpasses 15 hours).

2.12. Parasitoids of BMSB

Efforts to manage an invasive pest can indeed present a formidable challenge. These non-indigenous species, upon being introduced to new environments, inflict significant harm on the ecosystem, agriculture, and even human health. In the recently invaded areas, the alien pest often establishes itself rapidly due to the absence of natural enemies, its high adaptability, and the limited information available on its life history, thereby hindering the establishment of an effective management program (MCLAUGHLIN & DEARDEN 2019).

2.12.1. Parasitoids of BMSB in Native place

The species belonging to the genus *Trissolcus* (Hymenoptera: Scelionidae) are widely recognized as the most efficient and highly specialized parasitoids of BMSB within their natural habitat (ARAKAWA & NAMURA 2002, ARAKAWA et al. 2004, QIU 2007, YANG et al. 2009, LEE et al. 2013). In Beijing China, *Trissolcus japonicus* was determined to be the most prevalent species (YANG et al. 2009) Additionally, QIU et al. (2007) reported that this species completes 10 generations per year. In Japan, the primary parasitoid species identified was *Trissolcus mitsukurii* (Ashmead), which exhibited a total of 15 generations per year (ARAKAWA & NAMURA 2002, ARAKAWA et al. 2004). ARAKAWA et al. (2004) discovered that the longevity, body size, and egg production of *Tr. mitsukurii* experienced a notable enhancement after a duration of 7 days when nourished with eggs of BMSB, as opposed to being exposed to *Nezara viridula* (Linnaeus) or *Plautia stali* Scott. Despite the existence of reports regarding interspecific competition between *Anastatus* sp. (Hymenoptera: Eupelmidae) and *Tr. japonicus* (Yang) (synonym of *halyomorphae*), the overall parasitism levels did not show any decline (QIU 2007). The most predominant and effective parasitoid in China and Japan was *Tr. japonicus* and *Tr. mitsukurii* respectively. The parasitism rate was recorded in *Tr. mitsukurii* (84.7%), *Anastatus* sp. (77.2%), *Tr. japonicus* (70%) and *T. flavipes* (Thomson) (63.3%) (LEE et al. 2013). The list of potential parasitoids of BMSB in Asia was summarized by LEE et al. (2013) shown in Table 4.

Table 4. List of potential hymenopteran parasitoids of *Halyomorpha halys* in Asia summarized by LEE et al. (2013)

Species	Family	Host stage	Country
Acroclisoides sp	Pteromalidae	Eggs	China
Anastatus sp.	Eupelmidae	Eggs	China
Anastatus gastropachae (Ashmead)	Eupelmidae	Eggs	Japan
Bogosia sp.	Tachinidae	Eggs	Japan
Ooencyrtus nezarae (Ishii)	Encyrtidae	Eggs	Japan
Ooencyrtus	Encyrtidae	Eggs	China
Telenomus nigripedius (Nakagawa)	Scelionidae	Eggs	Korea
Telenomus mitsukurii (Ashmead)	Scelionidae	Eggs	China, Japan
Telenomus sp.	Scelionidae	Eggs	China,
Trissolcus itoi (Ryu)	Scelionidae	Eggs	Japan
Trissolcus plautiae (Watanabe)	Scelionidae	Eggs	Japan
Trissolcus flavipes (Thomson)	Scelionidae	Eggs	China,
Trissolcus japonicus (as *Tr. halyomorphae*)	Scelionidae	Eggs	China,

2.12.2. Native potential parasitoids of BMSB in Europe

Several research studies have been undertaken in diverse European locations to examine the viability of utilizing native European pentatomid's parasitoids as a natural enemy against BMSB (HAYE et al. 2014, ROVERSI et al. 2016, MORAGLIO et al. 2020, MORAGLIO et al. 2021, ROT et al. 2021, ANDREADIS et al. 2021, IACOVONE et al. 2022). HAYE et al. (2015) investigated the capacity of generalist egg parasitoids of European pentatomidae to target the eggs of BMSB. The study involved exposing BMSB and European Pentatomidae sentinel egg masses to two distinct climatic regions in Switzerland: The Delémont valley in Canton Jura and the Rhône valley in Canton Valais. Additionally, an assessment was carried out to evaluate the efficacy of indigenous stink bug parasitoids against BMSB through the implementation of "no choice black box test" and "no choice behavior test" where females of the parasitoid species were individually exposed to either frozen or unfrozen BMSB eggs to assess host acceptance, parasitism, and successful development. The scelionid *Tr. cultratus* (Mayr) and the eupelmid *Anastatus bifasciatus* (Geoffroy) were observed attacking freeze-killed sentinel egg masses of BMSB. On the other hand, fresh egg masses of native Pentatomidae occasionally hosted four species of Scelionidae wasps: *Trissolcus semistriatus* (Nees), *Tr. scutellaris* (Thomson), *Tr. cultratus*, and *Telenomus chloropus* (Thomson). *Te. chloropus* and *Tr. semistratus* did not yield any progeny when exposed to fresh BMSB eggs in no-choice tests. ROT et al. (2022) conducted research in Slovenia indicating that *A. bifasciatus* is identified as the prime candidate for augmentative biological control in Europe. This species is recognized as the most prevalent native egg parasitoid in Europe, with the ability to develop on viable BMSB eggs, as supported by previous studies (HAYE et al. 2015, COSTI et al. 2019, ABRAM et al. 2017, ROVERSI et al. 2016, STAHL et al. 2019a). Additionally, it has been revealed that there are three main groups of hymenopteran parasitoids that possess the ability to target BMSB eggs in areas that have been invaded. These groups are Scelionidae (*Telenomus*, *Trissolcus*, and *Gryon* spp.), Eupelmidae (*Anastatus* spp.), and Encyrtidae (*Ooencyrtus* spp.). However, it is worth noting that the current level of parasitism by native species is insufficient to effectively reduce the population of this pest below the economic thresholds (DIECKHOFF et al. 2017, ABRAM et al. 2017). Investigations in Southern Europe have shown that *A. bifasciatus* and especially *Ooencyrtus telenomicida* (Vassiliev) (Hymenoptera: Encyrtidae) could serve as effective biological control options for BMSB. Notably, *O. telenomicida* managed to parasitize 35.56% of the host eggs in laboratory settings. A successful emergence of new adults was observed in 22.92% of the eggs, resulting in a considerable decrease in BMSB egg hatching (over 70%) caused by this egg-parasitoid (ROVERSI et al. 2016).

2.12.3. Studies with the most promising parasitoids of BMSB

In 2017, the first reports of adventive populations of *Trissolcus japonicus* were recorded in Switzerland, then in Northern Italy in 2018 (SABBATINI PEVERIERI et al. 2018, STAHL et al. 2019b,). Additionally, in the Friuli Venezia Giulia region of northeastern Italy, Western Slovenia and France, the presence of another key parasitoids of BMSB, *Tr. mitsukurii*, was confirmed (COSTI et al. 2019, BOUT et al. 2021, ROT et al. 2022). These discoveries have introduced fresh avenues for the biological control of BMSB in Europe (STAHL et al. 2019b, SCACCINI et al. 2020). The introduction of host species repeatedly can expedite the dispersal of parasitoids beyond their original habitat (TORCHIN et al. 2004). According to bioclimatic envelope models, *Tr. japonicus* is anticipated to migrate alongside its host across Europe, colonizing regions that offer optimal conditions for its survival. These areas are situated in southwestern France, northeastern

Spain, northern Italy, western Slovenia, and Croatia (AVILA & CHARLES 2018). The coexistence of native and non-native species and their counterattack on BMSB could bring a positive array in controlling BMSB however, a great challenge and opportunity for the future biological control of BMSB, which also brings different risk factors to native species that should be assessed (HAYE et al. 2024).

The first report of *Tr. japonicus* outside its native range was in North America in 2014 and Europe in 2017, while *Tr. mitsukurii* was detected in Australia in the early 20th century and in Europe in 2016. The effectiveness of both parasitoids was observed in their native range. However, in invaded areas, *Tr. japonicus* exhibited a greater potential for habitat suitability on a global scale compared to *Tr. mitsukurii*. Additionally, *Tr. japonicus* showed higher potential suitability at lower latitudes on continental and national scales. These findings have significant implications for enhancing the efficacy of biological control against BMSB by strategically releasing parasitoids in areas where each species is most likely to thrive (TORTORICI et al. 2023).

KONOPKA et al. (2017) examined the potential co-occurrence of the non-native Asian egg parasitoids *Tr. japonicus* and the native European egg parasitoids *A. bifasciatus* as agents for classical biological control. The evaluation of adult aggressiveness following parasitization enabled the observation of interspecific competition between the two species, both in their larval and adult stages. The parasitoids *Tr. japonicus* and *A. bifasciatus* were found to engage in counterbalance competition, with *Tr. japonicus* demonstrating superiority as an extrinsic competitor due to its adult guarding the eggs and displaying more aggressiveness. On the other hand, *A. bifasciatus* demonstrated superiority in intrinsic competition, as its larvae were able to successfully develop from eggs that were multiparasitized and of varying ages. The results of the studies indicate that both parasitoid species can coexist and work together synergistically to combat BMSB.

The cold tolerance of potential bioagents of BMSB, namely *Trissolcus japonicus* and *Tr. cultratus*, was investigated by NYSTROM SANTACRUZ et al. (2017). These parasitoids were collected from four locations in Asia, including Beijing and Nanjing in China, Pucheon in South Korea, and Tsukuba in Japan. The study revealed that both populations of parasitoids exhibited the ability to withstand freezing temperatures and survive, indicating their cold tolerance and potential suitability for introduction.

An integrative physiologically based demographic model driven by weather patterns was created to assess the potential influence of natural enemies on the biological suppression of BMSB amidst present-day and future climate condition, focusing on European-Mediterranean region, resulted that *Tr. japonicus* and *Tr. mitsukurii*, possessing a strong ability to search for hosts, have the potential to effectively suppress BMSB on a regional scale. However, it is important to note that the necessary levels of parasitism required for economic control are not currently observed in either the native habitats of these parasitoids or the areas they have invaded. In addition, the egg hyperparasitoid *Anastatus. sinicus* (Chou & Chou) (Hymenoptera: Eupelmidae) suppressed the activities of the parasitoids in field condition (GUTIERREZ et al. 2023).

The parasitization rate of European parasitoids and *Tr. japonicus* and *Tr. cultratus* (Chinese strain) from the native range of BMSB indicated that both the European native parasitoids and non-native parasitoids were capable of parasitizing BMSB eggs. However, the parasitization rate of the non-native species was significantly higher compared to the European native species, with *Tr. japonicus* and *Tr. cultratus* (Chinese strain) causing 94.1% and 84.2% parasitization, respectively (HAYE et al. 2015). A similar finding was reported by ROT et al. (2022) where the parasitism rate increased significantly from 14% to 30.1% with the discovery of the non-native *Tr. mitsukurii*, which made a substantial contribution to the overall parasitism rate. Moreover, *A. bifasciatus* has been identified as the prevailing species among the native parasitoids of BMSB in Europe (HAYE et al. 2015, COSTI et al. 2019, ABRAM et al. 2017, ROVERSI et al. 2016, STAHL et al. 2019a). Furthermore, it has demonstrated the capability to coexist with non-native parasitoids (STAHL et al. 2019b), making it a promising contender for the implementation of augmentative control measures against BMSB. A study by DIECKHOFF et al. (2017) spanning nine years focused on native parasitoids of the brown marmorated stink bug (BMSB) in the United States. The results of the research showed that there was no observed rise in the parasitization rate. An attempt was made to implement classical biological control in North America using Asian *Trissolcus* sp., however, this species lacked target host specificity and was deemed too risky for release. Therefore, utilizing native parasitoids from the invaded region in an augmentative manner could offer an alternative control approach (RICE et al. 2014, HAYE et al. 2015). Details on the potential egg parasitoids of BMSB in the invaded regions are listed in Table 5.

Table 5. List of native and adventive hymenopteran parasitoids of *Halyomorpha halys* in USA and Europe

Parasitoid species	Family	Country/place	Reference
Anastatus reduvi (Howard)	Eupelmidae	U.S.A.	JONES et al. 2014, CORNELIUS et al. 2016, DIECKHOFF et al. 2017
A. mirabilis (Walsh & Riley)	Eupelmidae	U.S.A.	JONES et al. 2014
A.pearsalli (Ashmead)	Eupelmidae	U.S.A.	JONES et al. 2014, DIECKHOFF et al. 2017
Anastatus spp.	Eupelmidae	U.S.A.	JONES et al. 2014, DIECKHOFF et al. 2017
A. bifasciatus (Geoffroy)	Eupelmidae	Europe	HAYE et al. 2015, COSTI et al. 2019, ROT et al. 2022
Telenomus podisi (Ashmead)	Scelionidae	U.S.A.	JONES et al. 2014, CORNELIUS et al. 2016
Telenomus spp	Scelionidae	U.S.A.	JONES et al. 2014, CORNELIUS et al. 2016, DIECKHOFF et al. 2017
Telenomus chloropus (Thomson)	Scelionidae	Europe	HAYE et al. 2015, ROT et al. 2022
Trissolcus brochymenae (Ashmead)	Scelionidae	U.S.A.	JONES et al. 2014, CORNELIUS et al. 2016
Tr. hullensis (Harrington)	Scelionidae	U.S.A.	CORNELIUS et al. 2016
Trissolcus sp.	Scelionidae	U.S.A.	DIECKHOFF et al. 2017

Parasitoid species	**Family**	**Country/place**	**Reference**
Tr. edessae (Fouts)	Scelionidae	U.S.A.	DIECKHOFF et al. 2017
Tr. euschisti (Ashmead)	Scelionidae	U.S.A.	DIECKHOFF et al. 2017
Tr. semistriatus (Nees)	Scelionidae	Europe	HAYE et al. 2015, COSTI et al. 2019, ROT et al. 2022
Tr. scutellaris (Thomson)	Scelionidae	Europe	HAYE et al. 2015, COSTI et al. 2019, ROT et al. 2022
Tr. cultratus (Mayr)	Scelionidae	Europe	HAYE et al. 2015, COSTI et al. 2019, ROT et al. 2022
Tr. japonicus (Ashmead)	Scelionidae	Adventive species	HAYE et al. 2015, COSTI et al. 2019, ROT et al. 2022
Tr. mitsukurii (Ashmead)	Scelionidae	Adventive species	HAYE et al. 2015, COSTI et al. 2019, ROT et al. 2022
Gryon obesum (Masner)	Scelionidae	U.S.A.	CORNELIUS et al. 2016
Gryon sp.	Scelionidae	Europe	HAYE et al. 2015, COSTI et al. 2019, ROT et al. 2022
Ooencyrtus sp.	Encyrtidae	U.S.A.	DIECKHOFF et al. 2017
Ooencyrtus telenomicida (Vassiliev)	Encyrtidae	Europe	ROVERSI et al. 2016

3.0. MATERIALS AND METHODS

3.1. Collection and overwintering of BMSB adults

The overwintering adults of BMSB were hand collected from warehouses, and buildings at Budapest (N 47.4979°, E 19.0402°), as well as closed parasols outside restaurants in Budapest and Szentendre (N 47.6795°, E 19.0669°) at autumn during 2021 to 2023. Non-target Pentatomidae species were discarded. Details on adult BMSB collected from the wild (2021-2023) and experimentally reared between 2021 and 2024 are provided in Table 6.

Table 6. Overwintering of Male and Female *Halyomorpha halys* adults: Wild-Collected and Experimentally Reared

	Wild adult		**Experiment reared adult**	
Year	Male	Female	Male	Female
2021	739	665	120	96
2022	1449	1127	55	60
2023	418	367	63	69
2024	-	-	184	187

For overwintering the collected BMSB adult, males and females were separated in the laboratory and subsequently placed outdoors under semi-natural conditions sheltered by a roof to protect from rain and snow. The adults were kept in plastic boxes (Length 17 x Breadth 12 x Height 7 cm) along with pieces of cardboard covered with net and labelled with the date, the number of bugs, and the collection location. These boxes were then placed in insect rearing cages (BugDorms 4S2260 Insect Rearing Cage Width 24.5 x Depth 24.5 x Height 63.0 cm, Australian Entomological Supplies Pty Ltd) and left outside to overwinter naturally. Temperature was continuously monitored using T-Logg 160 Greisinger electronic GMBH, Germany and Tinytag Ultra 2-TGU-4510 Gemini Data Loggers, United Kingdom.

The BMSB male and female (wild collections during 2021 and 2022) for parasitoids studies were kept in a climate chamber for hibernation with controlled environmental conditions: temperature 4 ± 0.9 °C, relative humidity (RH) 70 ± 10%, and 8:16 h light: dark (L:D) photoperiod. The hibernating adults were transferred from the climate chamber to an outdoor environment (semi-natural conditions), sheltered under a roof to protect them from rain, and placed in Bug Dorms during the spring to regain activity. Food and water were provided.

3.2. Bugs rearing, phenology, and mortality assessment under outdoor conditions

During 2021 to 2023, three pairs of adults were released in a BugDorms, and five BugDorms were placed at three different sites- Site 1 (west) and Site 2 (east) of K building and Site 3 (south) of A building, in Buda Arboretum, Hungarian University of Agriculture and Life Sciences (Figure 2). In 2021, Site 3 was located on the east side of the K Building; however, due to unfavorable conditions at this location, where the location is densely covered with vegetation during summer, the site was relocated in 2022. Each year, a total of 45 pairs of BMSB adults were maintained, 15 pairs on each site. In each site, 5 BugDorms were placed and 3 pairs of adults were released into each BugDorms. To compensate for adult mortality, an additional 30–50 males and females were supplemented to replace dead individuals in each site (Figure 3). Adults were provided with beans (only in summer), sunflower seeds, peanuts, apples, and carrots, along with a water source consisting of a damp cotton cloth placed in a cap filled with tap water. Food and water were replenished twice weekly. Cardboard pieces were used as oviposition substrates. Once laid, egg masses were transferred individually into plastic boxes covered with nets (made from nylon socks). After hatching, nymphs from each egg mass were reared together and provided with same food and water, which were replaced twice weekly. Upon emergence, adults were paired, provided with continuous access to food and water, and observed for mating and oviposition; nymphal rearing for the summer generation was conducted in the same manner as for the overwintering generation. Data collection included oviposition dates, number of eggs per egg mass, hatching rates, first and last appearance of each nymphal stage, adult emergence, and mortality from egg to adult stages.

In 2024, a total of 131 females were selected from the overwintering population. Each female was paired with two males and reared individually in cylindrical plastic containers (8 cm diameter × 6 cm height). All pairs were maintained separately, with containers labeled and placed inside BugDorms under natural conditions, sheltered by a roof (Figure 4). If a male died, it was replaced, whereas if a female died, the sample was discarded.

The first three egg masses produced by each overwintering female were used to study life table parameters, degree days (DD), and development time. Egg masses were collected in separate containers, and upon hatching, water was provided using a damp cotton-filled bottle cap. First-instar nymphs were reared together until molting to the second instar, after which each nymph was transferred to an individual container for the remainder of the experiment.

For the summer generation, 66 daughters from different overwintering parents were selected, and each female was paired with two males from different parents to avoid sibling mating and minimize inbreeding. The first four egg masses from each female were collected, and nymphal rearing followed the same procedure as for the overwintering generation. After the first three egg masses from overwintering females and the first four from summer females, subsequent egg masses were used to assess generational mortality and study phenology.

Considering all eggs produced by each ovipositing female would have resulted in excessively large sample sizes; therefore, only the first three and four egg masses from each ovipositing female were selected for the overwintering and summer generations, respectively. However, for the evaluation of fecundity and hatching rate, all egg masses produced by every ovipositing female were considered.

Fecundity and hatching rates were calculated from the total number of egg masses laid per female. Data were recorded on the number of egg masses per female, eggs per mass, hatched eggs, and preoviposition duration. During the experiment, 2,143 second-instar nymphs from the overwintering generation and 2,057 from the summer generation were individually reared. Nymphs were observed daily to record mortality and the duration of each developmental stage until adulthood, with food and water replenished twice weekly. The food provided during the experiment remained constant throughout the study period, consisting of carrot, peanuts, and sunflower seeds. The experiment commenced on April 1, following reactivation of overwintering adults, and continued through December.

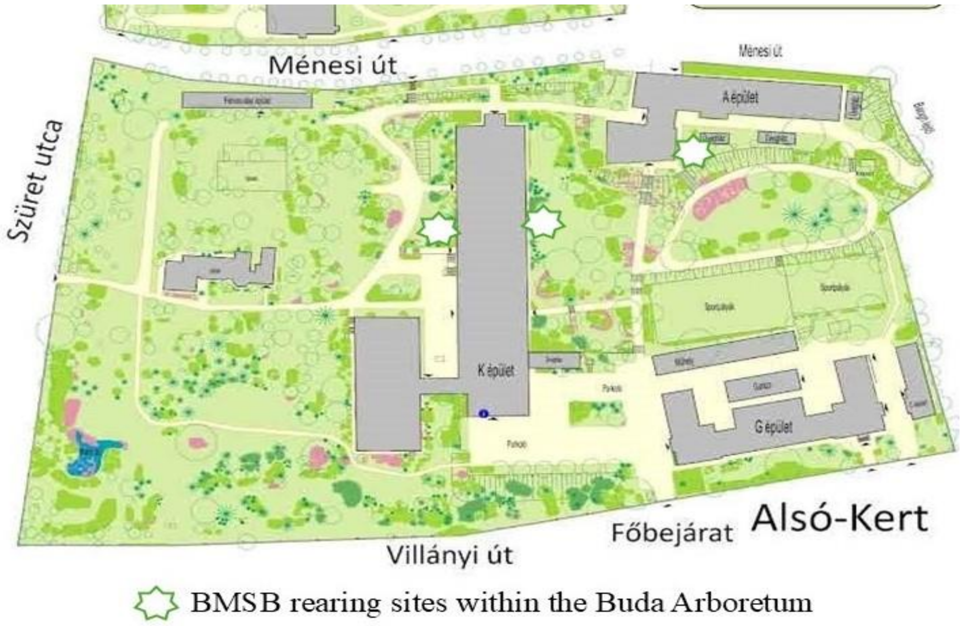


Figure 2. Locations of *Halyomorpha halys* rearing sites within the Buda Arboretum during 2021-2023

Figure 3. Group rearing of *Halyomorpha halys* pairs during 2021-2023 at three different sites in the Buda arboretum (Photo by Johnson Wahengbam, 2021)

Figure 4. Rearing of *Halyomorpha halys* 2nd-instar larvae individually in small plastic cups (right), with the cups placed inside BugDorms under a roof (left). (Photo by Luke Denis, 2024, Buda Arboretum, K Building)

3.2.1. Life table analysis

The parameters of the life table were determined in accordance with the methodologies established by BELLOWS et al. (1992) and HAYE et al. (2014). During the years 2021, 2022, and 2023, the mortality and survival rates of different stages of BMSB were calculated, since the adults were reared in group, it was not possible to evaluate the reproductive rate of each individual female. In 2024, the generational mortality, survival rates of various stages and reproductive rate (R_o) of BMSB were determined, as the fecundity of individual females was recorded during the studies.

Generational mortality and survival rates: Mortality linked to outdoor temperatures, along with background mortality due to various unidentified factors (such as food quality), was represented in terms of apparent mortality, actual mortality, mortality intensity (k-values), and generational mortality. Given that the research was carried out in semi-natural condition, the influence of predators and parasitoids was not taken into account.

Apparent mortality (qx) is the number of individuals dying (mainly from temperature) during a specific stage compared to the number entering that stage (lx). BMSB's apparent mortality was calculated using the number of dead individuals (dx) from each life stage (x), i.e., qx = dx/lx.

Real mortality (rx) is calculated as the fraction of individuals dying at each stage (dx) divided by the number of eggs at the beginning of the life table (rx = dx/l_0).

k-value (kx) = -log (1-qx). kx-values are the negative logarithm of (1-marginal attack rate (qx)) for a given factor, which expresses the intensity of mortality. A generation's mortality (Ks) represents the sum of all mortality factor k-values (summed over all life stages). Ks = $k_{eggs} + k_N1 + k_N2 + k_N3 + k_N4 + k_N5$.

As a proportion of the total generational mortality 100kx/Ks, this value shows the impact of mortality in each stage on BMSB's generational mortality.

The net reproductive rate of increase (R_0), which shows the number of times the population increases or decreases from one generation to the next (VAN DRIESCHE et al. 2008). Growing populations have R_0 values greater than one, whereas R_0 values less than 1 show that the population is declining and the *Ro* was calculated as follows:

Realized fecundity= Numbers of eggs laid/ numbers of females

For overwintering generation, = 5459 eggs laid by 77 females

For summer generation = 5257 eggs laid by 58 females

R_o overwintering generation = realized progeny/number of eggs in the overwintering generation, where realized progeny is the actual number of offspring produced by an individual that survives to a particular developmental stage under specific environmental or experimental conditions.

R_o summer generation = realized progeny/number of eggs in the summer generation

The R_o values for growing populations are greater than 1, whereas values for declining populations are less than 1.

3.2.2. Demographic growth parameters

The demographic growth parameters were calculated only for the 2024 summer generation following LI et al. (2014), as the age of the females is known for this population, since they were the offspring from the overwintering generation. The experiment was carried out under semi-natural outdoor conditions. A total of 66 females were used, of which 3 entered the overwintering phase without laying any eggs; therefore, these females were excluded from the data evaluation. Out of these 63, 34 died before reaching the diapause stage, while 29 successfully entered diapause. In our data analysis, we included all 63 females and accounted for their age until the last female's death before entering diapause, which occurred 88 days after the first adult emergence.

Egg laying to adult emergence, survival rate, daily fecundity, and daily sex ratio were used to construct $l_x m_x$ life tables ($l_x m_x$ is the net female maternity, l_x is the percentage of females alive at age X, and m_x is the mean number of female offspring produced by a female at age X) from which the following demographic growth parameters were calculated:

Net reproductive rates (the total number of offspring that an individual can produce during its lifetime), $R_o = \sum l_x m_x$, Mean generation time, $T = \sum X l_x m_x / R_o$, Intrinsic rate of natural increase, $r_m = \ln R_0 / T$, Finite rate of increase, $\lambda = \exp(r_m)$.

Mean estimates of demographic parameters along with standard errors were computed using the jackknife technique (MEYER et al. 1986, MAIA et al. 2000). To implement this technique, we initially calculated the population parameters based on all (n) individuals. For instance, the intrinsic rate r_{all} was determined using all individuals. Subsequently, we excluded individual i and employed the remaining n-1 individuals to compute the jackknife value $r_{i\text{-jack}}$. The pseudo value was then calculated as $r_{i\text{-pseudo}}$ as $r_{i\text{-pseudo}} = n \times r_{all} - (n - 1) \times r_{i\text{-jack}}$. This procedure was repeated until pseudo-values were obtained for all n possible exclusions from the original dataset. Finally, the n pseudovalue $r_{i\text{-pseudo}}$ were utilized to derive means and standard errors, applying the same methodology for R_0, T, r_m, and λ.

3.2.3. Degree days

Average daily temperature was calculated for the whole year from 2021 to 2024, and the accumulation of degree days was calculated using the critical lower threshold of 12.2ºC (HAYE et al. 2014). The accumulation of DD was calculated following average methods (NIELSEN & HAMILTON 2009a). From 2021 to 2024, DD accumulation was calculated using BMSB reared under natural temperature conditions in the Buda Arboretum from 1 April to key phenological stages, such as first oviposition and first adult emergence, for both overwintering and summer generations.

In 2024, degree days (DD) for each developmental stage were calculated, as nymphal instars were reared individually from 2nd instar onwards (overwintering generation, n = 2143; summer generation, n = 2057). The overwintered adults started regaining their activity from the beginning of April, and the individual female emergence date from overwintering was not recorded in the studies; thus, DD and duration of preoviposition for the overwintering generation were calculated from 1st April till the day before the first oviposition. In the summer generation, degree days (DD) and the duration of the preoviposition period were calculated for each ovipositing female from the date of adult emergence until the day preceding first oviposition. Degree-day accumulation from egg to adult for each nymphal instar was calculated from the beginning of a given developmental stage until moulting to the subsequent stage.

3.3. Studies on Egg Parasitoids of the Hungarian Population of BMSB

The surveys of parasitoids of BMSB were conducted in several parts of Hungary following two methods: assessing parasitism in naturally laid eggs in cages and collecting of wild egg masses.

3.3.1. Naturally laid eggs in cages

In 2021, the experiment on naturally laid eggs in cages was conducted from April to September. The cages used in this experiment (100 cm × 30 cm × 30 cm, with mesh size of 3 × 3 mm), following COSTI et al. (2018) (Figure 5) were tied to selected twigs of host plants, and three pairs of BMSB adults were introduced inside. The mesh size of the net was sufficiently large to permit the entry of parasitoids while preventing the escape of adult BMSB. The adults inside the cages were inspected and provided with a diet of beans, apple slices and carrot, and the foods were changed twice a week. Dead individuals were replaced with new adults as needed. This arrangement facilitated mating and egg-laying, allowing the eggs to be exposed to natural parasitism until they were ready to hatch. All egg masses were then collected and placed into separate petri dishes (15 × 100 mm) in the laboratory. Emerging BMSB nymphs were removed, and the remaining unhatched eggs were incubated under room condition to monitor parasitoid emergence. The cages were set up in 30 locations within the Buda Arboretum, Hungarian University of Agriculture and Life Sciences, Budapest (47.4822° N, 19.0402° E) focusing on the selected host plant species (*Syringa x hyacinthiflora* Lemoine*, Crataegomespilus dardaii* Simon-Louis*, Crataegus pinnatifida* Bunge*, Forsythia x intermedia* Zabel 'Spring glory', *Acer campestre* Linnaeus 'Zenta', *Ac. campestre* 'Red shine', *Carpinus betulus* Lindman 'Purpurea', *Fraxinus pennsylvanica* Marshall*, Malus* 'Eleyi', *Malus* 'Winter Gold', *Tilia tomentosa* Mill 'Wagner Janos', *Morus nigra* Linnaeus 'Nana', *Malus* 'Aldemahensis', *Prunus cerasifera* Ehrh*, Prunus serrulate* Lindley var. *hupehensis*, *Ac. platanoides* Linnaeus*, Ac. pseudoplatanus* Linnaeus and *Sorbus aria* Linnaeus 'Lutescens'). In 2022 the experiment was conducted in an apple orchard at the Hungarian University of Agriculture and Life Sciences Research and Experimental Farm in Budapest (Soroksár) (47.3966 °N, 19.1418 °E) from May to September. No insecticide treatments were applied in the orchard during the study year.

Figure 5. *Halyomorpha halys* eggs parasitoid studies conducted using field cages (100 × 30 × 30 cm; mesh size 3 × 3 mm) tied to twigs of a maple tree inside the Buda Arboretum. (Photo: Johnson Wahengbam, 2021)

3.3.2. Wild egg masses

During 2021 to 2022, a comprehensive search for wild egg masses of BMSB was conducted from June to September across various locations in Hungary (Table 8), along with a one-time collection in a few cities in Southeast Europe including Novi Sad (Serbia), Sofia (Bulgaria), and Oradea (Romania) (Figure 6). The survey was done with visual inspections of plants selected ad hoc, focusing on species frequently visited by BMSB such as *Ailanthus altissima* Miller (Simaroubaceae)*,* Sapindaceae- *Ac. negundo* Linnaeus*, Ac. pseudoplatanus* Linnaeus*, Ac.*

campestre Linnaeus, *Fraxinus pennsylvanica* Marshall (Oleaceae), *Populus alba* Linnaeus (Salicaceae), and *Celtis occidentalis* Linnaeus (Cannabaceae), among others. Details of the host plants on which BMSB egg masses and parasitized BMSB egg masses were found in Hungary during 2021 and 2022 are presented in Table 7.

Table 7. Host plants where *Halyomorpha halys* egg masses were collected with parasitized egg masses in Hungary in 2021 and 2022

Host plant	**Egg masses collected**	**Parasitized egg masses**
Ailanthus altissima	45	11
Acer pseudoplatanus	13	1
Fraxinus ornus	13	3
Populus alba	6	2
Celtis sp.	1	0
Acer negundo	10	4
Acer campestre	3	1
Allium porrum	1	1

In 2021, surveys were carried out in Budapest and Érd, and in 2022: Budapest, Tarcal and Szeged. The habitat types where wild egg masses were collected were categorised as urban sidewalk, urban park, and agricultural area. In Budapest, egg masses were collected from both urban area and agricultural areas, categorised as Budapest and Budapest (Soroksár) respectively. Further details on the collection sites are provided in Table 8.

Table 8. *Halyomorpha halys* wild egg masses collections coordinates in Hungary in 2020, 2021 and 2022

Location	Year	Coordinates
Érd	2021	47.3565ºN, 18.9206ºE
Budapest	2021 2022	47.4775ºN, 19.059944ºE; 47.465639ºN, 19.076444ºE; 47.398528ºN, 19.1495ºE; 47.478028ºN, 19.041472ºE; 47.481667ºN, 19.063889ºE; 47.4805ºN, 19.0369ºE; 47.426278ºN, 19.081389ºE
Szeged	2022	46.265917ºN, 20.110833ºE; 46.26175ºN, 20.108083ºE; 46.267083ºN, 20.108278ºE
Tarcal	2022	48.1286ºN, 21.3477ºE

The collected egg masses were individually placed in Petri dishes and kept under room conditions (~23°C) to monitor for the emergence of BMSB nymphs or adult parasitoids at the laboratories of the Department of Entomology, Hungarian University of Agriculture and Life Sciences. From each egg mass, the number of hatched nymphs, emerged parasitoids, and unhatched eggs was recorded. Identification of BMSB wild egg masses and 1st instar nymphs (if emerged) was carried out in accordance with the criteria described by KOBAYASHI (1967) and HOEBEKE & CARTER (2003).

3.3.3. Parasitoid identification

Once emerged, parasitoids were transferred into 1.5 mL microcentrifuge tubes (Eppendorf SE, Germany) containing ethanol (90% vol.) to ensure proper preservation prior to identification. Morphological identification was performed by Dr. Francesco Tortorici, Department of Agricultural, Forest and Food Sciences, University of Torino, Italy, relying on a set of taxonomic keys. For Eupelmidae, reference was made to ASKEW & NIEVES-ALDREY (2004) and PENG et al. (2020). Specimens of the genus *Trissolcus* Ashmead were identified using available identification keys and diagnostic characters and illustrations available in TALAMAS et al. (2017), TORTORICI et al. (2019), and MORAGLIO et al. (2021). For the genus *Telenomus* Haliday (Hymenoptera: Scelionidae), TORTORICI et al. (2024) was used. All specimens examined for morphological analysis have been deposited as vouchers in the entomological collections of the Department of Agricultural, Forest and Food Sciences (DISAFA), University of Torino (Italy).

3.3.4. Evaluation of parasitoid efficiency

The assessment of parasitoid efficiency was conducted following the methodology outlined by BIN & VINSON (1991) and ROT et al. (2021). The impact of the parasitoid, represented by the parasitism rate, was assessed for each location and year by calculating the number of parasitized eggs in relation to the total number of eggs collected from the field.

3.4. Statistical tools and analysis

Two sample Z test was used to compare the overwintering mortality between the wild-collected adults and experimentally reared adults and between male and female. Marascuilo's procedure was applied to test significant differences in overall mortality of overwintering adults among the study years.

Mortality of different developmental stages was compared among three study sites during 2021–2023. Marascuillo's procedure was applied to identify significant differences within and between study sites across BMSB developmental stages.

Comparison of the ratios of laid and hatched eggs throughout the experimental period were analyzed. For each subinterval of the experimental period, the ratios of laid and hatched eggs were calculated relative to the total numbers of laid and hatched eggs recorded in the experiment. These ratios were compared using pairwise binomial tests with Holm's correction. The binomial test is an exact test, i.e., it does not rely on large-sample normal approximations and specifically handles the conditional probability arising from the dependency of the subintervals within the total experimental period. Moreover, Holm's correction strictly controls the familywise error rate (FWER).

Comparison of the ratios of successful development (egg-to-adult) throughout the experimental period was calculated. The number of adults originating from the eggs laid at each subinterval relative to the number of eggs laid at that time subinterval. The ratios were then compared pairwise by using Fisher's exact test, which is not sensitive to low count data (e.g., zero) and does not rely on any distributional assumptions.

All statistical analyses were performed using the R software environment (v 4.5.1, R Core Team, 2025), utilizing the '*multicompView*' (GRAVES et al. 2024) package.

4.0. RESULTS

4.1. Overwintering survival

Based on the collection and overwintering of adult BMSB under natural temperature conditions described in the Materials and Methods, overwintering mortality of wild BMSB adults in the years 2021, 2022, and 2023 were recorded at 64.53%, 71.78% and 59.11% respectively. The mortality rates of overwintering adults in the experimental rearing of 2021, 2022, 2023, and 2024 were found to be 63.42%, 54.78%, 53.78% and 36.66% respectively. The mean temperatures during the overwintering period (mid-October to the end of March) were 6.08 °C in 2021, 8.52 °C in 2022, 8.9 °C in 2023 and 5.95°C in 2024 (mid-Oct to 20th Feb). The mortality rates of overwintering males and females were detailed in Table 9. Overwintering mortality was compared between wild-collected and experimentally reared adults and between sexes using a two-sample Z-test. Among wild-collected adults, overwintering mortality did not differ significantly between males and females in most years; however, in 2021, females exhibited significantly higher mortality than males. In experimentally reared adults, no significant sex-based differences in overwintering mortality were observed in 2021 and 2022; however, females exhibited higher mortality than males in 2023, whereas males showed higher mortality than females in 2024. Comparison of mortality rates among different years (2021-2023) between wild and experimentally reared adults showed that experimentally reared adults had significantly lower mortality rates than wild adults ($p < 0.05$) (Table 9). Marascuillo's multiple comparison procedure was used to test for differences in overwinter mortality proportions among years ($\alpha = 0.05$) for both wild and experimentally reared adults. The overall chi-square tests were significant, indicating heterogeneity in yearly mortality for both groups: the experimentally reared population ($\chi^2 > 7.81$, df = 3, $p < 0.05$) and the wild-collected population ($\chi^2 > 5.99$, df = 2, $p < 0.05$). Among wild adults, mortality rates in 2023 were significantly lower than those observed in 2022, but no significant difference with 2021. For experimentally reared adults, mortality rates in 2024 and 2023 were significantly lower than those in 2021 and 2022 (Table 9).

Table 9. Mortality rates of overwintering male and female *Halyomorpha halys* collected from the wild in Budapest and Szentendre (2021-2023) and experimentally reared adults (2021–2024) in the Buda Arboretum

Wild Adults collections							
	Overwintering population		Alive after overwintering		Mortality rate		Overall Mortality rate
Year	Male	Female	Male	Female	Male	Female	
2021	739	665	310	188	58.05a	71.73b	64.53Aa
2022	1449	1127	426	301	70.6a	73.29a	71.78Ab
2023	418	367	174	147	58.37a	59.95a	59.11Aac
					62.34±5.84(SD)	68.32 ±5.96(SD)	65.14±5.19(SD)
Experimental reared adult							
2021	120	96	41	38	65.83a	60.42a	63.42Bc
2022	176	175	67	81	61.93a	48.33a	57.83Bd
2023	223	198	143	86	65,08a	43.48b	45.61Bd
2024	184	187	107	128	41.85a	31.55b	36.66d
					56.54±12.87(SD)	45.95±11.95(SD)	50.88±11.2(SD)

(In the male and female mortality rate columns, different lowercase letters indicate significant differences between male and female mortality within the same year, as determined by a two-sample Z-test (α = 0.05). In the overall mortality column, different uppercase letters indicate significant differences between wild-collected and experimentally reared adults, based on a two-sample Z-test (α = 0.05), whereas different lowercase letters indicate significant differences among years within wild and experimental populations, as assessed using Marascuilo's multiple comparison procedure (α = 0.05).

4.2. Phenology

Overwintered adult BMSB originating from the overwintering cohorts described above became active in early April. In 2021, only a single generation was recorded, whereas from 2022 to 2024, two generations per year were observed. Oviposition by the overwintering population began on 18th June in 2021 and 11th June in 2023, at daily mean temperatures (DMS) of 23.15 ºC and 20.83 ºC, respectively. In 2022 and 2024, oviposition occurred earlier, starting on 30th May and 24th May, with DMS of 15.6 ºC and 18.92 ºC (Table 10). Peak oviposition occurred mostly in June, when DMS ranged between 20–25 ºC. In overwintering generation of 2021 to 2024, the periods during which the highest number of eggs were recorded: 28th to 3rd July in 2021 (Table 11), 11 to 13th June in 2022 (Table 12), 1st to 4th July in 2023 (Table 14), and 17th to 19th June in 2024 (Table 16). Details on oviposition in relation to temperature for the period 2021–2024 are provided in Appendices (A: 2). Adult emergence from the overwintering generation started from mid-July to the first week of September in 2022–2024, while in 2021, emergence was recorded from 13th August to 23rd September. The highest successful development from eggs to adults corresponded to oviposition periods occurred at 24th to 27th June in 2021 (Table 11), 2nd to 4th June in 2022 (Table 12), 11th to 13th June in 2023 (Table 14), and 24th May to 13th June in 2024 (Table 16). The summer generation-initiated oviposition on 4th August in 2022, 8th August in 2023 and 23rd July in 2024. Peak oviposition occurred approximately one week later and continued until the third week of August, when DMS ranged between 20–25 ºC. For summer generation, the periods where the highest numbers of eggs were recorded in 2022 during 23rd to 25th August (Table 13), in 2023, 13 to 15th August (Table 15) and in 2024, 7th to 9th Aug and 19th to 21st Aug (Table 17). The highest successful development from eggs to adults in the summer generation corresponding to oviposition dates was recorded on 13th to 15th August in 2022 (Table 14) and 7th to 21st August in 2023 (Table 14), and 29th July to 12th Aug in 2024 (Table 17).

Oviposition continued until 9th September in 2022 and 2024, although eggs laid after 2nd September did not hatch. In 2023, egg-laying ended on 29th August. Summer generation larvae hatched from mid-August, except in 2024 where hatching began on 2nd August. Larval periods of the overwintering generation generally spanned June to September, except in 2022 (until 29th August). Late overwintering larvae overlapped with early summer larvae (Table 10). Nymphs from eggs laid after 25th August (2022–2023) and 30th August (2024) failed to reach adulthood. Adult emergence from the summer generation occurred from the third week of September to mid-October in 2022 and 2023, and from the first week of September to the first week of November in 2024. In 2023, several 3rds–5th instar nymphs of the summer generation became inactive with the onset of autumn and died by early November. In 2024, 246 nymphal instars entered inactivity; 94 died by mid-December, and the remaining 152 overwintered but ultimately did not survive.

Table 10. Seasonal occurrence and daily mean temperature of *Halyomorpha halys* in Hungary during 2021, 2022,2023 and 2024

Year	**Generation**	**Eggs laying period**	**Average Daily Mean Temp.**	**Hatching period**	**Average Daily Mean Temp.**	**Larval period**	**Average Daily Mean Temp.**	**Adult emergence**	**Average Daily Mean Temp.**
2021	overwintering	18th June-23rd July	24.28 ºC	25th June-2nd Aug	24.13 ºC	25th June- 23rd Sep	21.73 ºC	13th Aug-23rd Sep	19.27 ºC
2022	overwintering	30th May-6th July	22.72 ºC	10th June-13th July	23.14 ºC	10th June-29th Aug	23.81 ºC	21st July-29th Aug	24.35 ºC
2022	summer	4th Aug-9th Sep	22.83 ºC	15th Aug-5th Sep	22.54 ºC	15th Aug- 18th Oct	17.43 ºC	25th Sept-18th Oct	13.75 ºC
2023	overwintering	11th June-18th July	22.86 ºC	20th Jun-25th July	23.88 ºC	20th June-8th Sep	22.65 ºC	21st July-8th Sept	21.82 ºC
2023	summer	8th Aug-28th Aug	22.89 ºC	15th Aug-5th Sep	23.01 ºC	15th Aug – 4th Nov	18.30 ºC	28th Sep-17th Oct	15.05 ºC
2024	overwintering	24th May-16th July	23.11 ºC	2nd June-18th Jul	23.11 ºC	2nd June- 18th Sep	23.79 ºC	14th July-8th Sep.	25.47 ºC
2024	summer	23rd July-9th Sep	21.41 ºC	2nd Aug-5th Sep	20.81 ºC	2nd Aug-Overwintering	14.68 ºC	8th Sep-4th Nov	14.12 ºC

[Overwintering- Some populations of larvae in 2024 summer generations undergoes diapause]

Table 11. Fertility and mortality data of overwintering generation of *Halyomorpha halys* in 2021 under outdoor conditions in Budapest, Hungary

Oviposition date	**Eggs laid (ex)**	**Proportion (%) (ex X 100/E)**	Eggs Hatched	**% mortality at different stages**						**Total mortality**	**% Successful development (egg –adult)**
				eggs	N1	N2	N3	N4	N5		
18th -21st Jun	16	1.5a	15b	6.3	40.0	77.8	100.0			100.0	0.0abc
22nd -24th Jun	52	4.9b	42cd	19.2	50.0	14.3	16.7	0.0	20.0	76.9	23.1bcd
25th -27th Jun	111	10.4c	85ef	23.4	23.5	18.5	7.6	6.1	0.0	58.6	**41.4de**
28th -30th Jun	**400**	**37.6e**	265g	33.8	35.9	18.2	25.9	5.8	6.2	77.3	22.8c
1st -3rd Jul	225	**21.2d**	**114f**	49.3	56.1	38.0	22.6	8.3	0.0	90.2	9.8ab
4th - 6th Jul	131	12.3c	66de	49.6	86.4	55.6	0.0	0.0	25.0	97.7	2.3a
7th - 9th Jul	54	5.1b	50cd	7.4	18.0	12.2	11.1	0.0	0.0	40.7	59.3e
10th- 12th Jul	15	1.4a	13b	13.3	100.0					100.0	0.0 abc
13th Jul	29	2.7ab	29bc	0.0	34.5	31.6	23.1	0.0	0.0	65.5	34.5cde
23rd Jul	30	2.8ab	0a	100.0						100.0	0.0 ab
Total	1063		679								

(No oviposition occurred from 14th July to 22nd July) (Bold letter indicates highest value within each column. The different letters represent significantly different ratios of laid and hatched eggs (pairwise binomial test with Holm's correction, $p<0.05$) as well as that of successful development (egg-to-adult) throughout the experimental period (Fisher's exact test with Holm's correction, $p<0.05$). The ratios with the highest values are indicated in bold font in each column)

Table 12. Fertility and mortality data of overwintering generation of *Halyomorpha halys* in 2022 under outdoor conditions in Budapest, Hungary

Oviposition date	**Eggs laid (ex)**	**Proportion (%) (ex X 100/E)**	**Eggs hatched**	**% mortality at different stages**						**Total mortality**	**% Successful development (egg –adult)**
				eggs	N1	N2	N3	N4	N5		
30th May-1st Jun	20	1.4a	6ab	70.0	50.0	66.7	0.0	0.0	0.0	95.0	5.0abc
2nd -4th Jun	28	1.9ab	28cd8	0.0	17.9	8.7	0.0	4.8	0.0	28.6	**71.4d**
5th -7th Jun	31	2.2ab	29cd	6.5	27.6	38.1	30.8	0.0	0.0	71.0	29.0bcd
8th -10th Jun	144	10.0d	89fg	38.2	55.1	45.0	22.7	11.8	20.0	91.7	8.3ab
11th -13th Jun	410	**28.6f**	**318i**	22.4	35.9	24.0	23.2	5.0	6.2	74.2	25.9c
14th -16th Jun	221	15.4e	107g	51.6	23.4	19.5	3.0	9.4	5.2	75.1	24.9c
17th -20th Jun	89	6.2c	42de	52.8	26.2	80.7	33.3	0.0	0.0	95.5	4.5a
21st -23rd Jun	268	18.7e	163h	39.2	38.7	20.0	21.3	3.2	4.9	78.4	21.6c
24th -26th Jun	125	8.7cd	64ef	48.8	37.5	32.5	14.8	4.4	0.0	82.4	17.6abc
28th -30th Jun	45	3.1b	0a	100.0						100.0	0.0a
1st -4th Jul	18	1.3a	0a	100.0						100.0	0.0abc
5th -6th Jul	36	2.5ab	11bc	69.4	27.3	12.5	14.3	0.0	0.0	83.3	16.7abc
Total	1435		857								

(Bold letter indicates highest value within each column. The different letters represent significantly different ratios of laid and hatched eggs (pairwise binomial test with Holm's correction, *p*<0.05) as well as that of successful development (egg-to-adult) throughout the experimental period (Fisher's exact test with Holm's correction, *p*<0.05). The ratios with the highest values are indicated in bold font in each column)

Table 13. Fertility and mortality data of summer generation of *Halyomorpha halys* in 2022 under outdoor conditions in Budapest, Hungary

Oviposition date	**Eggs laid (ex)**	**Proportion (%) (ex X 100/E)**	**Eggs hatched**	**% mortality at different stages**						**Total mortality**	**% Successful development (egg – adult)**
				Egg	N1	N2	N3	N4	N5		
4th-6th Aug	33	2.1a	0a	100.0						100.0	0.0ab
7th -9th Aug	77	4.8bc	55bc	28.6	50.9	48.2	21.4	0.0	18.2	88.3	11.7b
10th -12th Aug	169	10.6e	78c	53.9	35.9	30.0	14.3	10.0	7.4	85.2	14.8b
13th -15th Aug	146	9.2de	128d	12.3	24.2	28.9	20.3	1.8	3.7	64.4	**35.6c**
16th -18th Aug	169	10.6e	59bc	65.1	37.3	37.8	30.4	6.3	0.0	91.1	8.9b
19th -22nd Aug	60	3.8ab	58bc	3.3	63.8	23.8	18.8	7.7	0.0	80.0	20.0bc
23rd -25th Aug	385	**24.2f**	**289e**	24.9	73.0	57.7	78.8	28.6	60.0	99.5	0.5a
26th -29th Aug	115	7.2cd	45bc	60.9	57.8	79.0	100.0			100.0	0.0a
30th Aug-1st Sep	156	9.8de	38b	75.6	94.7	100.0				100.0	0.0a
2nd-5th Sep	168	10.6e	0a	100.0						100.0	0.0a
6th -9th Sep	113	7.1cd	0a	100.0						100.0	0.0a
Total	1591		750								

(Bold letter indicates highest value within each column. The different letters represent significantly different ratios of laid and hatched eggs (pairwise binomial test with Holm's correction, $p<0.05$) as well as that of successful development (egg-to-adult) throughout the experimental period (Fisher's exact test with Holm's correction, $p<0.05$). The ratios with the highest values are indicated in bold font in each column)

Table 14. Fertility and mortality data of overwintering generation of *Halyomorpha halys* in 2023 under outdoor conditions in Budapest, Hungary

Egg observed date	**Eggs laid (ex)**	**Proportion (%) (ex X 100/E)**	**Eggs hatched**	**% mortality at different stages**						**Total mortality**	**% Successful development (egg –adult)**
				eggs	N1	N2	N3	N4	N5		
11th -13th Jun	41	2.8a	41ab	0.0	2.4	0.0	17.5	0.0	0.0	19.5	**80.5d**
14th -16th Jun	82	5.6bcd	44ab	46.3	43.2	8.0	26.1	0.0	11.8	81.7	18.3ab
17th – 20th Jun	121	8.2de	70bc	42.2	50.0	11.4	6.5	3.5	0.0	76.9	23.1bc
21st -23rd Jun	181	12.3f	137d	24.3	53.3	12.5	5.4	5.7	4.0	73.5	26.5bc
24th -27th Jun	49	3.3ab	34a	30.6	47.1	0.0	11.1	0.0	37.5	79.6	20.4abc
28th -30th Jun	109	7.4cde	58ab	46.8	67.2	5.3	27.8	15.4	27.3	92.7	7.3a
1st -4th Jul	311	**21.2g**	**213e**	31.5	38.0	4.6	10.3	14.2	7.2	71.1	28.9bc
5th -7th Jul	144	9.8ef	107cd	25.7	29.9	8.0	13.0	1.7	0.0	59.0	40.9c
8th -11-Jul	187	12.7f	140d	25.1	26.4	21.4	19.8	3.1	1.6	66.8	33.2bc
12th – 14th Jul	174	11.8f	130d	25.3	30.0	19.8	16.4	4.9	8.6	69.5	30.5bc
15th – 18th Jul	70	4.8abc	36a	48.6	83.3	0.0	50.0	0.0	33.3	97.1	2.9a
Total	1469		1010								

(Bold letter indicates highest value within each column. The different letters represent significantly different ratios of laid and hatched eggs (pairwise binomial test with Holm's correction, *p*<0.05) as well as that of successful development (egg-to-adult) throughout the experimental period (Fisher's exact test with Holm's correction, *p*<0.05). The ratios with the highest values are indicated in bold font in each column)

Table 15. Fertility and mortality data of summer generation of *Halyomorpha halys* in 2023 under outdoor conditions in Budapest, Hungary

Egg observed date	**Eggs laid (ex)**	**Proportion (%) (ex X 100/E)**	**Eggs hatched**	**% mortality at different stages**						**Total mortality**	**% Successful development (egg – adult)**
				Eggs	N1	N2	N3	N4	N5		
7th – 9th Aug	79	12.01a	73de	7.6	39.7	27.3	0.0	0.0	0.0	59.5	**40.5b**
10th- 12th Aug	81	12.31a	68cd	16.1	32.4	34.8	40.0	0.0	5.6	79.0	**20.9b**
13th – 15th Aug	167	**25.38b**	**110e**	34.1	30.0	26.0	8.8	1.9	3.9	70.7	**29.3b**
16th – 18th Aug	58	8.81a	26ab	55.2	23.1	10.0	5.6	0.0	11.8	74.1	**25.9b**
19th – 21st Aug	81	12.31a	41bc	49.4	34.2	25.9	0.0	5.0	0.0	76.5	**23.5b**
22nd- 24th Aug	143	**21.73b**	**75de**	47.6	65.3	30.8	22.2	100.0			0.0a
25th – 28th Aug	49	7.45a	13a	73.5	69.2	100.0					0.00a
Total	658		406								

(Bold letter indicates highest value within each column. The different letters represent significantly different ratios of laid and hatched eggs (pairwise binomial test with Holm's correction, *p*<0.05) as well as that of successful development (egg-to-adult) throughout the experimental period (Fisher's exact test with Holm's correction, *p*<0.05). The ratios with the highest values are indicated in bold font in each column)

Table 16. Fertility and mortality data of overwintering generation of *Halyomorpha halys* in 2024 under outdoor conditions in Budapest, Hungary

Oviposition date	**Nos. of eggs laid**	**Eggs followed (ex)**	**Proportion (%) (ex X 100/E)**	**Eggs hatched**	**% mortality at different stages**						**Total mortality**	**% Successful development (egg – adult)**
					Eggs	N1	N2	N3	N4	N5		
24th-26th May	130	130	2.4c	116cd	10.8	22.4	12.2	13.9	10.3	24.6	64.6	**35.4i**
27th -29th May	218	218	4.0d	159de	27.1	7.6	17.7	20.7	13.5	16.9	68.4	**31.7hi**
30th May-1st June	359	359	6.6e	278gh	22.6	9.7	23.9	20.4	13.8	26.7	73.3	**26.7hi**
2nd-4th June	404	348	7.4ef	257fg	26.2	26.1	20.0	19.7	13.9	21.9	76.4	**23.6fghi**
5th-7th June	363	361	6.7e	275gh	23.8	30.2	19.3	21.9	14.1	21.2	77.3	**22.1ghi**
8th -10th June	471	497	8.6f	346h	30.4	28.3	31.1	15.2	24.8	15.6	81.5	18.1efgh
11th -13th June	353	388	6.5e	294gh	16.7	20.4	27.8	14.2	13.8	18.4	71.1	**28.0hi**
14th -16th June	255	263	4.7d	185e	26.6	29.7	47.7	23.5	17.3	23.3	84.4	12.9defg
17th -19th June	824	756	**15.1e**	**500i**	33.9	35.8	34.9	22.0	14.7	25.2	86.2	13.8def
20th -22nd June	372	291	6.8e	199ef	31.6	43.2	30.1	20.3	14.3	27.8	86.6	13.4cd
23rd -25th June	637	410	11.7g	274gh	33.2	61.0	29.0	40.8	35.6	44.8	96.1	3.9ab
26th -28th June	232	149	4.3d	97c	34.9	67.0	31.3	18.2	11.1	18.8	91.3	8.7abcd
29th June-1st July	416	153	7.6ef	92c	39.9	29.4	55.4	37.9	5.6	58.8	95.4	4.6a
2nd -4th July	72	43	1.3ab	18b	58.1	55.6	87.5	0.0	100.0		100.0	0.0abc
5th -7th July	81	81	1.4b	736b	91.4	100.0					100.0	0.0defghi
8th -10th July	154	154	2.8c	39b	74.7	33.3	19.2	0.0	0.0	4.8	87.0	13.0bcde
11th -13th July	40	40	0.73a	0a	100.0						100.0	0.00abcd
14th-16th July	78	78	1.43b	28b	64.1	28.6	15.0	23.5	0.0	7.7	84.6	15.38abcdefg
Total	5459	4719		3893								

(Bold letter indicates highest value within each column. The different letters represent significantly different ratios of laid and hatched eggs (pairwise binomial test with Holm's correction, $p<0.05$) as well as that of successful development (egg-to-adult) throughout the experimental period (Fisher's exact test with Holm's correction, $p<0.05$). The ratios with the highest values are indicated in bold font in each column)

Table 17. Fertility and mortality data of summer generation of *Halyomorpha halys* in 2024 under outdoor conditions in Budapest, Hungary

Oviposition date	**Nos. of eggs laid**	**Eggs followed (ex)**	**Proportion (%) (ex X 100/E)**	**Eggs hatched**	**% mortality at different stages**						**Total mortality**	**% Successful development (egg –adult)**
					Eggs	N1	N2	N3	N4	N5		
23rd-25th July	9	9	0.17a	0a	100.0						100.0	0.0abc
26th-28th July	50	50	0.95b	25bc	50.0	20.0	25.0	6.7	35.7	55.6	92.0	8.0abc
29th-31st July	640	620	12.17f	**427g**	31.1	24.6	23.9	19.2	26.8	41.4	86.3	**13.7c**
1st-3rd Aug	500	445	9.51e	328f	26.3	31.1	24.8	40.0	14.7	36.8	87.6	**12.4c**
4th-6th Aug	536	543	10.20e	**439g**	19.2	34.6	15.7	32.6	29.5	44.4	88.2	**11.8c**
7th-9th Aug	819	710	**15.58g**	**477g**	32.8	34.6	18.9	23.7	24.9	47.6	89.3	**10.7bc**
10th-12th Aug	595	599	11.32ef	**428g**	28.6	35.5	25.7	33.2	19.7	57.3	92.2	**7.9bc**
13th-15th Aug	584	468	11.11ef	331f	29.3	31.7	34.5	38.5	22.0	60.6	94.0	5.9ab
16th-18th Aug	230	230	4.38d	163e	29.1	35.6	37.1	27.3	31.3	90.9	98.7	1.3a
19th-21st Aug	773	406	**14.70g**	283f	30.3	32.9	41.6	50.5	41.8	93.8	99.5	0.5a
22nd-24th Aug	133	123	2.53c	64d	48.0	26.6	61.7	44.4	100.0		100.0	0.0a
25th-27th Aug	169	169	3.21c	0a	100.0						100.0	0.0a
28th-30th Aug	137	109	2.61c	44cd	59.6	20.5	22.9	29.6	47.4	30.0	93.6	6.4abc
31stAug-2nd Sep	54	46	1.03b	18b	60.9	38.9	72.7	100.0			100.0	0.0abc
9th Sep	28	28	0.53b	0a	100.0						100.0	0.0abc
Total	5257	4555		3027								

(No oviposition from 3rd Sep to 8th Sep) (Bold letter indicates highest value within each column. The different letters represent significantly different ratios of laid and hatched eggs (pairwise binomial test with Holm's correction, *p*<0.05) as well as that of successful development (egg-to-adult) throughout the experimental period (Fisher's exact test with Holm's correction, *p*<0.05). The ratios with the highest values are indicated in bold font in each column)

4.2.1. Degree days (DD) and development time

Degree days (DD) and development times were calculated for all developmental stages of BMSB reared in 2024 at the Buda Arboretum under natural temperature conditions. The average egg-to-adult development time was 48.74 ± 0.25 (SE) days for the overwintering generation and 67.57 ± 0.56 (SE) days for the summer generation. In the overwintering generation, the longest and shortest egg-to-adult durations were 81 and 34 days, respectively, while in the summer generation, they were 92 and 41 days. The average preoviposition period was 65.54 ± 0.99 (SE) days in the overwintering generation (Calculations began on 1st April, when overwintered BMSB adults resumed activity, since the exact emergence date from overwintering for each individual was not recorded) and 13.98 ± 0.44 (SE) days in the summer generation. In the overwintering generation, the longest and shortest preoviposition periods were 93 and 52 days, respectively; in the summer generation, they were 24 and 7 days. Daily mean temperatures during oviposition, nymphal, and adult emergence periods are presented in Table 9. In the overwintering generation, the highest DD accumulation occurred in the 5th nymphal stage (137.66 DD). While, in the summer generation, the highest DD was in the 2nd instar (117.6 DD), followed by the 5th instar (107.56 DD). The 5th nymphal stage had the longest development time: 9.98 days in the overwintering generation and 31 days in the summer generation. During the preoviposition period, DD accumulation was 342.30 ± 8.59 (SE) DD in the overwintering generation and 185.74 ± 6.65 (SE) DD in the summer generation. Total DD for egg-to-adult development was 611.32 ± 2.76 (SE) DD for the overwintering generation and 569.16 ± 2.24 (SE) DD for the summer generation. Average DD accumulation and development times for each stage are listed in Table 18.

The accumulation of degree days (DD) from 1 April to first oviposition, first hatching, and first adult emergence of BMSB individuals was evaluated for both generations reared under natural temperatures at the Buda Arboretum during 2021–2024. In the overwintering generation, first oviposition occurred between 214.77 - 254.86 DD, first hatching between 309.50 - 325.64 DD, and first adult emergence between 689.27 - 878.87 DD. In the summer generation (2022–2024), first oviposition occurred between 850.70 - 958.33 DD, first hatching between 909.60 - 1089.67 DD, and first adult emergence between 1317.55 - 1532.95 DD.

Table 18. Development time and degree days (DD) of different stages of *Halyomorpha halys* in Budapest, Hungary under outdoor conditions in 2024

Stage	**Overwintering Populations**		**Summer populations**	
	Development time (Days) (mean±SE)	Degree days (mean±SE)	Development time (Days) (mean±SE)	Degree days (mean±SE)
Preoviposition	65.54±0.99 (N= 77)	342.30±8.59 (N= 77)	13.98±0.44 (N= 63)	185.74±6.65 (N=63)
Eggs	8.43±0.05	88.05±0.59	5.95±0.03	87.67±0.79
N1	6.72±0.05	75.25±0.84	5.5±0.03	77.37±0.95
N2	8.92±0.06	109.69±0.97	9.12±0.07	117.60±1.25
N3	7.14±0.07	92.85±1.14	8.47±0.14	88.97±1.27
N4	7.91±3.60	107.86±1.34	12.82±0.27	89.98±1.32
N5	9.98±0.14	137.66±1.76	31.13±0.46	107.56±1.58
Eggs-adult	48.74±0.25 (N= 784)	611.32±2.76 (N= 784)	67.57±0.56 (N= 371)	569.16±2.24 (N= 371)

[N= sample size]

4.2.2. Life table analysis

From 2021 to 2024, hatching rates in the overwintering generation were 63.88%, 59.72%, 68.75%, and 60.43%, respectively, while in the summer generation they were 47.14% (2022), 61.70% (2023), and 66.88% (2024). In the overwintering generation of 2021 to 2023, early instars recorded up to 40% (1^{st}–3^{rd}), and up to 10% in later instars (4^{th}–5^{th}) (Table 21). In 2024, however, 5th instar mortality (14%) exceeded that of the 4th (9.62%) and 3rd instars (12.93%) (Table 19). In the summer generation, mortality followed a similar pattern, with higher in the 1st–3rd instars (up to 25%) and lower in later instars, except in 2024 where the 5th instar mortality (24%) was the highest among all stages (Table 20). The total percent mortality rate of the overwintering generation of 2021, 2022, 2023, and 2024 (Table 19) was 91.63%, 79.58%, 72.22% and 82.67% respectively, and in the summer generation of 2022, 2023, and 2024 (Table 20) was 96.73%, 90.04% and 94.50% respectively. Reproductive parameters in 2024 showed that the average number of eggs laid per female was 70.9 in the overwintering generation and 90.64 in the summer generation. A single female produced a maximum of 7 egg masses in overwintering generation and 9 egg masses in summer generations. The net reproductive rate of increase (R_o) was 5.39 for the overwintering generation and 2.21 for the summer generation (Tables 19 & 20).

Table 19. Age-specific life table for the overwintering generation of *Halyomorpha halys* studied under outdoor temperature in Budapest, Hungary 2024

Stage	**lx (Alive)**	**dx (Dead)**	**Apparent mortality qx=dx/lx**	**Real mortality rx=dx/lo**	**K value (-log(1-qx))**	**% generation mortality (100 kx/Ks)**
Egg	4719	1533	0.32	0.32	0.17	22.42
N1	3186	1003	0.31	0.54	0.16	21.57
N2	2183	615	0.28	0.67	0.14	18.88
N3	1568	318	0.20	0.74	0.10	12.93
N4	1250	194	0.16	0.78	0.07	9.62
N5	1056	238	0.23	0.83	0.11	14.57
New generation adults	818					
Total mortality%	82.67					
sex ratio	0.5				Ks=0.76	
realized fecundity	70.9					
realized progeny	29423.5					
Ro	5.39					
adult female	415					

(% generational mortality represents the stage-specific proportion of individuals that die during a given life stage, k-value (Kx) quantifies the contribution of each life stage to total generational mortality, Ks is the sum of Kx and realized progeny is the multiplication of number of female and fecundity)

Table 20. Age-specific life table for the summer generation of *Halyomorpha halys* studied under outdoor temperatures in Budapest, Hungary 2024

stage	**lx (Alive)**	**dx (Dead)**	**Aparent mortality Qx=dx/lx**	**Real mortality rx=dx/lo**	**K value (-log(1-qx))**	**% generation mortality (100 kx/Ks)**
Egg	4274	1154	0.27	0.27	0.14	10.85
N1	3120	1063	0.34	0.25	0.18	14.36
N2	2057	554	0.27	0.13	0.14	10.82
N3	1503	473	0.31	0.11	0.16	13.03
N4	1030	273	0.27	0.06	0.13	10.61
N5	757	386	0.51	0.09	0.31	24.58
Diapause adult	371	136	0.37	0.03	0.20	15.74
Overwintered adults	235					
Total mortality%	94.50					
sex ratio	0.5				Ks= 1.26	
realized fecundity	90.64					
realized progeny	11601.92					
Ro	2.21					
adult female	128					

(% generational mortality represents the stage-specific proportion of individuals that die during a given life stage, k-value (Kx) quantifies the contribution of each life stage to total generational mortality, Ks is the sum of Kx and realized progeny is the multiplication of number of female and fecundity)

Table 21. Percent generational mortality and total mortality percent of different stages of *Halyomorpha halys* in Budapest, Hungary during 2021, 2022 and 2023

Stage	% generational mortality (100*kx/Ks)					
	2021		2022		2023	
	Overwintering generation	Summer generation	Overwintering generation	Summer generation	Overwintering generation	Summer generation
eggs	18.38	-	31.14	21.92	29.24	20.36
N1	22.71	-	29.00	23.84	39.62	21.47
N2	10.37	-	20.59	15.57	9.11	13.06
N3	8.86	-	12.37	11.22	12.15	5.53
N4	1.89	-	3.56	1.82	4.87	0.54
N5	1.80	-	3.35	2.20	5	6.77
Diapause adults	36.23	-	-	23.13	-	32.55
Total mortality %	91.63	-	79.58	96.73	72.22	90.04

(% generational mortality represents the stage-specific proportion of individuals that die during a given life stage. From 2021 to 2023, fecundity of individual females was not recorded; therefore, only mortality across different developmental stages is presented. Mortality for each developmental stage was calculated following the life-table approach used in Tables 19 and 20. Detailed calculations are provided in Appendices (A: 3).

4.2.3. Demographic growth parameters

In the 2024 summer generation, demographic growth parameters were calculated; the recorded mean generation time (T) was 80.444±0.636 (SE) days, net reproductive rate (R_o): 88.921±7.459 (SE), intrinsic rate of increase (r_m): 0.057±0.001 (SE), and finite rate of increase (λ): 1.058±0.001 (SE).

4.2.4. Mortality of BMSB at different stages across different studies sites during 2021 to 2023

Comparison of egg hatch rates and mortality rates of nymphal instars of BMSB at three sites (Site 1, Site 2, and Site 3) in Buda Arboretum, including within- and between-site comparisons using Marascuillo's multiple comparison procedure. No significant differences were observed among the three sites, except for egg hatch rates. However, significant differences were detected in mortality among different developmental stages within each site (Table 22).

Table 22. Comparison of egg hatch rates and nymphal stage mortality of *Halyomorpha halys* at three study sites in Buda Arboretum during 2021–2023.

Nymphal instar	**Year**	**Overwintering generation**			**Summer generation**		
		Site 1	Site 2	Site 3	Site 1	Site 2	Site 3
Hatch rate	2021	0.74B (537)	0.48A (265)	0.58A (261)			
1st		0.36Ac (400)	0.44Ac (127)	0.63Bc (122)			
2nd		0.19Ab (257)	0.20Ab (71)	0.46Bbc (56)			
3rd		0.21Ab (209)	0.12Aab (57)	0.27Ab (30)			
4th		0.06Ba (165)	0.02Aba (50)	0.00Aa (22)			
5th		0.06Ba (155)	0.02Aba (49)	0.00Aa (22)			
Hatch rate	2022	0.68B (679)	0.57A (236)	0.50A (520)	0.61C (676)	0.49B (493)	0.33A (444)
1st		0.39Ad (460)	0.36Ab (135)	0.30Ab (262)	0.60Ac (412)	0.40Bb (241)	0.60Ab (146)
2nd		0.31Acd (282)	0.15Ba (87)	0.29Ab (183)	0.42Ab (165)	0.34Ab (145)	0.41Aab (58)
3rd		0.20Abc (194)	0.12Aa (74)	0.18Ab (130)	0.41Ab (95)	0.29Abb (96)	0.18Ba (34)
4th		0.04Aa (150)	0.03Aa (65)	0.08Aab (106)	0.07Aa (56)	0.03Aa (68)	0.11Aa (28)
5th		0.07Aa (149)	0.05Aa (63)	0.03Aa (97)	0.10Aa (52)	0.08Aa (66)	0.00Aa (25)
Hatch rate	2023	0.60A (558)	0.66A (421)	0.76B (475)	0.65A (156)	0.59A (185)	0.57A (345)
1st	2023	0.36Ab (336)	0.44Ac (278)	0.39Ac (359)	0.29Aa (101)	0.42Aba (110)	0.45Ba (195)
2nd		0.07Ab (215)	0.08Aab (155)	0.14Ac (220)	0.18Aa (72)	0.27Aa (64)	0.32Aa (108)

Nymphal instar	**Year**	**Overwintering generation**			**Summer generation**		
		Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
3rd		0.14Aa (199)	0.14Ab (142)	0.14Ab (190)	0.08Aac (59)	0.09Aac (47)	0.15Aac (73)
4th		0.05Aa (171)	0.11Aab (122)	0.04Ab (163)	0.02Abc (54)	0.02Abc (43)	0.03Abc (62)
5th		0.10Aa (162)	0.03Aa (109)	0.04Aa (156)	0.06Ab (53)	0.43Bb (42)	0.03Ab (60)

[Values in parentheses indicate sample size (n)] (Different letters denote statistically significant differences according to Marascuilo's multiple comparison procedure ($p < 0.05$). Uppercase letters indicate comparisons among study sites within the same developmental stage, whereas lowercase letters indicate comparisons of mortality among developmental stages within the same site)

4.3. Parasitoid Studies

4.3.1. Naturally laid eggs in cages

In 2021, 85 egg masses were collected from 30 cages in Buda Arboretum, and no parasitism was observed. In 2022, the experiment was conducted in an apple orchard at Budapest (Soroksár), where a total of 47 egg masses were collected. Only three egg masses were parasitized, comprising 62 eggs. From these parasitized egg masses, nine parasitoids emerged, all identified as *A. bifasciatus* (Table 23). The overall parasitism rate was 0.79%, with nine parasitized eggs out of 1,141 collected. In both 2021 and 2022, egg laying began in July and continued until early September. In 2022, all parasitized egg masses were found during the first half of August, with no parasitism recorded in other months.

Table 23. Details of *Halyomorpha halys* egg masses laid in mesh cages with associated parasitoids emerged (Budapest and Soroksár)

Year	Egg masses (30 cages)	Eggs	Hatched nymphs	Unhatched eggs	Parasitized egg masses	% Hatched	% Unhatched	% Parasitized	Parasitoids	Parasitoids species
2021	85	1823	920	903	0	50.47	49.53	0	0	-
2022	47	1141	1086	46	3	95.26	4.03	0.79	9	*Anastatus bifasciatus*

4.3.2. Wild egg masses

In 2021, wild egg masses were collected from three sites in Hungary: Érd, Soroksár, and Budapest Centre (Table 7). The numbers of egg masses collected was 11 from Soroksár, 26 from Budapest Centre, and 16 from Érd. Notably, no parasitoids emerged from the samples collected in Érd. A total of 288 and 475 eggs were collected from Soroksár and Budapest Centre, respectively. In Soroksár, 13 parasitoids emerged, resulting in parasitization rate of 4.51%, while in Budapest Centre, 54 parasitoids emerged, corresponding to a parasitization rate of 11.37%.

In Soroksár, *A. bifasciatus* were recorded from one fully parasitized egg mass. In Budapest Centre, the parasitoid species identified were *A. bifasciatus* and *Ooencyrtus* sp. Co-occurrence of multiple *Ooencyrtus* sp. and *A. bifasciatus* within a single egg mass was also recorded.

In 2021, BMSB egg masses were also collected from cities in Southeast Europe: Oradea, Sofia and Novi Sad. A total of 17 egg masses were collected from Oradea, comprising 395 eggs. Out of these, 112 parasitoids emerged, resulting in parasitisation rates of 28.35%. The identified species included *A. bifasciatus, Tr. mitsukurii* and *Tr. basalis* (Wollaston). Co-occurrence between *Tr. mitsukurii* and *Tr. basalis*, as well as between *Tr. mitsukurii* and *A. bifasciatus*, within single egg masses were recorded. In Sofia, only two egg masses were collected, containing a total of 33 eggs. Of these, seven parasitoids emerged, resulting in 21.21% parasitisation and identified as *A. bifasciatus*. In Novi Sad, four egg masses were collected, with only one parasitized. Two parasitoid species emerged from this egg mass: *A. bifasciatus* and the non-native species *Tr. japonicus*.

Table 24. Details on wild egg masses of *Halyomorpha halys* collected in 2021 and 2022 along with the associated parasitoids emerged

Location	**Year**	**Habitat**	**Egg masses**	**Eggs**	**Hatched nymphs**	**Unhatched eggs**	**Parasitized egg mass**	**% Hatched**	**% Unhatched**	**% Parasitized**	**Parasitoids emerged**
Budapest (Soroksár) (HU)	2021	Orchard Agricultural field	11	288	204	71	1	70.83	24.65	4.51	13
Budapest (HU)	2021	Urban Park, sidewalk	20	475	213	219	4	44.84	46.11	11.36	54
Érd (HU)	2021	Orchard	16	383	325	58	0	84.86	15.14	0.00	0
Oradea (RO)	2021	Urban Park, sidewalk	17	395	113	170	10	28.61	43.04	28.35	112
Sofia (BU)	2021	Urban Park, sidewalk	2	33	0	33	1	0.00	78.79	21.21	7
Novi Sad (SR)	2021	Urban Park, sidewalk	4	107	28	79	1	26.17	58.88	14.95	16
Szeged (HU)	2022	Urban sidewalk	45	1076	770	306	9	71.56	21.56	6.88	74
Budapest (HU)	2022	Urban Park, sidewalk	38	859	156	703	13	18.16	69.38	12.46	107
Tarcal (HU)	2022	Urban sidewalk	1	26	24	2	0	92.31	7.69	0.00	0
Budapest (Soroksár) (HU)	2022	Orchard, Agricultural field	6	110	29	81	1	26.36	59.09	14.55	16

[HU: Hungary, RO: Romania, SR: Serbia, BU: Bulgaria]

In 2022, egg masses were collected from various locations in Hungary: Budapest (Budapest Centre, Csepel, and Soroksár) Szeged, and Tarcal (Table 7). Only one egg mass was collected in Tarcal, with no evidence of parasitization. A total of 45, 38 and six egg masses were collected from Szeged, Budapest Centre, and Soroksár, respectively, corresponding to 1,076, 859 and 110 eggs. The highest number of parasitoids emerged from Budapest Centre (107 parasitoids), followed by Szeged (74 parasitoids) and Soroksár (16 parasitoids). The parasitization rates recorded were 12.46% for Budapest Centre, 14.55% for Soroksár and 6.88% for Szeged (Table 24.). The details of parasitoid species corresponding to their collection locations are presented in Figure 5 and Table 25.

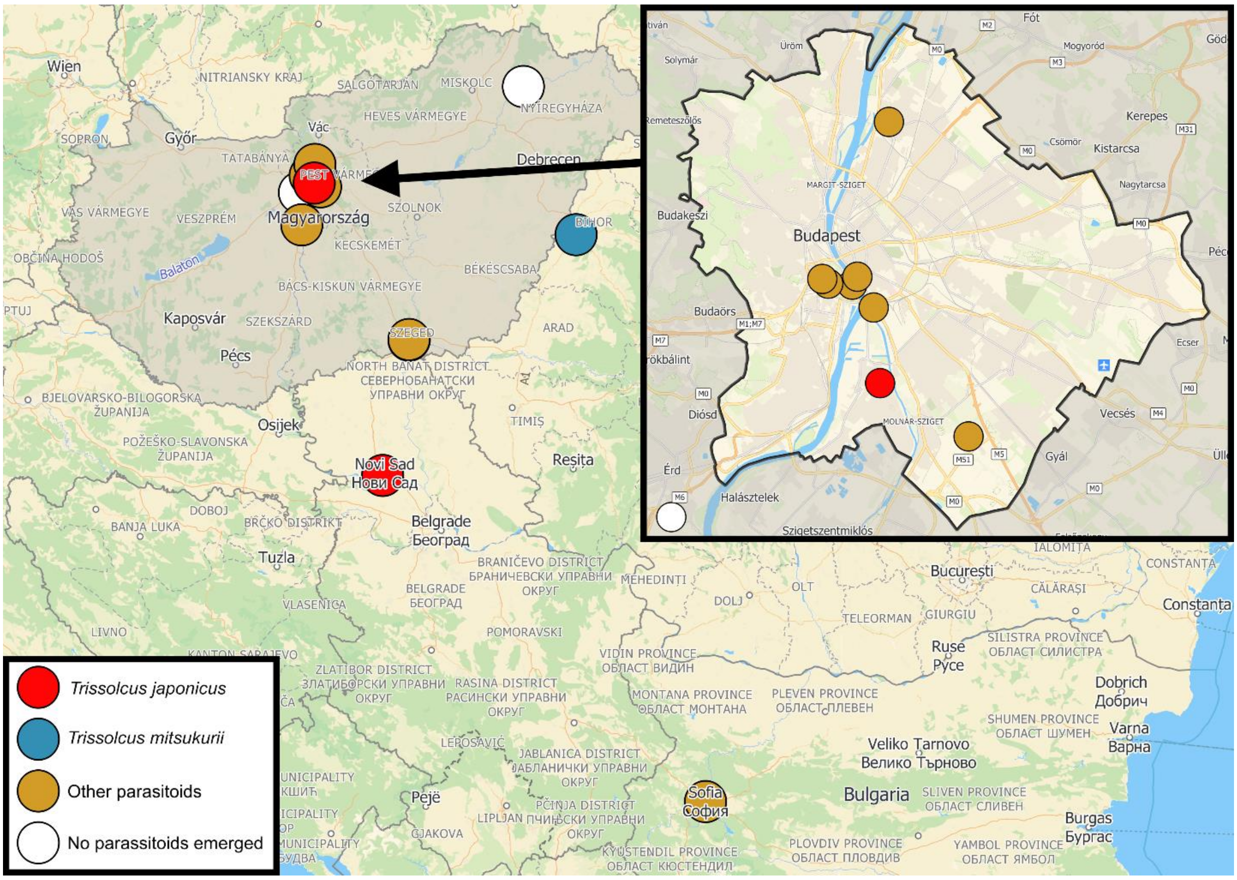


Figure 6. *Halyomorpha halys* wild egg masses collection sites in Hungary and neighbouring countries (between 2021-2022)

In 2022, only *A. bifasciatus* was recorded from Soroksár. In Budapest Centre, *A. bifasciatus, Ooencyrtus* sp., *Tr. japonicus, Tr. basalis* and *Tr. colemani* (Crawford) were identified. Furthermore, *A. bifasciatus* and *Tr. japonicus* were observed in the same egg mass. In Szeged, the parasitoids species recorded were *A. bifasciatus, Ooencyrtus* sp., and *Telenomus truncatus* (Nees von Esenbeck) (Table 25).

Overall, only 33 out of 160 egg masses were collected from agricultural areas, whereas 79.4% of the egg masses were collected from urban areas (Table 24). Furthermore, the only species observed in the agricultural landscapes was *A. bifasciatus*, with just 29 parasitoid individuals recorded from these areas out of a total emergence of 388 parasitoids.

Among the ornamental plants, the highest number of BMSB egg mass was collected from *A. altissima*. The highest number of parasitized egg masses were found in the *A. altissima,* contributed 48% of the parasitized egg masses collected (Table 7).

Table 25. Parasitoid species recorded from wild egg masses of *Halyomorpha halys* in 2021 and 2022 (Hungary and its neighbourhood)

Location	**Year of collection**	***Anastatus bifasciatus***	***Trissolcus japonicus***	***Trissolcus mitsukurii***	***Trissolcus colemani***	***Trissolcus basalis***	***Telenomus truncatus***	***Ooencyrtus* sp.**
Budapest (HU)	2021	13	0	0	0	0	0	6
Budapest (Soroksár) (HU)	2021	13	0	0	0	0	0	0
Érd (HU)	2021	0	0	0	0	0	0	0
Oradea (RO)	2021	68	0	23	0	3	0	0
Sofia (BU)	2021	5	0	0	0	0	0	0
Novi Sad (SR)	2021	2	13	0	0	0	0	0
Szeged (HU)	2022	48	0	0	0	0	3	2
Budapest (HU)	2022	70	21	0	2	1	0	3
Budapest (Soroksár) (HU)	2022	13	0	0	0	0	0	0
Tarcal (HU)	2022	0	0	0	0	0	0	0

[HU: Hungary, RO: Romania, SR: Serbia, BU: Bulgaria]

5.0. DISCUSSION

The present studies aimed to provide details on the phenology and reproductive biology of BMSB in Hungary, which would contribute to a better understanding on the development of strategies for the management of this invasive pest in Hungary and Europe. In addition, a comprehensive survey was carried out to identify and assess the potential egg parasitoids associated with BMSB.

5.1. Phenology, life cycle and biological parameters of BMSB

BMSB adults undergo winter diapause regulated by photoperiod, which allows them to complete a variable number of generations across both native and invaded regions, depending on local temperature and other environmental factors such as food availability and precipitation (SAULICH & MUSOLIN 2018). In Europe, studies on BMSB biology have been conducted in several locations, showing substantial variation in overwintering adult mortality: 39% in Switzerland (HAYE et al. 2014), 71–81% in western Slovenia (ROT et al. 2022), and 86% in northern Italy (COSTI et al. 2017). In the present study, the average mortality rates of overwintered BMSB adults were 65.14% for wild-collected individuals and 50.88% for those reared experimentally. According to SCACCINI et al. (2019) due to its cold-intolerant nature, exposure to low temperatures during the winter and extreme spring frost events can greatly contribute to a greater mortality rate for BMSB and survival rates decline at temperature below 5ºC. The low survival can also be attributed to an insufficient accumulation of nutritional reserves as the summer generation enters diapause earlier (FUNAYAMA et al. 2012). The reason for low survival in wild overwintered populations may be due to the continuously supplied food source in the experimental rearing. According to FUNAYAMA (2012), low nutrient reserves when entering diapause exhibited lower survival rates during overwintering.

Overwintering adult regain activity begins at a photoperiod of 13 h and above 14 °C average daily temperature (MAISTRELLO 2024), Voltinism and the timing of first oviposition are strongly influenced by spring temperatures. Under warmer spring conditions, oviposition occurs earlier and can result in the completion of a second generation (STÖCKLI et al. 2020). Our findings indicate the exit from overwintering occurred when the daily mean temperature was above 14 ºC and the photoperiods above 12h, typically beginning in late March to early April, aligned with the studies conducted in Italy and Slovenia (COSTI et al. 2017, ROT et al. 2021) where overwintering adults become active when daily temperatures exceed 14°C. BMSB has one or two generations in native areas such as China, Japan and Korea (LEE et al. 2013) as well as in the invaded region of the north-east USA (NIELSEN & HAMILTON 2009a, LESKEY et al. 2012). In Europe, some studies on the biology of BMSB have been carried out so far. In Switzerland, BMSB had a single generation in 2014 (HAYE et al. 2014), although, two generation was recorded during 2018–2019, possibly due to climate change (STÖCKLI et al. 2020). BMSB exhibits two generations per year in Italy (COSTI et al. 2017), Turkey (ÖZDEMIR et al. 2023), and Western Slovenia (ROT et al. 2022), with potential for three generations in parts of Azerbaijan and Ukraine (MAISTRELLO 2024). In contrast to Western Slovenia, only one generation occurs in central Slovenia (BOHINC et al. 2024). Temperature is a key factor: colder climates support a single generation, while warmer regions allow two or more. Southern Europe and warm regions of the United States remain at risk from such rapid population growth and spread (NIELSEN et al. 2008, COSTI et al. 2017).

In the present study, a univoltine life cycle was recorded in 2021, while bivoltinism was observed from 2022 to 2024. In 2021, the average monthly temperatures in April and May were 10.57 °C and 14.23 °C, respectively. Oviposition began in mid-June, followed by adult emergence in mid-August. Similar results were reported by HAYE et al. (2014), who observed a single generation with oviposition starting in mid-June and adult emergence in mid-August, attributed to low spring temperatures below 15 °C. From 2022 to 2024, spring temperatures were consistently higher than those recorded in 2021. The mean monthly temperatures for April and May were 11.94 °C and 18.59 °C in 2022, 11.81 °C and 17.66 °C in 2023, and 14.80 °C and 18.74 °C in 2024. These elevated spring temperatures likely corresponded with earlier oviposition, occurring 18, 7, and 25 days earlier than in 2021, respectively. Notably, the average daily temperature in March 2024 exceeded that of all previously studied years, likely contributing to the earlier onset of oviposition and adult emergence (Table 10). Comparable spring temperature patterns have been reported in Western Slovenia (ROT et al. 2022) and in Modena Province, Italy (COSTI et al. 2017), where April temperatures above 15 °C were associated with oviposition beginning in mid-May.

Our findings indicated that the rise in spring temperatures during 2022, 2023, and 2024 resulted in earlier oviposition compared to 2021, leading to the earlier appearance of first-generation adults in the second half of July. This pattern is consistent with previous studies (ZHANG et al. 1993, COSTI et al. 2017, ROT et al. 2022). These adults-initiated oviposition from the last week of July through early August, continuing until 9 September in 2022 and 2024. However, eggs laid at the end of August failed to develop into adults, and those deposited after 2 September did not hatch. Summer generation adult emergence began in September and extended into early November. Similar observations have been reported in Western Slovenia, where nymphs emerging from September-laid eggs did not reach adulthood (ROT et al. 2022), and in Italy, where second-instar nymphs appearing after 25 August failed to complete development (COSTI et al. 2017). The present study demonstrates that climate change has a significant impact on BMSB populations. Rising spring temperatures are likely to shift the species from univoltine to bivoltine, posing a considerable risk for population growth in the future. Under warmer spring conditions, oviposition and the second generation could begin earlier, potentially leading to outbreaks.

In Swiss univoltine populations, development lasts between 2 and 4 months. By contrast, in bivoltine populations, the first generation emerging in early summer develops more rapidly (50.0 days) than the second generation (56.8 days) (MAISTRELLO 2024). In the present study, the development time from egg to adult was 48.74 days in the overwintering generation and 67.57 days in the summer generation. In the summer generation, development from the first to fourth nymphal instars lasted 5 to 12 days, whereas the fifth instar required 31 days. MUSOLIN et al. (2019) reported that under short day lengths, nymphal development was faster, and adult diapause was induced, whereas long day lengths promoted reproduction, with the critical day length for diapause induction around 15.5 hours at 24 °C. Additionally, low temperatures can induce diapause in both nymphal and adult stages (NIVA & TAKEDA, 2003). In the present study, the photoperiod from early August was less than 14 hours and dropped below 12 hours from October onward. At the onset of autumn, most of the nymphal population was in the fifth instar. The prolonged development observed in the fifth instar, even under photoperiods shorter than 12 hours, was likely due to low temperatures, with an average daily temperature of 13.2 °C in October. Consequently, only a few individuals reached adulthood by the first week of November. Additionally, in 2024, a portion of the population—5% of fourth instars and 30% of fifth instars—failed to reach the adult stage and entered diapause. This population did not survive overwintering, possibly due to lower accumulation of nutritional reserves compared to adults (FUNAYAMA et al. 2012). The present study demonstrates that the development of BMSB is strongly influenced by both temperature and photoperiod. Even under photoperiods shorter than 15 hours, low temperatures can substantially delay or halt nymphal development. Further research is needed to clarify how temperature and photoperiod interact to affect nymphal development in BMSB. Additionally, adults emerging in late autumn and early winter enter diapause immediately after emergence. It is therefore important to investigate whether these adults possess sufficient nutritional reserves to survive the winter, or whether inadequate nutrition could trigger premature emergence from overwintering sites, as low nutrient levels influence diapause termination (FUNAYAMA 2012).

In Europe, degree days (DD) are commonly calculated using a 12.2 °C threshold, which represents the lower developmental threshold of BMSB. This value was proposed by HAYE et al. (2014) because it provides the best agreement between accumulated degree days and observed insect phenology under European climatic conditions. The same threshold has also been successfully applied in Western Slovenia (ROT et al. 2022). In Switzerland, the overwintering generation from egg to adult emergence required 588.24 DD (HAYE et al. 2014). In Western Slovenia, values were 530 DD for the overwintering, 545 DD for the summer generation, and 179 DD for the summer generation preoviposition period (ROT et al. 2022). In this study, DD from egg to adult emergence was 611.32 ± 2.76 (SE) for the overwintering generation and 569.16 ± 2.24 (SE) for the summer generation, with a preoviposition period of 185.74 DD in summer generation.

Degree-day (DD) accumulation from 1 April to first oviposition, first hatching, and first adult emergence of BMSB reared under natural temperature at Buda Arboretum, was recorded from 2021 to 2024. Overwintered BMSB adults begin oviposition at 214–255 DD and adult emergence at 689-878 DD, oviposition by summer generation at 850-958 DD. Considering these values, there is potential for overlaps between late stages of the overwintering generation and early stages of the summer generation. This overlap can contribute to the timing and magnitude of population peaks, highlighting the importance of monitoring both early and late developmental stages for effective pest management. Incorporating these thresholds into predictive models can help forecast periods of peak activity and optimize the timing of interventions.

The fecundity of BMSB is strongly influenced by temperature, photoperiod (GOVINDAN & HUTCHISON 2020, REZNIK et al. 2022), genetics, geographic location, rearing conditions, and collection date (NIELSEN et al. 2008). In overwintering generations, a single female lays 70.9 eggs in Switzerland (HAYE et al. 2014), 174 eggs in Western Slovenia (ROT et al. 2022), and 285 eggs in Northern Italy (COSTI et al. 2017). For summer generations, fecundity per female was 76 eggs in Western Slovenia and 214.7 eggs in Northern Italy. In the present study, females produced up to 7 egg masses (70.9 eggs) in the overwintering generation and 9 egg masses (90.4 eggs) in the summer generation. ROT et al. (2022) noted lower fecundity in Western Slovenia compared to Northern Italy and Asia, likely due to higher latitude and less favorable temperatures. Similarly, the low fecundity observed here may result from geographic and climatic constraints, including prolonged exposure to low temperatures, which reduces fecundity but can increase longevity (SCACCINI et al. 2019). Photoperiod also affects ovarian development, which declines below 15 hours (REZNIK et al. 2022), with some development may occur at 13 or 13.5 h (WATANABE 1979), almost none was reported at below12 h (WATANABE 1980, FUJIIE 1985). In this study, adult emergence of the summer generation began in mid-July and peaked in mid-August, when photoperiods were below 15 hours, likely contributing to reduced fecundity. In this study, carrots, sunflower seeds, and peanuts were used to rear BMSB, and this diet was constant throughout the experiment, but the effects of diet on adult longevity or fecundity were not assessed. Previous research suggests diet composition can influence these traits; for example, combining carrots with peanut and soybean diets improved survival and egg production compared to single diets

(FUNAYAMA 2006). Mixed diets generally support greater survival and reproduction in laboratory colonies than restricted diets (DINGHA & JACKAI 2017), indicating that diet quality, alongside abiotic factors like temperature, may affect BMSB longevity and fecundity. The net reproductive rate of increase (R_0) in Hungary in 2024 was 5.39 for the overwintering generation and 2.21 for the summer generation, considerably lower than reported in Western Slovenia (14.84 and 5.64) (ROT et al. 2022) and Northern Italy (24.04 and 5.44) (COSTI et al. 2017), but similar to the univoltine overwintering generation of the Swiss population (5.69) (HAYE et al. 2014). Previous studies were conducted under similar conditions, considering only temperature as a major factor affecting fecundity, mortality, and development duration. The R_0 value in the present studies indicates slower population growth. However, these comparisons do not account for fertility and mortality factors influenced by diet or by predators and parasitoids; therefore, the actual R_0 under field (natural) conditions may differ once the effects of diet and natural enemies are considered. Additionally, in the summer generation of 2024, demographic growth parameters were assessed under natural temperature conditions. The average temperature from the onset of female reproductive age to the last oviposition was 24.1 °C. The recorded intrinsic rate of increase (representing the population's potential growth rate under specific environmental conditions) (r_m) was 0.057 ± 0.00 (SE), and the finite rate of increase (λ) was 1.058 ± 0.00 (SE) aligned with earlier studies which conducted under laboratory conditions at constant temperature at between 23 °C to 25 °C: GOVINDAN & HUTCHISON (2020), ($r_m = 0.0606 \pm 0.00$, and $\lambda = 1.062 \pm 0.00$ at 23 °C), NIELSEN et al. (2008) ($r_m = 0.07$ at 25 °C) and MERMER et al. (2023) ($r_m = 0.06$ at 25 °C). The generation time (T) defined as the duration from female birth to death—was reported in earlier studies as 79 days at a constant temperature of 23 °C (GOVINDAN & HUTCHISON 2020) and 103 days at 25 °C (MERMER et al, 2023). In the present study, the recorded T was 80 days. Since this study was conducted under natural temperature conditions, the duration for each female was counted from birth until entering diapause, with 33 out of 63 individuals entering diapause. In this experiment, λ values above 1 and positive r_m indicate a growing population. As the study was conducted outdoors with protection from natural enemies, temperature can be considered the primary factor influencing population growth. These demographic parameters may vary annually in response to environmental changes.

In the present studies, total percent mortality from eggs to adult was high, 81.52% in the overwintering generation and 93.76% in the summer generation (2021–2024), indicating strong developmental losses. Overwintering generation mortality (eggs to adult) was lower in Italy (56%) (COSTI et al. 2017) and Slovenia (60%) (ROT et al. 2022) but similar in Switzerland (86.7%) (HAYE et al. 2014), while summer generation mortality (eggs to adult) was also high in Italy

(97%) and Slovenia (89%) (COSTI et al. 2019; ROT et al. 2022). The high mortality of the summer generation is likely due to cold autumn temperatures affecting the late developmental stages, as well as the low survival of diapausing adults. These findings align with European patterns and highlight the importance of considering seasonal differences in survival when predicting population dynamics.

The present research confirmed that the shift from one to two generations per year of BMSB in Hungary may be triggered by changes in climatic conditions, which in turn increases the risk of crop damage and nuisance from overwintering populations. Compared to studies conducted in Northern Italy (COSTI et al. 2017) and Western Slovenia (ROT et al. 2022), the reproductive rate in Hungary is lower could be due to genetic, differences in geographic location and climate. It should be noted that all studies were conducted under semi-natural conditions with diet provided throughout the experimental period; therefore, differences in reproductive rate cannot be attributed to food limitation during the experiments. However, under true field (natural) conditions, particularly in early spring when BMSB regains activity, food availability is likely to be limited, which may further influence reproductive performance. Nevertheless, life table and population growth parameters from the current study indicate a rising population trend. Therefore, under conditions where the temperature in April exceeds 11 °C and in May exceeds 15 °C, egg-laying is expected to begin in the 3rd or 4th week of May. This can lead to the early emergence of new adults and the production of a second generation, potentially resulting in high populations of nymphs and adults during July, August, and September. Conversely, low autumn temperatures and photoperiods below 15 hours induce adult diapause and slow or halt nymphal development, leading to high mortality. However, if warm autumn conditions prevail, nymphal development may proceed faster, as short photoperiods can trigger accelerated development (MUSOLIN et al. 2019). Such conditions could result in larger overwintering adult populations. If winter temperatures remain warm, survival rates could further increase—for instance, a 1 °C rise above 4 °C can enhance survival by 13% (KIRITANI et al. 2007). In the absence of natural enemies, if these factors prevail, it may contribute to significant population increases of BMSB in subsequent years. There has been an interest among researchers for years in finding the best measures to manage BMSB effectively in newly invaded areas. The current study provides phenological and biological parameters on BMSB in Hungary that can be used to optimize and adapt control measures for the pest's most vulnerable life stages as well as in developing a pest forecasting model.

5.2. Survey on egg parasitoids of *Halyomorpha halys* in Hungary

A survey examining the egg parasitoids of BMSB in Hungary was carried out in 2021 and 2022, during which we identified multiple species of egg parasitoids, including one non-native species. In addition, wild egg masses were obtained from cities in Southeast Europe, specifically Oradea, Sofia, and Novi Sad. This led to the identification of various species of egg parasitoids, including two non-native species. In Hungary, six species of egg parasitoids were discovered, namely *A. bifasciatus, Ooencyrtus sp., Tr. japonicus, Tr. basalis, Tr. colemani,* and *Te. truncatus. Trissolcus japonicus* is a non-European species that was documented for the first time in Hungary. *Anastatus bifasciatus* was found to be the most predominant and abundant native parasitoid of BMSB eggs in Hungary, aligning with earlier European research findings (COSTI et al. 2019, MORAGLIO et al. 2020, ZAPPONI et al. 2020, ROT et al. 2021, KONJEVIĆ et al. 2024). In addition, the genus *Anastatus* was among the most retrieved native parasitoids from BMSB eggs in the United States (DIECKHOFF et al. 2017, JONES et al. 2014).

In 2017 and 2018, an adventive population of *Tr. japonicus* was discovered in Canton Ticino, Switzerland (STAHL et al. 2019b). Later, *Tr. japonicus* was reported from Northern Italy in 2018 (SABBATINI PEVERIERI et al. 2018), Western Slovenia in 2020 (ROT et al. 2021), Germany in 2021 (DIECKHOFF et al. 2021), and in 2024 in Southwestern France (MARTEL et al. 2024), and Serbia (KONJEVIĆ et al. 2024). A recent investigation identified *Tr. japonicus* in Hungary for the first time and in Novi Sad, which aligned with the record of *Tr. japonicus* from Serbia by KONJEVIĆ et al. (2024). The invasion of BMSB in North America and Europe has led to the documentation of non-native parasitoids such as *Tr. japonicus* and *Tr. mitsukurii* in invaded areas. In addition, bioclimatic envelope models suggest that *Tr. japonicus* exhibits distinct geographic distribution patterns in Europe, thriving in regions regarded as most suitable for its establishment, including Southwestern France, Northeastern Spain, Northern Italy, Western Slovenia, and Croatia (AVILA & CHARLES 2018, ROT et al. 2021). *Trissolcus mitsukurii*, an Asian egg parasitoid of BMSB, was first detected in northern Italy in 2016 (SABBATINI PEVERIERI et al. 2018) and has since been recorded in several parts of Europe, including western Slovenia (ROT et al 2021), Serbia (KONJEVIĆ et al. 2024), and France (BOUT et al. 2021). In the present investigation, *Tr. mitsukurii* was not recorded from Hungary. However, *Tr. mitsukurii* was identified in egg masses collected from Oradea, Romania, which is the first report of this species in Romania. According to TORTORICI et al. (2023), BMSB can thrive and establish in Europe, with the most suitable habitats located in France, Italy, Greece, and some locations in Germany, the Netherlands, and the Balkan Peninsula. Furthermore, the two non-indigenous egg parasitoid species of BMSB*, Tr. japonicus* and *Tr. mitsukurii*, were modeled to exhibit distinct geographic distribution patterns in

Europe, with *Tr. japonicus* preferring lower latitudes, primarily in the southern part of Europe, and *Tr. mitsukurii* preferring higher latitudes such as Northern and Western France, Belgium, the Netherlands, Denmark, Germany, and Scandinavia. Importantly, it has become apparent that the central part of Europe is favorable to both parasitoid species. Furthermore, Northern Europe, Northern and Eastern Spain, Northern Italy, and the Hungarian Plain may provide ideal conditions for these two *Trissolcus* species but not for BMSB (TORTORICI et al. 2023). In the current studies, *Tr. mitsukurii* was found in Oradea, located near southeastern Hungary. Consequently, as Hungary is in the preferred zone of these *Trissolcus* species, there is a high probability that *Tr. mitsukurii* is present but undetected in Hungary or may establish populations in the near future.

Anastatus bifasciatus was the most prevalent BMSB egg parasitoid in this study. This observation highlights the ability of native parasitoids to adopt new hosts, indicating their potential to increase the mortality of suitable invasive pest species as also recorded in earlier studies (HAYE et al. 2015, COSTI et al. 2019, ABRAM et al. 2017, ROVERSI et al. 2016, STAHL et al. 2019a). Recently, *Tr. mitsukurii*, a non-native parasitoid, was found co-parasitizing BMSB eggs with *A. bifasciatus*, a native parasitoid, thus increasing the overall parasitism rate on BMSB in Slovenia (ROT et al. 2021). An attempt to assess the possible coexistence of an Asian egg parasitoid, *Tr. japonicus,* and a native European egg parasitoid, *A. bifasciatus,* a classical biological control of BMSB was conducted in Italy (authorization number DG/DISR/DISR05/0013647-19/04/2018) by the Italian Ministry of Agriculture (SABBATINI PEVERIERI et al. 2018). KONOPKA et al. (2017) revealed that both species can coexist and possibly act synergistically in increasing rates of BMSB egg mortality. The interspecific competition of adults and larvae between these two parasitoid species revealed that they engaged in counterbalance competition, where *Tr. japonicus* was superior as an extrinsic competitor because adults guarded host eggs more aggressively, while *A. bifasciatus* was superior in intrinsic competition because its larvae were more successful in developing from multiparasitized and multi-age BMSB eggs. Critically, whether the benefits of non-indigeneous parasitoids outweigh the risks to non-target species needs to be evaluated in invaded regions. Three-year studies in Switzerland and Italy revealed that *Tr. japonicus* parasitizes 15 of 18 non-target pentatomid species, though most experienced lower parasitism rates than BMSB, suggesting partial temporal refuges. *Pentatoma rufipes*, the most affected non-target species, may face a higher parasitism risk (HAYE et al. 2024). In the present study, the co-occurrence of native and non-native species in a single egg mass was recorded, such as *A. bifasciatus* and *Tr. japonicus*, *Tr. mitsukurii* and *Tr. basalis*, and *Tr. mitsukurii* and *A. bifasciatus*. Therefore, it is feasible that these species could be utilized in future efforts to target the eggs of BMSB, provided that the nature of the interaction between the parasitoid species is carefully examined and demonstrated to be beneficial.

Sentinel egg masses on artificial substrates provide a rapid and convenient method for evaluating the presence of natural enemies (JONES et al. 2014), and sentinel egg masses can exhibit higher parasitism and predation rates than eggs laid in sleeve cages (COSTI et al. 2019). However, sentinel eggs may underestimate true parasitism rates and misrepresent parasitoid community composition, as they lack host-associated cues present in wild egg masses (JONES et al. 2014). To compensate for the lack of host- and plant-associated cues and to simulate more natural conditions, eggs naturally laid in cages were used in the present study. The average rate of parasitism observed in naturally laid eggs in cages was 0% in 2021, with a marginal increase to 0.79% in 2022. Thus, this method was ineffective for monitoring parasitoid activity in Hungary. The low level of parasitism observed in naturally laid eggs in cages may be attributed to physical barriers, despite the mesh size being sufficiently adequate to allow parasitoids to enter through the netting. COSTI et al. (2019) noted a similar outcome when using mesh cages. The collection of wild egg masses was more effective than naturally laid eggs in mesh cages for measuring parasitism rates and parasitoid species diversity, with overall parasitism rates of 5.29% and 8.47% in 2021 and 2022, respectively. Research conducted in Western Slovenia revealed that the average rate of parasitism over two years was 3.0% and 14.4%, with the peak parasitism rate reaching 30.1% (ROT et al. 2021). The level of parasitism observed in this project peaked at 14.55%, which was lower than that reported in Western Slovenia. In the present study, predation was not recorded, and unhatched eggs were not dissected to quantify levels of failed parasitism.

In the present study, urban areas recorded a higher number of BMSB egg masses and a greater diversity of parasitoids than agricultural areas. In urban regions, *A. bifasciatus, Ooencyrtus* sp., *Tr. japonicus, Tr. basalis, Tr. colemani*, and *Te. truncatus* were recorded in Hungary, in Oradea, *A. bifasciatus, Tr. mitsukurii*, and *Tr. basalis* were found, in Sofia, Bulgaria, only *A. bifasciatus* was observed, and in Novi Sad, Serbia, *A. bifasciatus* and *Tr. japonicus* were recorded. In orchards and agricultural areas surveyed in Hungary, only *A. bifasciatus* was recorded. The survey was conducted randomly in urban and agricultural areas; however, a larger portion of the survey was concentrated in urban areas. Consequently, a more detailed survey across various orchards and agricultural sites in Hungary is needed to better assess the presence of BMSB egg masses and parasitoid diversity. Urban ornamental hosts such as *Ailanthus altissima*, *Ilex aquifolium*, *Paulownia tomentosa*, and *Pyrus persica* support complete development from egg to adult, providing continuous resources for both pests and parasitoids (LESKEY et al. 2014). Higher egg densities and parasitism rates in the upper tree canopy further distinguishing urban habitats from orchards and crops (COTTRELL et al. 2023). In the present studies, *A. bifasciatus* and *Tr. japonicus*, recorded the most commonly found BMSB egg parasitoids in Hungary. In Western Slovenia, *A. bifasciatus* was the most dominant and widespread species of BMSB eggs, followed by *Tr. mitsukurii* (ROT et al. 2021). Interestingly, Serbia reported a higher incidence of BMSB egg masses in hazelnut orchards, whereas most parasitized eggs were collected from urban regions, possibly due to pesticide applications in orchards. *Anastatus bifasciatus* was identified as the most dominant and widespread species in Serbia. In addition, *Tr. japonicus* and *Tr. mitsukurii* were also detected, however, the impact of these parasitoids on BMSB population densities is not yet assessable, given that parasitoid populations are in early developmental stages (KONJEVIĆ et al. 2024). In the present investigation, no plant protection products were applied in the agricultural areas (i.e., apple orchards) surveyed at the Hungarian University of Agriculture and Life Sciences Research and Experimental Farm in Budapest (Soroksár) that could have influenced parasitism or species richness. It can be assumed that *Tr. japonicus* may still be in a preliminary stage of its spread across Hungary. However, a more detailed survey is required to better estimate its distribution, abundance, and impacts on BMSB. In addition, further research is needed to determine the geographic origin of the adventive *Tr. japonicus* and *Tr. mitsukurii* strains using molecular tools. Such investigations could provide greater insight into introduction pathways for adventive biological control agents. The survey of various plant species in Hungary indicated that most wild egg masses (50.56%) and parasitoids (47.83%) were collected from *Ai. altissima*, which aligns with earlier findings (BERGMANN et al. 2016, RICE et al. 2014, BAKKEN et al. 2015). NIELSEN & HAMILTON (2009b) reported that host plant species such as *Ai. altissima, Paulownia tomentosa* (Thunberg) Steudel (Paulowniaceae), *Acer* spp., and *Fraxinus* spp. play a crucial role in sustaining BMSB populations, especially during the early stages of invasion into a new area. The dispersal capability among various host plants is important for the development and survival of BMSB, although this insect can complete its life cycle on *Ai. altissima* and *P. tomentosa* (FUNAYAMA 2002, 2004, RICE et al. 2014). These findings are consistent with our observations, since the majority of BMSB egg masses were gathered from woody ornamental plants, as listed in Table 7, with the highest recorded from *Ai. altissima*.

6.0. CONCLUSION AND RECOMMENDATION

During the present investigation, research was conducted between 2021 and 2024 to examine the phenology, life cycle, and key biological parameters of BMSB in Hungary. In addition, a comprehensive survey was carried out to identify and assess the potential egg parasitoids associated with BMSB.

6.1. Phenology, life cycle and biological parameters of BMSB

1. Overwintering mortality of BMSB adults was higher in wild populations than in those reared under experimental conditions. Moreover, males exhibited higher mortality rates than females.
2. The emergence of BMSB adults from overwintering occurred when the daily mean temperature exceeded 14 °C and the photoperiod longer than 12 hours, typically beginning in late March to early April. In the present study, a univoltine life cycle was recorded in 2021, whereas bivoltinism was observed from 2022 to 2024, coinciding with higher spring temperatures during those years than in 2021. Voltinism and the timing of first oviposition in BMSB are strongly influenced by spring temperatures. Under warmer spring conditions, oviposition occurs earlier, which can facilitate the completion of a second generation.
3. In the univoltinism (2021), oviposition began in mid-June and continued until the third week of July, and adult emergence started in mid-August and lasted until the third week of September. In the bivoltinism (2022–2024), the overwintering generation-initiated oviposition in late May, which continued until mid-July, with adult emergence beginning after mid-July. The summer generation commenced oviposition in late July or early August and continued until early September. Eggs laid at the end of August failed to develop into adults, and those deposited after 2 September did not hatch. Adult emergence of the second generation began in September and extended into early November. The late nymphal stages of first generation overlap with the early stages of second generation. Pest management measures should be targeted during the stages when the pest is most active to achieve optimal control.
4. The development time from egg to adult averaged 48.74 days in the overwintering generation and 67.57 days in the summer generation. In the summer generation, the first to fourth nymphal instars developed within 5–12 days, while the fifth instar required about 31 days, likely due to low autumn temperatures (mean daily temperature of 13.2 °C in October). As most nymphs were in the fifth instar during autumn, only a few reached adulthoods by early November. Additionally, about 5% of fourth instars and 30% of fifth

instars entered diapause but did not survive overwintering, possibly due to insufficient nutritional reserves.

5. Degree days (DD) have been studied using a 12.2 ºC as minimum threshold temperature (HAYE et al. 2014). DD from egg to adult emergence was 611.32 ± 2.76 (SE) for the overwintering generation and 569.16 ± 2.24 (SE) for the summer generation. Degree-day (DD) accumulation from 1 April to first oviposition, first hatching, and first adult emergence of BMSB reared under natural temperature at Buda Arboretum from 2021 to 2024; in the overwintering generation, first oviposition occurred at 214.77–254.86 DD, first hatching at 309.50–325.64 DD, and first adult emergence at 689.27–878.87 DD. In the summer generation (2022–2024), these events occurred at 850.70–958.33 DD, 909.60–1089.67 DD, and 1317.55–1532.95 DD, respectively. These findings provide valuable data for developing pest forecasting models for BMSB in Hungary.
6. Females produced up to a maximum of 7 egg masses in the overwintering generation and 9 egg masses in the summer generation. Average fecundity of a single female was 70.9 eggs in overwintering generation and 90.4 eggs in summer generation.
7. The net reproductive rate of increase (R_0) was 5.39 for the overwintering generation and 2.21 for the summer generation. Additionally, in the summer generation of 2024, demographic growth parameters were assessed under semi-natural conditions. The average temperature from the onset of female reproductive age to the last oviposition was 24.1 °C. The recorded intrinsic rate of increase (r_m) was 0.057 ± 0.00 (SE), and the finite rate of increase (λ) was 1.058 ± 0.00 (SE).
8. The study was conducted outdoors with protection from precipitation and natural enemies; therefore, fertility and mortality factors influenced by diet or predation/parasitization were not considered. Temperature can thus be regarded as the primary factor affecting population growth. These demographic parameters may vary annually in response to environmental fluctuations, and the actual net reproductive rate (R_0) under field conditions may differ from the values obtained in this study.
9. The study found that the reproductive rate of the BMSB population originated from Budapest and Pest County (Central Hungary) is lower than in Mediterranean regions, likely due mainly to geographic and climatic differences. However, population growth data indicate an increasing trend, suggesting that under favorable climatic conditions, the population could increase.
10. The research provides key phenological and biological insights that can help optimize control strategies targeting the pest’s most vulnerable stages and support the development of a forecasting model for effective management.

6.2. Survey on egg parasitoids of *Halyomopha halys* in Hungary

1. Surveys of eggs parasitoids associated with BMSB were conducted in multiple regions (mostly in Central Hungary) across Hungary using two methods: assessing parasitism in naturally laid eggs inside cages and collecting wild egg masses.
2. The study recorded very low parasitism rates in naturally laid BMSB eggs in caged—0% in 2021 and only 0.79% in 2022—indicating that this method was ineffective in Hungary. *Anastatus bifasciatus* was the only parasitoid species detected during the study.
3. During 2021 to 2022, a comprehensive search for wild egg masses of BMSB was conducted from June to September across various locations in Hungary (mainly in Central Hungary), along with a one-time collection in a few cities in Southeast Europe including Novi Sad (Serbia), Sofia (Bulgaria), and Oradea (Romania).
4. Several native European parasitoids belonging to the families Encyrtidae, Eupelmidae, and Scelionidae were recorded successfully parasitizing the eggs of BMSB under field conditions, with the most common species recorded being *Anastastus bifasciatus.* In addition, *Trissolcus japonicus* and *Tr. mitsukurii* were documented for the first time in Hungary and Oradea (Romania), respectively. The study observed the coexistence of native and non-native parasitoid species within single BMSB eggs mass—such as *Anastatus bifasciatus* with *Trissolcus japonicus* or *Tr. mitsukurii*—demonstrating that multiple species can simultaneously exploit the same host. This finding highlights the importance of carefully assessing these interspecific interactions before introducing non-native parasitoids for augmentative biological control.
5. The study suggests that urban areas contain a higher diversity of parasitoid species and more BMSB egg masses compared to agricultural areas. However, since the survey was limited to specific locations, expanding survey across a wider range of urban and agricultural areas across country would provide more comprehensive data on parasitoid abundance and diversity.
6. The study highlights *Ailanthus altissima* as one of the most favored host plants for BMSB in Hungary. Along with other urban tree species, it serves as an ecological reservoir that supports parasitoid survival and dispersal, highlighting the need to include urban habitats in BMSB monitoring and management.
7. Further research is needed to understand interactions between native and non-native species and how non-native species adapt to new environments. Furthermore, incorporating genetic studies to determine the geographic origin of the adventive *Tr. japonicus* and *Tr. mitsukurri* strains using molecular tools. Such investigations could provide greater insight into the opportunities for adventive biological control.

7.0. NEW FINDINGS

1. First report of several native European parasitoids belonging to the families Encyrtidae (*Anastatus bifasciatus*), Eupelmidae (*Ooencyrtus* sp), and Scelionidae (*Trissolcus japonicus, Tr. basalis, Tr. colemani, Tr. mitsukurii* and *Telenomus truncatus*) successfully parasitizing eggs of *Halyomorpha halys* under field conditions in Hungary. The most common species recorded was *Anastatus bifasciatus*.
2. First detection of the non-indigenous egg parasitoids *Trissolcus japonicus* in Hungary (Budapest, 2022) and *Tr. mitsukurii* in Romania (Oradea, 2021), respectively.
3. Shift in voltinism of BMSB from univoltine to bivoltine in Budapest (Central Hungary) possibly in response to rising temperatures. Voltinism and the timing of first oviposition in BMSB are strongly influenced by spring temperatures; under warmer spring conditions, oviposition occurs earlier, enabling completion of a second generation.
4. Studying in Budapest, outdoor condition, using a BMSB population originated from Pest County (Central Hungary), the Degree-day (DD) requirement of the different developmental stages was determined. Degree-day (DD) accumulation from 1 April to first oviposition, first hatching, and first adult emergence of BMSB between 2021 and 2024; in the overwintering generation, first oviposition occurred at 214.77–254.86 DD, first hatching at 309.50–325.64 DD, and first adult emergence at 689.27–878.87 DD. In the summer generation (between 2022 and 2024), these events occurred at 850.70–958.33 DD, 909.60–1089.67 DD, and 1317.55–1532.95 DD, respectively.

8.0. SUMMARY

The Brown Marmorated Stink Bug (BMSB), *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae), is native to Korea, Japan, Taiwan, and China, and has rapidly invaded North America and Europe. In Hungary, it was first reported in 2013 at the Buda Arboretum, Budapest, and by 2018 had spread across the country. BMSB is a highly polyphagous pest, causing severe damage to horticultural and agricultural crops and creating public nuisance through overwintering aggregations. Globally, it has caused substantial economic losses, including $37 million in U.S. apples and €500 million in Italy. In Hungary, studies found 94% of dry bean seeds and 100% of sampled green hot peppers damaged. While research on BMSB's bio-ecology and potential parasitoids has been conducted in Europe, Hungary lacks comprehensive studies on parasitoid communities, seasonal dynamics, and biological parameters. In the present studies, research was conducted between 2021 and 2024 to examine the phenology, life cycle, and key biological parameters of BMSB in Hungary. In addition, a comprehensive survey was carried out to identify and assess the potential egg parasitoids associated with BMSB.

This study demonstrates that temperature strongly influence the biology, phenology, and population dynamics of BMSB in Hungary. Seasonal variations in temperature and day length affect overwintering success, voltinism, fecundity, and developmental duration, highlighting the species' phenotypic plasticity. Overwintering mortality was high (65.14% in wild populations, 50.88% in lab-reared individuals), likely due to low temperatures and pre-diapause nutrient accumulation, with lower mortality in reared bugs likely linked to continuous food availability. Overwintering adults regain activity when average temperatures exceeded 14 °C and photoperiods surpassed 12 h

Warmer spring temperatures from 2022–2024 than in 2021 triggered earlier exit from diapause, earlier oviposition, and produced second generation, shifting from univoltine to bivoltine life cycles. Development from eggs to adults was shorter for overwintering (48.74 days) than summer (67.57 days) generations, with extended development particularly in the fifth nymphal instar, due to lower autumn temperatures can substantially slow or even arrest nymphal development. High late-autumn nymphal mortality, often due to unsuccessful diapause, underscores the sensitivity of the species to low temperatures. These observations showed the delicate balance between climatic conditions and the insect's developmental physiology. Even slight deviations in temperature and day length may determine whether a generation completes successfully or is partially lost due to incomplete development before winter onset.

Degree days (DD) were estimated for the first time in Hungary, providing a baseline for predictive modeling. Total heat accumulation from egg to adult was 611.32 DD for the overwintering and 569.16 DD for the summer generation. Degree-day (DD) accumulation from 1 April to key phenological stages during 2021–2024 showed that, in the overwintering generation, first oviposition occurred at 214.77–254.86 DD, hatching at 309.50–325.64 DD, and adult emergence at 689.27–878.87 DD. In the summer generation, these events occurred at 850.70–958.33 DD, 909.60–1089.67 DD, and 1317.55–1532.95 DD, respectively. These data are crucial for refining pest forecasting and integrating BMSB phenology into regional management.

Fecundity differed seasonally: overwintering females laid 70.9 eggs on average, summer females 90.4, reflecting higher reproduction under warmer, longer-day conditions. Net reproductive rates (R_0 = 5.39 overwintering, 2.21 summer) were lower than Mediterranean populations, indicating moderated growth under Central European climates. Intrinsic (r_m = 0.057) and finite (λ = 1.058) rates show populations can sustain growth in the absence of natural enemies, under favorable conditions likely enhancing reproduction and overwintering survival. The low fecundity in Hungary is likely due to temperature and photoperiods, where warmer temperature and long day periods play a significant role on ovarian development and egg production. Nonetheless, demographic growth parameters confirm that BMSB can maintain viable populations across successive seasons.

Warmer spring and summer temperatures may allow two full generations per year, with oviposition beginning earlier when April and May temperatures exceed 11 °C and 15 °C, respectively. To produce the 2nd generation, adult emergence must occur before the end of July, when the photo periods are still above 15h. Overlapping generations could increase crop damage and overwintering populations, while cold autumns limit reproduction and increase mortality. However, if autumn continues to warm under ongoing climate change, delayed diapause induction could favor faster development, greater survival, and higher population. These phenological and demographic insights are vital for predicting emergence, timing control measures, and developing region-specific management strategies.

This study provides the first comprehensive survey of BMSB egg parasitoids in Hungary, conducted in 2021–2022. Six species were identified: *Anastatus bifasciatus*, *Ooencyrtus* sp., *Trissolcus japonicus*, *Tr. basalis*, *Tr. colemani*, and *Telenomus truncatus*. Notably, *Tr. japonicus*, an Asian species, was recorded in Hungary for the first time, highlighting ongoing non-native parasitoid expansion in Central Europe. The native *A. bifasciatus* remained the most abundant and widely distributed species. Additionally, *Tr. mitsukurii* was recorded at Oradea, suggesting potential establishment in Hungary.

Coexistence of native and exotic parasitoids within single egg mass—e.g., *A. bifasciatus* with *Tr. japonicus* or *Tr. mitsukurii*—demonstrates the complexity of trophic interactions and underscores the need for careful evaluation before using non-native species for biological control. Parasitism in naturally laid eggs in mesh cages was very low (0–0.79%), whereas wild egg masses reached 14.55%. These findings indicate that the parasitoid community in Hungary is still developing, with low densities of key species like *Tr. japonicus*. Long-term monitoring will be essential to track establishment, assess parasitism trends, and evaluate the potential of parasitoids to manage BMSB populations effectively.

The survey revealed that urban areas had higher parasitoid diversity and more BMSB egg masses than agricultural sites. *A. bifasciatus* dominated both habitats, while *Tr. japonicus* occurred only in Budapest, suggesting cities may serve as initial establishment points for adventive species. Host plants influenced distribution, with over half of BMSB eggs and parasitoids found on *Ailanthus altissima*, highlighting its role as an ecological reservoir. The two-year, localized study may underestimate true parasitoid diversity and abundance. Furthermore, molecular analysis of *Trissolcus* species was not performed, leaving their origins uncertain. Future research should include genetics and long-term monitoring across the country to assess establishment and coexistence with native *A. bifasciatus*. The dominance of native species alongside emerging non-natives indicates a transitional parasitoid community. Native and exotic species may jointly suppress BMSB, but ongoing surveillance, molecular identification, and ecological studies are essential to guide biological control and understand parasitoid dynamics in Central Europe.

APPENDICES

A1: Bibliography

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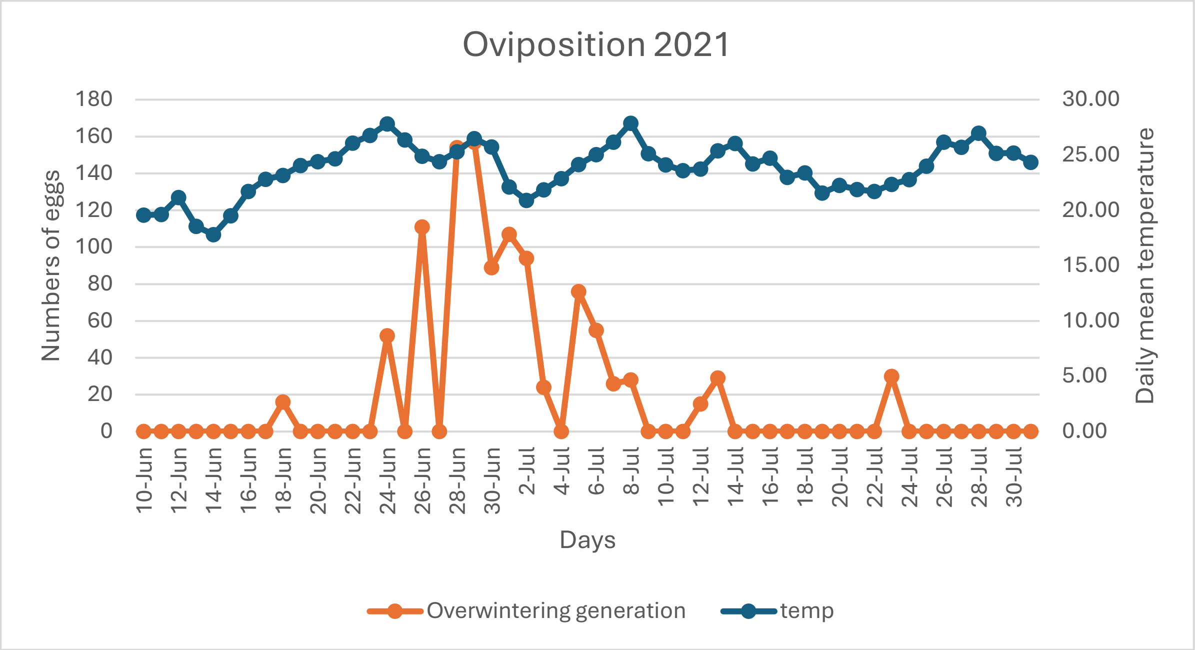
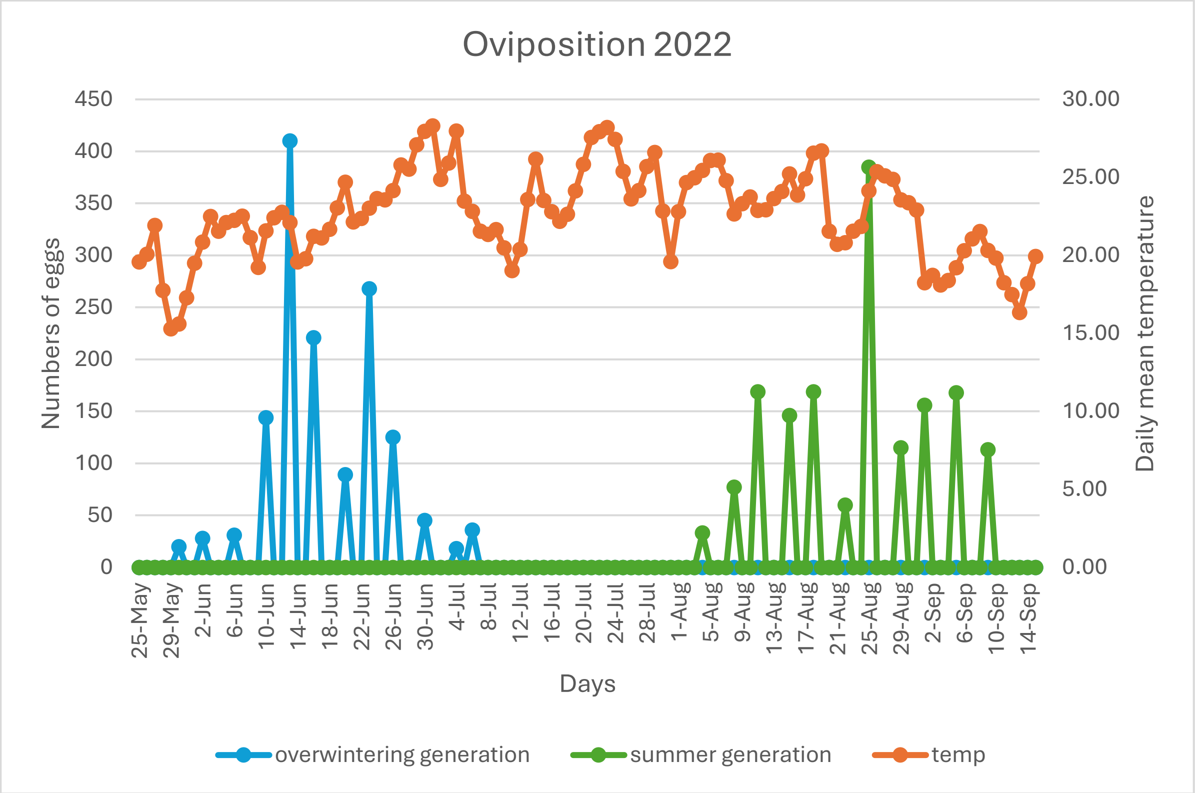
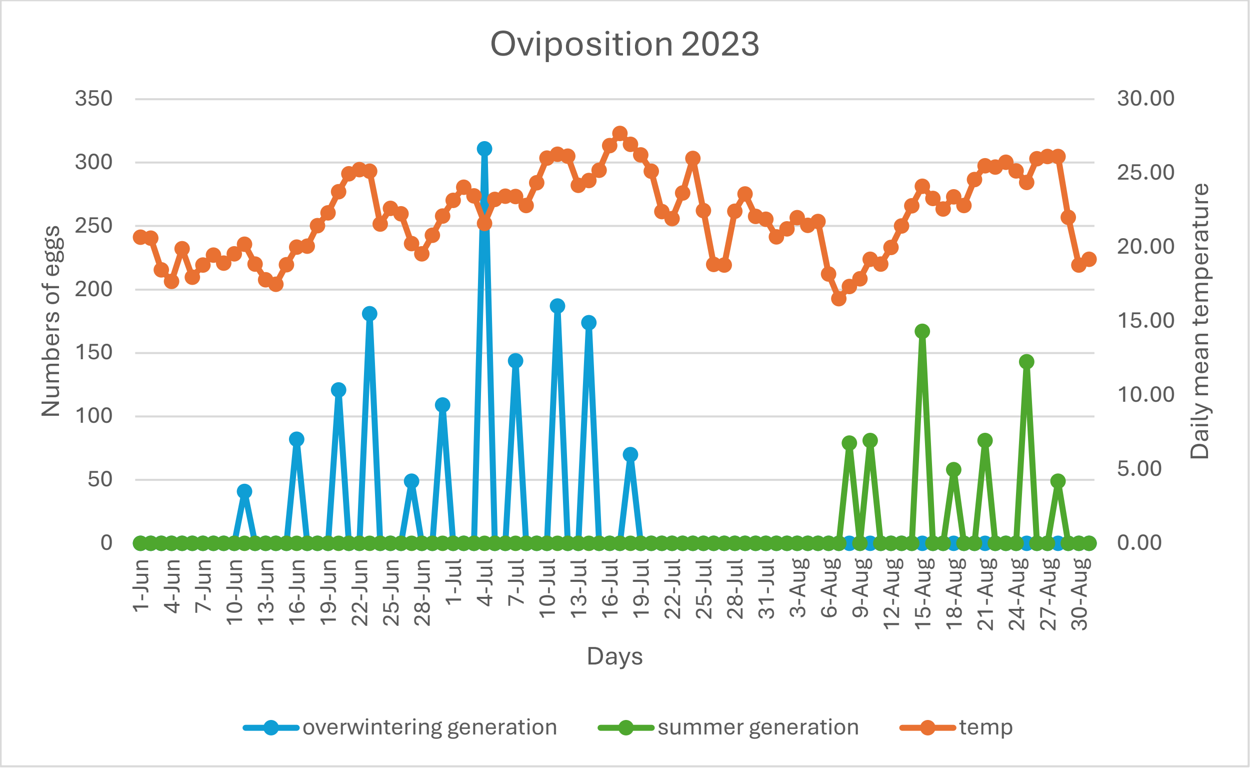
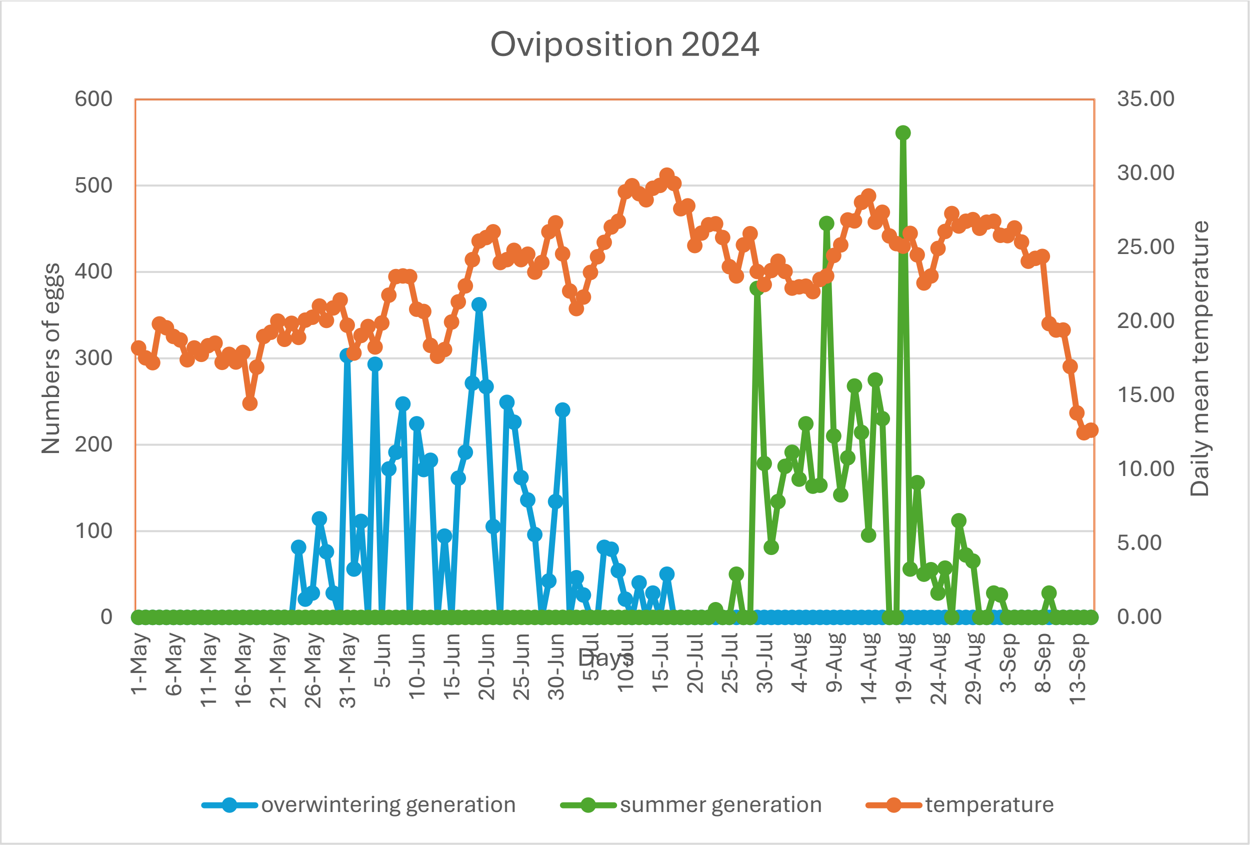
A2: Seasonal oviposition patterns of the BMSB in Budapest (2021–2024)






Oviposition 2023
Numbers of eggs
0
50
100
150
200
250
300
350
Daily mean temperature
0.00
5.00
10.00
15.00
20.00
25.00
30.00
1-Jun
4-Jun
7-Jun
10-Jun
13-Jun
16-Jun
19-Jun
22-Jun
25-Jun
28-Jun
1-Jul
4-Jul
7-Jul
10-Jul
13-Jul
16-Jul
19-Jul
22-Jul
25-Jul
28-Jul
31-Jul
3-Aug
6-Aug
9-Aug
12-Aug
15-Aug
18-Aug
21-Aug
24-Aug
27-Aug
30-Aug
Days
overwintering generation
summer generation
temp


Oviposition 2024
Numbers of eggs
0
100
200
300
400
500
600
Daily mean temperature
0.00
5.00
10.00
15.00
20.00
25.00
30.00
35.00
1-May
6-May
11-May
16-May
21-May
26-May
31-May
5-Jun
10-Jun
15-Jun
20-Jun
25-Jun
30-Jun
5-Jul
10-Jul
15-Jul
20-Jul
25-Jul
30-Jul
4-Aug
9-Aug
14-Aug
19-Aug
24-Aug
29-Aug
3-Sep
8-Sep
13-Sep
Days
overwintering generation
summer generation
temperature

A3: Generational mortality of the BMSB in Budapest (2021–2023) using life table analysis

a. 2021 Overwintering generation

Stage	lx	dx	Aparent mortality Qx=dx/lx	Real mortality rx=dx/lo	K value (-log(1-qx))	% generation mortality (100 kx/Ks)
eggs	1063	384	0.36	0.36	0.19	17.86
N1	679	295	0.43	0.28	0.25	22.71
N2	384	88	0.23	0.08	0.11	10.37
N3	296	59	0.20	0.06	0.10	8.86
N4	237	11	0.05	0.01	0.02	1.89
N5	226	10	0.04	0.01	0.02	1.80
New generation adults	216	129	0.60	0.12	0.39	36.23
overwintered adult	87					
total%mortality	91.82			Ks=1.09		

b. 2022 Overwintering generation

Stage	lx	dx	Aparent mortality Qx=dx/lx	Real mortality rx=dx/lo	K value (-log(1-qx))	% generation mortality (100 kx/Ks)
eggs	1435	578	0.40	0.40	0.22	32.45
N1	857	305	0.36	0.21	0.19	27.69
N2	552	154	0.28	0.11	0.14	20.59
N3	398	71	0.18	0.05	0.09	12.37
N4	327	18	0.06	0.01	0.02	3.56
N5	309	16	0.05	0.01	0.02	3.35
New generation adults	293					
total% mortality	79.58				Ks=0.69	

c. 2022 Summer generation

Stage	lx	dx	Aparent mortality Qx=dx/lx	Real mortality rx=dx/lo	K value (-log(1-qx))	% generation mortality (100 kx/Ks)
eggs	1591	841	0.53	0.53	0.33	21.92
N1	750	419	0.56	0.26	0.36	23.84
N2	331	137	0.41	0.09	0.23	15.57
N3	194	62	0.32	0.04	0.17	11.22
N4	132	8	0.06	0.01	0.03	1.82
N5	124	9	0.07	0.01	0.03	2.20
New generation adults	115	63	0.55	0.04	0.34	23.13
overwintered adult	52					
total% mortality	96.73				Ks=1.49	

d. 2023 Overwintering generation

Stage	lx	dx	Aparent mortality Qx=dx/lx	Real mortality rx=dx/lo	K value (-log(1-qx))	% generation mortality (100 kx/Ks)
eggs	1469	459	0.31	0.31	0.16	29.05
N1	1010	402	0.40	0.27	0.22	39.36
N2	608	67	0.11	0.05	0.05	9.05
N3	541	78	0.14	0.05	0.07	12.07
N4	463	28	0.06	0.02	0.03	4.84
N5	435	27	0.06	0.02	0.03	4.97
New generation adults	408					
total% mortality	72.23				Ks=0.56	

e. 2023 Summer generation

Stage	lx	dx	Aparent mortality Qx=dx/lx	Real mortality rx=dx/lo	K value (-log(1-qx))	% generation mortality (100 kx/Ks)
eggs	658	252	0.38	0.38	0.21	20.36
N1	406	162	0.40	0.25	0.22	21.47
N2	244	65	0.27	0.10	0.13	13.06
N3	179	22	0.12	0.03	0.06	5.53
N4	157	2	0.01	0.00	0.01	0.54
N5	155	23	0.15	0.03	0.07	6.77
New generation adults	132	71	0.54	0.11	0.34	32.55
overwintered adult	61					
total%mortality	90.73				Ks=1.03	

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