



**Hungarian University of Agriculture and Life
Sciences**

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

The Thesis of PhD dissertation

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)

1.0. INTRODUCTION AND AIMS

The brown marmorated stink bug (BMSB), *Halyomorpha halys* (Stål, 1855) (Hemiptera: Pentatomidae), is native to Korea, Japan, Taiwan, and China (ZHU et al. 2012). It invaded North America, first recorded from Allentown, Pennsylvania, in 1998 (HOEBEKE & CARTER 2003), and is now found in 47 U.S. states and four Canadian provinces (NORTHEASTERN IPM CENTER 2023). In Europe, first reported in Switzerland in 2008 (WERMELINGER et al. 2008), it has spread widely (EPPO 2025, MAISTRELLO 2024). BMSB is polyphagous, active above 15 °C, with one or more generations per year, cause nuisance by overwintering aggregations (LEE & LESKEY 2015), and reduces crop quality, causing major losses: USD 37 million in mid-Atlantic USA apples (UNITED STATES APPLE ASSOCIATION 2010), €500 million in Italy (COMMISSION IMPLEMENTING REGULATION (EU) 2020/465), and projected billions in New Zealand GDP (CLOUGH 2017).

BMSB was first recorded in Budapest, Hungary, in 2013 (VÉTEK et al. 2014). By 2016, surveys confirmed widespread distribution, with mass occurrences in southern Hungary, particularly Pécs. Severe infestations affected dry beans and green hot peppers, damaging 94% of seeds and 100% of sampled fruits, respectively (VÉTEK & KORÁNYI 2017). Nuisance problems gained media attention in 2017 (VÉTEK et al. 2018).

BMSB biology, phenology, temperature requirements, and natural enemies have been studied in the USA and Europe to support sustainable management (NIELSEN et al. 2008; HAYE et al. 2014; COSTI et al. 2017; ROT et al. 2022). Recovery of non-native egg parasitoids, *Trissolcus japonicus* and *Tr. mitsukurii*, from the invaded regions has opened new opportunities for biological control of BMSB (SABBATINI PEVERIERI et al. 2018; STAHL et al. 2019)

1.1. Objectives

The invasion of BMSB in Hungary threatens horticultural crops and causes nuisance through overwintering aggregations (WERMELINGER et al. 2008). Hungary's continental climate, with highs of 23–28 °C (occasionally >35 °C) and lows of –3 to –7 °C (sometimes <–10 °C) (ANONYMOUS, 2025), is suitable for BMSB establishment and overwintering. However, detailed studies on its biology, life history, phenology, voltinism, and potential parasitoids in Hungary are lacking. This study aims to address these gaps to support improved pest management strategies.

- 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. MATERIALS AND METHODS

2.1. Collection and overwintering of BMSB adults

Overwintering BMSB adults were collected from warehouses, buildings, and closed parasols in Budapest (47.4979° N, 19.0402° E) and Szentendre (47.6795° N, 19.0669° E) during autumn 2021–2023. Non-target Pentatomidae were discarded. In the laboratory, males and females were separated and kept outdoors under semi-natural conditions, sheltered from rain and snow, in plastic boxes (17 × 12 × 7 cm) with cardboard, covered with netting, and labeled by date, number, and location. Boxes were placed in BugDorm (BugDorms 4S2260; 24.5 × 24.5 × 63.0 cm; Australian Entomological Supplies Pty Ltd) to overwinter naturally, with temperature continuously recorded using T-Logg 160 and Tinytag Ultra 2 loggers.

Wild-collected adults used for parasitoid studies (2021–2022) were overwintered in a climate chamber (4 ± 0.9 °C, 70 ± 10% RH, 8:16 h L:D) and transferred to semi-natural outdoor BugDorms in spring, with food and water provided.

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

From 2021 to 2023, adult BMSB were maintained in BugDorms at three sites in the Buda Arboretum (Hungarian University of Agriculture and Life Sciences): west and east of the K Building and south of the A Building. Five BugDorms per site, three adult pairs each BugDorms (15 pairs per site; 45 pairs total). To compensate for mortality, 30–50 adults were added per site as needed. Adults were fed beans (summer only), sunflower seeds, peanuts, apples, carrots, and water twice weekly. Egg masses were collected individually and nymphs reared together in net-covered boxes. Emerged adults were paired and monitored for mating and oviposition; summer-generation nymphs were reared similarly. Recorded data included oviposition timing, eggs per mass, hatching rate, nymphal development, adult emergence, and mortality from egg to adult.

In 2024, 131 overwintering females, each paired with two males and reared individually in labeled cylindrical containers (8×6 cm) in BugDorms under roof-sheltered natural conditions. Dead males were replaced, and replicates were discarded if females died. The first three egg masses per female were used to assess life table parameters, degree days (DD), and development time. Eggs were collected individually, and first-instar nymphs were reared together until the second instar, then individually. Water was supplied via a damp cotton-filled bottle cap.

For the summer generation, 66 daughters from different overwintering parents were each paired with two unrelated males. The first four egg masses per female were collected, with nymphs reared similarly. Subsequent egg masses were used to assess generational mortality and phenology, while all egg masses were included in fecundity and hatching-rate analyses.

Recorded data included egg masses per female, eggs per mass, hatched eggs, and preoviposition duration. In total, 2,143 second-instar nymphs (overwintering) and 2,057 (summer) were reared individually. Nymphs were monitored daily for mortality and development, with constant food throughout the experiment (carrots, peanuts, sunflower seeds) and water replenished twice weekly. The experiment began from April 1 through December.

2.2.1. Life table analysis

Life table parameters were estimated following Bellows et al. (1992) and Haye et al. (2014). Between 2021 and 2023, mortality and survival of BMSB life stages were calculated under semi-natural conditions; individual female reproductive rates could not be assessed due to group rearing. In 2024, generational mortality, stage-specific survival, and reproductive rate (R_0) were determined using individually recorded female fecundity. Mortality associated with outdoor temperature and background mortality from unidentified factors (e.g., food quality) was expressed as apparent mortality, real mortality, mortality intensity

(k-values), and generational mortality. Predator and parasitoid effects were not considered. Apparent mortality (q_x) is the proportion of individuals dying at a given life stage relative to the number entering that stage (l_x): $q_x = d_x/l_x$, where d_x is the number of deaths in stage x . Real mortality (r_x) is the fraction of individuals dying at each stage relative to the initial number of eggs (l_0): $r_x = d_x/l_0$. k-value (k_x) = $-\log(1 - q_x)$. A generation's mortality (K_s) represents the sum of all mortality factor k-values (summed over all life stages). $K_s = k_{\text{eggs}} + k_{N1} + k_{N2} + k_{N3} + k_{N4} + k_{N5}$. As a proportion of the total generational mortality $100k_x/K_s$, this value shows the impact of mortality in each stage on BMSB's generational mortality.

Net reproductive rate (R_o) indicates population growth from one generation to the next (VAN DRIESCHE et al. 2008). Populations grow when $R_o > 1$ and decline when $R_o < 1$. $R_o =$ realized progeny/number of eggs in the generation. Here, "realized progeny" refers to the actual number of offspring produced by an individual surviving to a given developmental stage under the experimental conditions. For the overwintering generation, 5,459 eggs were laid by 77 females; for the summer generation, 5,257 eggs were laid by 58 females.

2.2.2. Demographic growth parameters

Demographic growth parameters were calculated only for the 2024 summer generation following LI et al. (2014), as female ages were known from the overwintering generation. The experiment was conducted under semi-natural outdoor conditions with 66 females; three that did not lay eggs were excluded. Of the remaining 63, 34 died before entering diapause, and 29 survived to diapause. All 63 females were included in the analysis, with age tracked until the last female died before diapause (88 days).

Egg laying, survival to adult emergence, daily fecundity, and daily sex ratio were used to construct $l_x m_x$ life tables, where l_x is the proportion of females surviving

to age x and m_x is the mean number of female offspring produced per female at age x . From these life tables, key demographic 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, $r_m = \ln R_o / T$, Finite rate of increase, $\lambda = \exp(r_m)$.

Mean estimates of demographic parameters and their standard errors were calculated 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-jack} . Pseudovalues were then computed as:

$$r_{i-pseudo} = n \cdot r_{all} - (n - 1) \cdot r_{i-jack}$$

This process was repeated for all n individuals. The resulting pseudovalues were used to calculate the mean and standard error for r_m , R_o , T , and λ .

2.2.3. Degree days

Average daily temperatures from 2021 to 2024 were used to calculate degree-day (DD) accumulation with a lower developmental threshold of 12.2 °C (Haye et al. 2014), following standard methods (Nielsen & Hamilton, 2009). DD were calculated for BMSB reared under natural temperatures in the Buda Arboretum from 1 April to key phenological stages, including first oviposition and adult emergence, for both overwintering and summer generations.

In 2024, DD were calculated for each developmental stage, as nymphs from the 2nd instar onward were reared individually (overwintering, $n = 2,143$; summer, $n = 2,057$). For the overwintering generation, DD and preoviposition were calculated from 1 April to the day before first oviposition, as individual emergence dates were unknown. For the summer generation, DD and preoviposition were calculated for each female from adult emergence to the day

before first oviposition. DD for each instar were calculated from the start of the stage until moulting to the next.

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

Parasitoid surveys of BMSB in Hungary were conducted using two methods: assessing parasitism in naturally laid eggs in cages and collecting wild egg masses.

2.3.1. Naturally laid eggs in cages

In 2021, this experiment was conducted from April to September. Cages (100 × 30 × 30 cm, 3 × 3 mm mesh) (Costi et al. 2018) were placed on twigs of selected host plants, and three adult BMSB pairs were introduced. The mesh allowed parasitoid entry but prevented adult escape. Adults were fed beans, apples, and carrots, with food replaced twice weekly and dead adults substituted. Eggs were exposed to natural parasitism, then collected and placed in Petri dishes (15 × 100 mm) in the laboratory. Emerging nymphs were removed, and unhatched eggs were monitored for parasitoids. Experiments were set up at 30 locations in the Buda Arboretum, Budapest. In 2022, the experiment was repeated in an apple orchard at the Hungarian University of Agriculture and Life Sciences Experimental Farm, Soroksár (47.3966° N, 19.1418° E), from May to September (no insecticide use).

2.3.2. Wild egg masses

From 2021 to 2022, wild BMSB egg masses were surveyed across Hungary from June to September, with single collections in Novi Sad (Serbia), Sofia (Bulgaria), and Oradea (Romania). Visual inspections targeted frequently visited plant species, including *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). In 2021, surveys were conducted in Budapest and Érd, and in 2022 in Budapest (urban- Budapest

and agricultural areas-Budapest–Soroksár), Tarcál, and Szeged. Habitats were classified as urban sidewalk, urban park, or agricultural areas. Collected egg masses were placed individually in Petri dishes (~23 °C) to monitor nymph or parasitoid emergence. Hatched nymphs, emerging parasitoids, and unhatched eggs were recorded. Egg masses and first-instar nymphs were identified following Kobayashi (1967) and Hoebeke & Carter (2003).

2.3.3. Parasitoid identification

Emerging parasitoids were preserved in 1.5 mL microcentrifuge tubes with 90% ethanol for identification. Morphological identification was performed by Dr. Francesco Tortorici (DISAFA, University of Torino) using taxonomic keys. Eupelmidae; Askew & Nieves-Aldrey (2004) and Peng et al. (2020); *Trissolcus* spp. using Talamás et al. (2017), Tortorici et al. (2019), and Moraglio et al. (2021); and *Telenomus* using Tortorici et al. (2024). All specimens were deposited as vouchers in the DISAFA entomological collection, University of Torino, Italy.

2.3.4. Evaluation of parasitoid efficiency

Parasitoid efficiency was assessed for each location and year following Bin & Vinson (1991) and Rot et al. (2021).

2.4. Statistical tools and analysis

Overwintering mortality was compared between wild-collected and experimentally reared adults, and between sexes, using two-sample Z-tests. Marascuilo's procedure tested differences in diapause adult mortality among years and developmental stages mortality across and within three study sites (2021–2023). Ratios of eggs laid and hatched eggs per subinterval were compared using pairwise binomial tests with Holm's correction, and egg-to-adult development ratios were compared with Fisher's exact test. All analyses were performed in R (v4.5.1 R Core Team, 2025) using the multcompView package (GRAVES et al. 2024).

3.0. RESULTS AND DISCUSSION

3.1. Overwintering survival

Overwintering mortality of wild BMSB adults was high: 64.53% (2021), 71.78% (2022), and 59.11% (2023), while experimentally reared adults showed lower mortality: 63.42% (2021), 54.78% (2022), 53.78% (2023), and 36.66% (2024). Mortality was significantly lower in experimentally reared adults ($p < 0.05$). Reported overwintering mortality studied in Europe under natural temperature includes Switzerland: 39% (HAYE et al. 2014), western Slovenia: 71–81% (ROT et al. 2022), and northern Italy: 86% (COSTI et al. 2017). High mortality reflects the cold-intolerant nature of BMSB, with survival declining below 5 °C and during frost (SCACCINI et al. 2019). Lower survival of wild adults may result from limited nutrient reserves at diapause entry, whereas continuous food in experimental rearing likely enhanced survival (FUNAYAMA et al. 2012).

3.2. Phenology

Overwintered adult BMSB became active in early April. One generation occurred in 2021, and two generations per year from 2022–2024. Oviposition of the overwintering generation began in mid-June in 2021 and 2023, but earlier in late May in 2022 and 2024, at daily mean temperatures (DMS) of 15.6–23.15 °C. Peak oviposition generally occurred in June at 20–25 °C. The highest egg deposition dates were 28 June–3 July (2021), 11–13 June (2022), 1–4 July (2023), and 17–19 June (2024). Adult emergence from these eggs occurred mid-July to early September (2022–2024) and 13 August–23 September (2021). Maximum egg-to-adult development corresponded to oviposition on 24–27 June (2021), 2–4 June (2022), 11–13 June (2023), and 24 May–13 June (2024).

Summer generation oviposition began on 23 July 2024, 4 August 2022, and 8 August 2023, with peak oviposition about one week later. Highest egg numbers occurred on 23–25 August (2022), 13–15 August (2023), and 7–9 and 19–21 August (2024). Eggs laid after 2 September did not hatch, and nymphs from eggs

laid after 25 August (2022–2023) or 30 August (2024) failed to reach adulthood. Adult emergence occurred from the third week of September to mid-October (2022–2023) and from the first week of September to the first week of November (2024). In 2023, several 3rd–5th instar nymphs became inactive with autumn onset and died by early November. In 2024, of 246 nymphal instars that entered inactivity, 94 died by mid-December, and the remaining 152 overwintered but ultimately did not survive.

Spring temperatures influenced the number of generations and the timing of oviposition. In 2021, mean April and May temperatures were 10.57 °C and 14.23 °C, resulting oviposition in mid-June. From 2022 to 2024, higher spring temperatures (April: 11.81–14.80 °C; May: 17.66–18.74 °C) corresponded with earlier oviposition, occurring 7–25 days earlier than in 2021. Notably, March 2024 had the highest average daily temperature among all study years, likely contributing to the earlier onset of oviposition and adult emergence.

This study shows that BMSB life cycles in the region are strongly influenced by temperature and photoperiod. Overwintering adults became active at mean daily temperatures above 14 °C and photoperiods >12 h, consistent with observations in Italy and Slovenia (COSTI et al. 2017, ROT et al. 2021). The univoltine pattern in 2021 was likely due to cooler spring temperatures, whereas warmer springs from 2022–2024 allowed a second generation, aligning with reports from Western Slovenia, Italy, Switzerland, and the USA (NIELSEN & HAMILTON 2009, COSTI et al. 2017, ROT et al. 2022, STÖCKLI et al. 2020).

3.2.1. Degree days (DD) and development time

Degree days (DD) and development times were calculated for all developmental stages in 2024 in Buda Arboretum at natural temperature. 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 (calculated from 1st April) and 13.98 ± 0.44 (SE) days in the summer generation.

In Swiss univoltine populations, development lasts 2–4 months, whereas 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. MUSOLIN et al. (2019) showed that short day lengths accelerate nymphal development and induce adult diapause, while long days promote reproduction, with a critical photoperiod of ~ 15.5 h at 24 °C, and diapause can also be induced by low temperatures in both nymphs and adults (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 this stage, 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 fourth instars 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).

During the preoviposition period, DD accumulation using a 12.2 °C threshold was 342.30 ± 8.59 (SE) DD in the overwintering generation (calculated from 1st April) 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. In Europe, degree days (DD) have been studied using a 12.2 °C threshold (HAYE et al. 2014). In Switzerland,

the first generation from egg to adult emergence required 588.24 DD (HAYE et al. 2014). In Western Slovenia, values were 530 DD for the first generation, 545 DD for the second, and 179 DD for the second generation's preoviposition period (ROT et al. 2022).

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 adults begin oviposition at 214–255 DD and adult emergence at 689–878 DD, with summer generation oviposition at 850–958 DD. Considering these values, overlaps between late stages of the overwintering generation and early stages of the summer generation are possible. Such overlaps can influence 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 intervention timing.

3.2.2. 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). From 2021–2023, in both generations, mortality was highest in early instars (1st–3rd) and lower in later instars, but in 2024 the 5th instar showed the highest mortality in both overwintering (14%) and summer (24%) generations. The 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.

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. 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, egg production ranges from 76 eggs in Western Slovenia to 214.7 eggs in Northern Italy. 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). 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 where photoperiod below 15h reduces ovarian development (REZNIK et al. 2022).

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). In the present investigation, BMSB were reared on carrots, sunflower seeds, and peanuts, but the effects of diet on adult longevity and fecundity were not examined. Previous studies indicate that diet composition influences these traits, with mixed diets (e.g., carrots with peanut and soybean) improving survival and

egg production compared with single diets (FUNAYAMA 2006; DINGHA & JACKAI 2017).

3.2.3. Demographic growth parameters

In the summer generation of 2024, demographic growth parameters were calculated under natural temperature conditions; the recorded mean generation time (T) was 80.444 ± 0.636 (SE) days, net reproductive rate (R_0): 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).

The mean temperature from the onset of female reproduction to the last oviposition was 24.1 °C, and the intrinsic (r_m) and finite (λ) rates of increase were consistent with laboratory studies at constant temperatures of 23 – 25 °C (GOVINDAN & HUTCHISON 2020; NIELSEN et al. 2008; MERMER et al. 2023). Previous studies reported generation times (T) of 79 days at 23 °C (GOVINDAN & HUTCHISON 2020) and 103 days at 25 °C (MERMER et al. 2023), whereas in this outdoor study T was measured from birth to diapause entry, with 33 of 63 females entering diapause. Positive r_m and $\lambda > 1$ indicate population growth. As the study was conducted outdoors with protection from parasitoids/predators and precipitation, temperature was likely the main factor affecting population growth, though demographic parameters may vary annually.

This study suggests climate-driven changes may allow BMSB to shift from one to two generations per year in Hungary, raising risks of crop damage and overwintering nuisance, though reproductive rates remain lower than in Mediterranean regions (COSTI et al. 2017). Our findings indicate population growth, with early spring egg-laying potentially producing a second generation. Warm autumns may enable summer instars to reach adulthood, increasing overwintering populations, while mild winters further boost survival (e.g., a 1 °C rise above 4 °C increases survival by 13%; KIRITANI et al. 2007). Without natural enemies, these conditions may drive substantial growth in following years.

These phenological and biological data can improve timing of control measures and pest forecasting in Hungary.

3.3. Parasitoid Studies

3.3.1. Naturally laid eggs in cages

In 2021, 85 BMSB egg masses were collected from 30 cages in the Buda Arboretum, with no parasitism observed. In 2022, 47 egg masses were collected in a apple orchard (Soroksár); three egg masses (62 eggs) were parasitized identified as *Anastatus bifasciatus*, with a parasitism rate of 0.79%. In both years, oviposition occurred from July to early September, with parasitized egg masses in 2022 appearing only in early August

3.3.2. Wild egg masses

In 2021, wild BMSB egg masses were collected from Soroksár (11), Budapest Centre (26), and Érd (16). No parasitoids emerged from Érd. From 288 eggs in Soroksár, parasitism was 4.51% (13 *A. bifasciatus* from one egg mass); from 475 eggs in Budapest Centre, parasitism was 11.37% (54 parasitoids, *A. bifasciatus* and *Ooencyrtus* sp., including co-occurrence in one mass). From neighboring cities of Hungary, Oradea, 17 egg masses (395 eggs) yielded 112 parasitoids (28.35%), mainly *A. bifasciatus*, with co-occurrence of *Tr. mitsukurii* with *Tr. basalis* and *A. bifasciatus* from single egg mass. In Sofia, two egg masses (33 eggs) produced seven *A. bifasciatus* (21.21%). In Novi Sad, one of four egg masses was parasitized by *A. bifasciatus* and non-native *Tr. japonicus*.

In 2022, BMSB egg masses were collected in Hungary from Budapest (Centre, Csepel, Soroksár), Szeged, and Tarcsl. Only one mass from Tarcsl had no parasitization. Szeged (45), Budapest Centre (38), and Soroksár (6) yielded 1,076, 859, and 110 eggs, with 74, 107, and 16 parasitoids, respectively, corresponding to parasitism rates of 6.88%, 12.46%, and 14.55%. Species found were *Anastatus bifasciatus*, *Ooencyrtus* sp., *Trissolcus japonicus* (Budapest), *Tr. basalis*, *Tr. colemani*, and *Telenomus truncatus*.

Multiple egg parasitoid species, including two non-natives, were identified in Hungary and neighboring regions. Hungary recorded six species—*Anastatus bifasciatus*, *Ooencyrtus* sp., *Trissolcus japonicus*, *Tr. basalis*, *Tr. colemani*, and *Telenomus truncatus*—with *Tr. japonicus* reported for the first time. *Tr. mitsukurii* was first recorded in Romania. *A. bifasciatus* was the most common native species, consistent with prior European and U.S. studies. (JONES et al. 2014, COSTI et al. 2019, MORAGLIO et al. 2020, ROT et al. 2021).

Adventive populations of *Tr. japonicus* have been reported in Switzerland, Italy, Slovenia, Germany, France, and Serbia (SABBATINI PEVERIERI et al. 2018, STAHL et al. 2019, ROT et al. 2021, DIECKHOFF et al. 2021, MARTEL et al. 2024, KONJEVIĆ et al. 2024). Bioclimatic models indicate *Tr. japonicus* prefers southern Europe, while *Tr. mitsukurii* favors higher latitudes, with central Europe suitable for both (TORTORICI et al. 2023). Although not detected in Hungary, *Tr. mitsukurii* was found at neighboring city (Oradea), suggesting it may already be present or appear soon.

Co-occurrence of native and non-native parasitoids within single egg masses, observed here and in other studies, indicates potential for combined biological control, though interspecific interactions and non-target effects require careful evaluation (KONOPKA et al. 2017). Potential impacts on non-target species remain a concern. In Switzerland and Italy, *Tr. japonicus* parasitized 15 of 18 non-target pentatomid species, usually at lower rates than BMSB, with *Pentatoma rufipes* most affected (HAYE et al. 2024).

Urban areas in Hungary had higher BMSB egg densities and greater parasitoid diversity than agricultural areas. The survey was conducted randomly in urban and agricultural areas but focused more on urban sites. A more extensive survey across orchards and agricultural areas in Hungary is needed to better assess BMSB egg masses and parasitoid diversity.

4.0. CONCLUSION AND RECOMMENDATION

Between 2021 and 2024, research was conducted in Hungary to examine the phenology, life cycle, and key biological parameters of BMSB, along with a survey to identify and assess its potential egg parasitoids.

4.1. 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.
2. BMSB adults emerged from overwintering when daily mean temperatures exceeded 14 °C and day length exceeded 12 hours, typically in late March–early April. A univoltine in 2021, and bivoltinism from 2022–2024, linked to warmer springs. Spring temperatures strongly affect voltinism and first oviposition, with warmth enabling earlier egg-laying and a possible second generation.
3. In 2021 (univoltine), oviposition occurred from mid-June to late July, with adult emergence from mid-August to late September. In 2022–2024 (bivoltine), the overwintering generation laid eggs from late May to mid-July, and adults emerged after mid-July. The summer generation oviposited from late July/early August to early September; eggs laid after 2 September failed to hatch. Second-generation adults emerged from September to early November, with late overwintering generation nymphs overlapping early summer generation stages. Pest management should target periods of peak activity for effective control.
4. Egg-to-adult development averaged 48.74 days in the overwintering generation and 67.57 days in the summer generation. In summer, the first to fourth nymphal instars developed in 5–12 days, while the fifth instar took ~31 days, likely due to low autumn temperatures (mean 13.2 °C in October). Most nymphs remained in the fifth instar in autumn, so few reached adulthoods by early November. About 5% of fourth instars and

30% of fifth instars entered diapause but did not survive winter, likely from insufficient nutritional reserves.

5. Degree days (DD) were calculated using a 12.2 °C minimum threshold at natural temperature conditions (HAYE et al. 2014). Egg-to-adult DD averaged 611.32 ± 2.76 (overwintering) and 569.16 ± 2.24 (summer). From 1 April to key life stages at Buda Arboretum (2021–2024): overwintering generation—first oviposition 214.77–254.86 DD, first hatching 309.50–325.64 DD, adult emergence 689.27–878.87 DD; summer generation—first oviposition 850.70–958.33 DD, hatching 909.60–1089.67 DD, adult emergence 1317.55–1532.95 DD. These findings provide valuable data for developing pest forecasting models for BMSB in Hungary.
6. Females produced up to 7 egg masses in the overwintering generation and 9 in the summer generation, with average fecundity of 70.9 and 90.4 eggs per female, respectively.
7. The net reproductive rate of increase (R_0) was calculated in 2024, 5.39 for the overwintering generation and 2.21 for the summer generation. In summer 2024, demographic growth parameters were assessed under semi-natural conditions (mean 24.1 °C), the 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, so diet- or parasitization/predation-related fertility and mortality were not considered. Temperature was the main factor affecting population growth. Demographic parameters may vary annually, and actual field R_0 may differ from these values.
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.

4.2. Survey on egg parasitoids of *Halyomorpha 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—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 and 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 *Anastatus bifasciatus*. Alongside native parasitoid species, *Trissolcus japonicus* and *Tr. mitsukurii* were documented for the first time in Hungary and Romania, respectively. The study observed the coexistence of native and non-native parasitoid species within single BMSB eggs mass—such as *A. bifasciatus* with *Tr. 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. Therefore, integrating urban habitats into pest monitoring and management is essential for enhancing the natural control of BMSB populations.
 7. Further research is required to better understand the interactions between native and non-native species, as well as the mechanisms by which 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.

5.0. 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 *Trissolcus 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.

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LIST OF PUBLICATIONS

PUBLICATIONS RELATED TO THE TOPIC OF THE THESIS

Journal articles:

Wahengbam, J., Király, K. D., Radácsi, P., Fail, J., Véték, G., Tortorici, F., & Hári, K. (2025). First records of egg parasitoids of *Halyomorpha halys* (Stål, 1855) (Hemiptera, Pentatomidae) in Hungary. *NeoBiota*, 103, 215-230. <http://doi.org/10.3897/neobiota.103.162386> (Scopus Q1, SJR:1.061)

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