JEE ISSN: 2288-1220
https://doi.org/10.5141/jee.25.039
Journal of Ecology and Environment (2025) 49:16

RESEARCH

Phenology of *Epilachna quadricollis* (Dieke) (Coccinellidae: Epilachnini) in Korea

Jang-Hoon Lee*

Research Institute for Natural Science, Dongguk University, Seoul 04620, Republic of Korea

ARTICLE INFO
Received May 3, 2025
Revised June 9, 2025
Accepted June 11, 2025
Published on July 15, 2025

***Corresponding author**
Jang-Hoon Lee
E-mail ecojhl@dongguk.edu

Background: *Epilachna quadricollis* (Dieke) (Coccinellidae: Epilachnini) is the only known species in Korea that hibernates as a 4th instar larva, unlike most phytophagous coccinellids, which overwinter as adults. This study was conducted to understand its distribution, seasonal phenology, developmental patterns, and reproductive traits through field surveys across Korea and laboratory observations, providing baseline data for future studies on its ecological adaptations.
Results: *Epilachna quadricollis* undergoes four larval instars and overwinters as a mature 4th instar larva. Except for slight variation observed in the 2nd instar, head capsule width was a reliable indicator for distinguishing larval developmental stages. The mean duration of the development from oviposition to the new 4th instar was 43.1 days. Females laid a mean of 51.5 ± 2.8 (SE) eggs per cluster on the underside of leaves from June to mid-August, with a mean fecundity of 338.4 ± 93.2 (SE) eggs. Pupation began in late April, with adult emergence from mid-May. Oviposition began approximately 39 days after adult emergence and lasted for 19 days. The phenology of *E. quadricollis* was estimated by reorganizing multi-year field collection and observation records, and its feeding and development were closely linked to the phenology of *Fraxinus* spp.
Conclusions: This study provides detailed insight into the life history, seasonal development, and reproductive traits of *E. quadricollis*. Its univoltine cycle, closely synchronized with the phenology of *Fraxinus* spp., highlights the species' dependence on host plant availability. Larval stages can be reliably distinguished based on morphological characteristics, especially head capsule dimensions. The extended preoviposition period suggests that reproduction is regulated by photoperiod. Its confirmed distribution across several offshore islands—including Deachungdo Island, Jejudo Island, and Ulleungdo Island—highlights the need to investigate potential dispersal mechanisms and population connectivity.

Keywords: distribution, *Epilachna quadricollis*, life history traits, phenology

Introduction

Epilachna quadricollis (Dieke) (Coccinellidae, Epilachnini) is known to be distributed in Korea, China, and Taiwan (Borowski 2020; Jadwiszczak and Węgrzynowicz 2003). Unlike most species belonging to the ladybird beetle family, Coccinellidae, which exhibit carnivorous characteristics, the Epilachnini tribe including *E. quadricollis* demonstrates herbivorous behavior and is classified as paraphyletic group within the Coccinellidae (Lee 2015; Park and Yoon 1991). While most species of phytophagous ladybird beetles overwinter as adults, *E. quadricollis* is the only species known to overwinter as larvae in Korea. In taxonomic studies by Chûjô (1940) and Bielawski (1980), this insect has been recorded as a species distributed in North Korea.

Epilachna quadricollis inhabits mountainous areas and causes damage by feeding on the leaf tissue of *Fraxinus rhynchophylla* Hance, *Fraxinus sieboldiana* BL., and *Ligustrum obtusifolium* S. et Z., making the number of damaged leaves easy to identify with the naked eye. In South Korea, localized damage to *Fraxinus* spp. has been observed more frequently than damage to *Ligustrum* trees in mountainous areas. Because of the lack of information on distribution, phenology, development, and reproductive biology of this beetle in Korea and globally, field and laboratory studies were conducted to fill these knowledge gaps. The objectives of the current study are to describe the phenological characteristics of *E. quadricollis* within its natural habitat and to obtain data on its distribution in Korea, as well as life history traits, including voltinism, longevity, and fecundity.

Materials and Methods

Collection and site information of *E. quadricollis*

From 1983 to 1988, collections and observations were carried out at five sites in Gyeonggi Province—Mt. Cheonggyesan, Kwangjun-ri, Mt. Namhansan, Mt. Wangbangsan, and Mt. Yongmoonsan—with each site surveyed three to ten times. From 2017 to 2018, sampling and monitoring were conducted at five new locations across South Korea, due to the disappearance of populations at the original sites in Gyeonggi Province. Each site was monitored between three and nine times during the study period: Mt. Samgaksan on Daecheongdo Island (an island in the westernmost part of South Korea), Mt. Seonginbong on Ulleungdo Island (an island in the easternmost part), Mt. Halla on Jejudo Island (an island in the southernmost part), Mt. Mani on Ganghwado Island (an island in the mid-western part), and Mt. Tohamsan (located in the southeastern part of the mainland). All collection sites were mixed forests containing either *Fraxinus* spp., *L. obtusifolium*, or both. Except for Ulleungdo, all specimens were collected from *Fraxinus* spp., whereas on Ulleungdo, collections were made exclusively from *Ligustrum foliosum* Nakai.

The initial observation of adult *E. quadricollis* in Gwangjeon-ri, Namyangju County (Gyeonggi Province) occurred on June 14, 1983. Collections were carried out every 1–2 weeks until early November, yielding a total of 10 collections and observations. Through these efforts, the entire life cycle was observed in the field, from adults to eggs and from first to 4th instar larvae, including overwintering larvae. Based on the season-long collection in 1983, subsequent collections were conducted during the research period to supplement information on the onset and end of overwintering, as well as developmental patterns in the field.

Geographic information for the study area was obtained using Google Earth (Google Earth LLC 2024). Weather data for the survey areas were obtained from the Automated Synoptic Observing System and the Automatic Weather Station via the Korea Meteorological Administration's Meteorological Data Open Portal (Korea Meteorological Administration 2015). Weather data for the survey sites were collected from weather stations in close proximity. However, for past survey sites where there were no neighboring weather stations (Mt. Cheonggyesan, Kwangjun-ri, Mt. Namhansan, and Mt. Wangbangsan) during 1983–1988, data from the Seoul Weather Observatory were used as a reference. The Seoul Weather Observatory is situated 19–38 km from each of these sites. Details of these locations, including the years, their coordinates, and annual average temperatures, are presented in Table 1.

Table 1 Geographic and climatic information of the collection sites of *Epilachna quadricollis* in Korea

Collection sites[b]	Year	Coordinate	Elevation (m.a.s.l)	Yearly average temp. (°C)[a]
Mt. Wangbangsan,	1984	37°53′38″ and 37°53′51″N by	257–262	11.6
Gyeonggi Province	1988	127°06′32″ and 127°06′57″E		12.1
Mt. Cheonggyesan,	1986	37°26′30″ and 36°26′37″N by	80–120	11.2
Gyeonggi Province	1988	127°03′07″ and 127°03′17″E		12.1
Kwangjunri,	1983	37°41′27″ and 37°41′32″N by	50–70	12.4
Gyeonggi Province	1984	127°07′55″ and 127°08′04″E		11.6
	1985			11.6
	1986			11.2
Mt. Yongmoonsan,	1983	37°32′40″ and 37°32′44″N by	196–203	10.8
Gyeonggi Province		127°34′53″ and 127°35′00″E		
Mt. Namhansan,	1984	37°28′52″ and 37°28′54″N by	377–381	11.6
Gyeonggi Province	-85	127°11′04″ and 127°11′06″E		11.6
Mt. Manisan, Incheon	2017	37°37′22″ and 37°37′23″N by	157–167	11.5
	2018	126°25′30″ and 126°25′31″E		11.3
Mt. Samgaksan,	2018	37°48′55″ and 37°48′56″N by	292–297	11.8
Daecheongdo, Inchon		124°41′57″ and 124°41′59″E		11.0
Mt. Tohamsan,	2017	35°47′06″ and 35°48′02″N by	731–689	12.3
Gyeongsangbuk Province	2018	129°20′40″ and 129°20′48″E		12.1
Ulleungdo Island,	2017	37°29′09″ and 37°29′12″N by	273–250	13.1
Gyeongsangbuk Province	2018	130°53′34″ and 130°53′36″E		13.0
Mt. Hanllasan,	2017	33°21′24″ and 33°21′28″N by	1,096–1,099	10.2
Jeju Province	2018	126°27′47″ and 126°27′48″E		10.0

m.a.s.l: meters above sea level.
[a]The annual average temperature was obtained from data recorded at a nearby weather station. [b]The collection sites from 1984–1988 were located 9.9 to 37.7 km from the weather station, while those from 2017–2018 were 2.0 to 17.7 km away from the nearest weather station.

Phenology estimations of *E. quadricollis* in the central region

Insect phenology involves the timing of life events, including the number of generations (voltinism) (Gaytán et al. 2022). The seasonal timing and duration of life stages can vary greatly based on climate (Duan et al. 2018). For this reason, data from geographically distinct locations such as Daecheongdo, Ulleungdo, Mt. Hallasan, and Mt. Tohamsan were excluded from central-region phenology estimates.

Phenology was based on collection and observation data concerning developmental stages—such as overwintering larvae, pupae, adult emergence, oviposition, and larval development—gathered from six sites located within 36°26′–37°54′N and 126°25′–127°35′E in the Incheon and Gyeonggi Province areas. Mt. Manisan in Incheon was included in the phenological estimation along with past data from Gyeonggi Province, due to their similar geographic and climatic conditions (Table 1). Fifty records of collections and observations over 13 survey seasons—varying by area and year—were compiled monthly and every ten days to illustrate the occurrence of *E. quadricollis* by developmental stage. It is important to note that the life cycle illustrated for *E. quadricollis* represents a composite from several study periods and may be slightly longer than what would be observed within a single year.

Immature stage measurements and stage-specific development periods

Immature stage measurements

Adult *E. quadricollis* were collected from Kwangjun-ri in 1983 and reared on *F. rhynchophylla*. Their offspring were used to measure the immature stages. All experiments, including measurements and rearing of both adults and immatures, were conducted under ambient laboratory conditions (25°C ± 1°C, 65% ± 5% RH., with natural photoperiod), unless otherwise stated.

Larvae were classified from first to 4th instars based on the number of molts evidenced by exuviae. Larvae were measured under a microscope using an ocular micrometer (0.01 mm, 1 Div.) calibrated with a stage micrometer to determine their instar-specific body and head capsule sizes. Newly hatched larvae, newly molted 2nd, 3rd, and 4th instar larvae, mature 1st, 2nd, and 3rd instar larvae on the verge of molting into the next instar, and mature 4th instar larvae just before overwintering were used as specimens for measurement. The head capsule width was measured at the broadest part of the head, viewed dorsal and frontally. Body width was measured at the 3rd abdominal segment. Measurements that incorporated spines (scoli) involved the distance between the distal points of the subdorsal scoli on both sides of the 3rd abdominal segment. The body length measurement did not include the spines; the distance from the anterior end of the head (in dorsal view) to the posterior end of the abdomen was measured. All measurements were made to the nearest 0.01 mm.

Stage specific developmental period

To determine the stage-specific developmental periods of *E. quadricollis*, overwintering larvae collected from Mt. Namhansan on March 22, 1988, and their offspring were used for the study. The hibernating larvae were put in large plastic Petri dishes (150 × 25 mm) lined with paper towels, containing 10–20 individuals per dish, and observed daily to examine developmental changes. To maintain humidity within the large petri dishes, filter paper slightly moistened with water using a pipette (Ø55 mm, Whatman no.2) was placed inside. Upon pupation, individuals were immediately separated and placed individually in smaller Petri dishes (Ø 60 ×15 mm) to measure the duration until adulthood.

The adults emerging from pupae were reared in groups (4 males: 4 females) in cylindrical transparent plastic tubes (Ø9 × 16.5 cm, 3 mm thick), which served as rearing containers. Both ends of the tubes were covered with plastic Petri dish lids (Ø9 × 15 mm). As food, bouquets were made by inserting three small twigs (16 cm long, each with three leaves) into a vial (6 cm × Ø2.5 cm), and the junction between the vial opening and the twigs was sealed with Parafilm to prevent water leakage. A total of four rearing containers were maintained, and the offspring of the adults were used to assess the developmental duration of immature stages.

Newly laid egg masses in the rearing containers were randomly selected and individually transferred to Petri dishes (Ø 90 × 15 mm) containing fresh food leaves, and the egg period, defined as the time until hatching into the 1st instar larva (n = 51). To separate egg masses laid in the rearing containers without causing damage, leaves with attached egg masses were carefully detached or only parts with egg mass were excised, minimizing impact on the eggs.

Newly hatched larvae were randomly selected to measure the duration of each larval stage. Each larva was reared individually up to the 4th instar, and the duration of each developmental stage was recorded (Table 2). To minimize disturbance when separating the 1st instar larvae (newly hatched) or 2nd and 3rd instar larvae (newly molted), the leaf to which they were attached was gently removed, minimizing handling shock.

Reproductive schedule: adult longevity, fecundity, and oviposition periods

To obtain data on reproductive traits such as lifespan, egg production, and oviposition period, *E. quadricollis* adults were collected from the field (Mt. Namhansan on May 29, 1986) immediately after emergence and before feeding, and brought to the laboratory. They were identi-

Table 2 Measurements of the immature stages of *Epilachna quadricollis* (in millimeters)

Stardium	Length of body excluding spine		Width of body including spine		Width of body excluding spine		Breadth of head-capsule	
	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*
Egg	0.93 ± 0.04^{a,*}	20			0.42 ± < 0.01^{a}	20		
New L1	0.99 ± 0.01^{b}	10	1.34 ± 0.01^{a}	10	0.47 ± < 0.01^{b}	10	0.41 ± < 0.01^{a}	10
Mature L1	1.86 ± 0.01^{c}	10	1.41 ± 0.02^{b}	10	0.75 ± 0.01^{c}	10	0.40 ± 0.01^{a}	10
New L2	1.86 ± 0.01^{c}	10	2.02 ± 0.02^{c}	10	0.79 ± 0.01^{c}	10	0.55 ± 0.02^{b}	10
Mature L2	2.52 ± 0.01^{e}	10	2.35 ± 0.03^{d}	10	1.26 ± 0.01^{e}	10	0.60 ± 0.02^{c}	10
New L3	2.31 ± 0.01^{d}	10	3.03 ± 0.01^{e}	10	1.15 ± 0.01^{d}	10	0.77 ± 0.01^{d}	10
Mature L3	4.03 ± 0.03^{g}	10	3.98 ± 0.02^{f}	10	2.09 ± 0.02^{g}	10	0.79 ± 0.01^{d}	10
New L4	3.86 ± 0.01^{f}	10	4.93 ± 0.03^{g}	10	1.95 ± 0.02^{f}	10	1.17 ± 0.01^{e}	10
Mature L4	6.80 ± 0.04^{h}	10	6.27 ± 0.02^{h}	10	3.22 ± 0.02^{g}	10	1.18 ± 0.01^{e}	10

Values are mean ± standard error.
*Means in the same column followed by the same letter are not significantly different (ANOVA, $p < 0.05$).

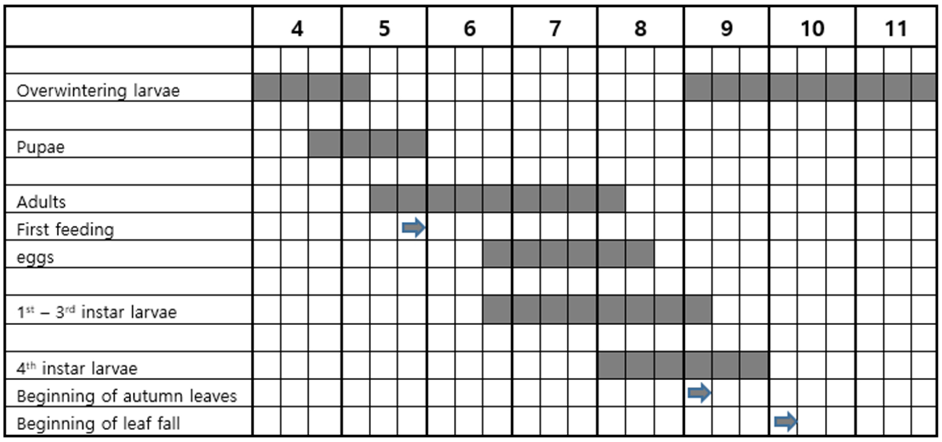

Fig. 1 Life history of *Epilachna quadricollis* in Central Korea. The activity periods of *E. quadricollis* were estimated based on collections and observations conducted between 1983–1988 and 2017–2018 in the Gyeonggi Province and Incheon regions, and represent a composite of data from 13 survey seasons.

fied as newly emerged based on their pale body coloration, a characteristic feature observed immediately after eclosion. They were placed in large Petri dishes (150 × 25 mm) and were fed leaves of *F. rhynchophylla*. Following mating within the Petri dishes, the pairs were isolated and reared in separate rearing containers (Ø9 × 16.5 cm high) and fresh food was supplied as needed by replacing it with fresh leaves. According to rearing records, adult beetles typically began feeding 2–5 days after emerging from pupae, with mating observed to begin approximately 13–20 days' post emergence. Rearing containers were checked daily for survival and the presence of eggs until female death. Males were not replaced if they died before the female, as the average longevity of *E. quadricollis* shows no significant difference between the sexes. Eight pairs of *E. quadricollis* were checked. The preoviposition and oviposition periods, along with fecundity, were recorded for each female. Longevity was assessed for both males and females. Egg masses laid by each female were individually transferred to Petri dishes (Ø 90 × 15 mm). The total number of eggs laid per mass was recorded.

Statistical analysis

The variation in size (mm) among immature developmental stages was assessed using one-way analysis of variance (ANOVA), while differences in longevity between female and male adult ladybugs were assessed with a Student's t-test. The developmental period across immature stages was analyzed with the Kruskal–Wallis test due to non-normality (Shapiro–Wilk test, $p < 0.05$). All measurements were reported as the mean ± standard error (SE), with the range represented by the 95% confidence interval (CI). Statistical analyses were conducted using SAS 9.4 (SAS Institute Inc. 2012), and differences were considered significant at $p < 0.05$.

Results

Phenology of *E. quadricollis* in the field

Pupation of overwintering larvae begins in late April, with the emergence of new adults from mid-May in the field. *E. quadricollis* undergoes three molts after hatching from eggs, and overwinter as mature 4th instar larvae, as shown in Figure 1.

Oviposition generally starts approximately 40 days following adult emergence (Fig. 1), which closely corresponds to the preoviposition period of 38.8 days measured in the laboratory (Table 4). From August onwards, both young larvae and mature (4th instar) larvae are commonly observed in surveyed areas (Fig. 1). In early to mid-September, both overwintering larvae and actively feeding 4th instar larvae were observed to coexist (Fig. 1), indicating variation among individuals in the timing of developmental progression and entry into diapause, rather than a synchronized transition into overwintering across the population.

This study confirmed the presence of *E. quadricollis* throughout South Korea, including the mainland with surveys at five sites in Gyeonggi Province from 1983 to 1988, as well as in regions ranging from Deacheongdo Island on the west to Ulleungdo on the east, and Jeju Province in the south where studies were carried out between 2017 and 2018 (Table 1).

Measurements of immature stages and development periods

The eggs are laid in clusters on the undersurfaces of leaves, lying flat against the undersurface rather than being attached at one end and projecting downward like those of *Epilachna vigintioctomaculata* (Moschulsky) (Coccinellidae) and related species. The eggs are 0.9–1.0 mm long and 0.42 mm wide (Table 2) and pale yellowish cream in color. The duration of the egg stage ranges from 4 to 10 days (5.5–6.8 CI), with a mean of approximately 6.2 days (Table 3). Egg masses contain between 21 and 97 eggs (45.8–57.2 CI), with a mean of about 52 eggs (Table 4).

The larva hatches by chewing the end of a thin, membrane-like sac enclosing the ovum, and subsequently develops through four larval instars. Feeding begins shortly after eclosion, and the larvae feed mainly on the undersides of leaves, although the 4th instar larvae occasionally feed on the upper sides. The developmental periods of larvae, excluding the overwintering 4th instar, were longest during the 3rd instar. There were no statistically significant differences among the 1st, 2nd instars, and the pupal stage (Table 3).

The changes in the measurements of head capsule width and body size (width and length) across developmental stages were examined (Table 2). The width of the head capsule increased with developmental stage, and within the same stage, the size difference between new and mature larvae was only significant at the 2nd instar (0.55 vs. 0.6, $p < 0.05$), with little difference observed at the other stages (1st, 3rd, and 4th instars). Conversely the body size (length and width) of mature larvae was significantly larger than that of new larvae at the same instar across all larval stages ($p < 0.05$). Changes in larval length and width before and after molting were compared (Table 2). No significant difference in size (length and width, excluding spines) were found between mature 1st instar and newly molted 2nd instar larvae, both measuring 1.86 mm in length, while the width was 0.75 mm in the mature 1st instar and 0.79 mm in the new 2nd instar. After the 2nd instar, the body size was shown to be smaller immediately after molting compared to before molting ($p < 0.05$). In contrast, spine-inclusive width measurements were consistently larger post-molting.

Reproductive schedule: adult longevity, fecundity, oviposition periods

The mean lifespan for females was 63.8 days, which was

Table 3 Developmental periods of the immature stages of *Epilachna quadricollis* under laboratory conditions

Host plant used for food	Duration of stage (days ± SE, 95% CI)					
	Egg	L1	L2	L3	L4	Pupa
Fraxinus rhynchophylla	6.2 ± 0.3[a] (5.5–6.8)	11.1 ± 0.4[b] (10.3–11.9)	12.0 ± 0.8[bd] (10.4–13.6)	13.8 ± 0.6[e] (12.5–15.1)	8–9 mo	11.5 ± 0.2[bc] (11.1–11.9)
No. individuals examined	54	31	31	31		21

Reared at ambient laboratory conditions (25°C ± 1°C, 65% ± 5% RH) with natural day length.
Means within a row followed by the same letter are not significantly different (Kruskal–Wallis test, $p < 0.05$).

Table 4 Reproductive schedules of *Epilachna quadricollis* fed on *Fraxinus rhynchophylla* under laboratory conditions

Reproductive traits	Mean ± SE (95% CI)	*n*
Longevity (in days) of males	56.6 ± 5.0[a,*] (44.7–68.6)	8
Longevity (in days) of females	63.8 ± 5.0[a] (52.0–75.5)	8
Preoviposition period (in days)	38.8 ± 4.1 (29.1–48.4)	8
Oviposition period (in days)	19.4 ± 4.4 (8.9–29.9)	8
Postoviposition period (in days)	5.6 ± 1.1 (3.0–8.2)	8
Fecundity (total no. of eggs laid per female)	338.4 ± 93.2 (118.0–558.7)	8
No. of eggs per mass	51.5 ± 2.8 (45.8–57.2)	52

Reared at ambient laboratory condition (25°C ± 1°C, 65% ± 5% RH) with natural day length.
[*]Longevity was compared between sexes using Student's t-test ($p > 0.05$). Means within a column followed by the same letter are not significantly different.

slightly longer compared to 56.6 days for male (Student's t-test, $p = 0.3312$). The oviposition period lasted 19 days, during which a mean of 338 eggs was produced. Eggs were laid in masses, with a mean of 52 eggs (range: 21–97) per mass. The preoviposition period extended for 39 days following adult eclosion (Table 4).

Discussion

Phenology of *E. quadricollis* in the field

The life cycle pattern of *E. quadricollis* closely resembles that of *Epilachna admirabilis*, which, according to Imai (2004), is distributed from northern to southern Japan, from Hokkaido to Kyushu. It is the only known species in Japan that overwinter as larvae (Katakura 1976). Research has shown that oviposition increases significantly during the shift from long to short photoperiods (Imai 2004; Katakura 1976). *Epilachna quadricollis* begins oviposition in late June (Fig. 1), shortly after the summer solstice, when day length starts to decrease. This timing suggests that its reproductive activity is similarly influenced by photoperiodic changes. Additionally, the cessation of feeding activity in September may be associated with a seasonal decline in the quality or availability of *Fraxinus* foliage, which is primarily influenced by environmental variables such as photoperiod, humidity, precipitation, and temperature (Han and Sim 1989; Keenan and Richardson 2015; Zhang et al. 2020). Variability in feeding duration among populations suggests that local environmental factors may further contribute to regional differences in host phenology, particularly in the timing of leaf senescence. At Mt. Tohamsan, where *Ligustrum* and *Fraxinus* coexist, *E. quadricollis* adults, eggs, and 1st instar larvae were observed on *Fraxinus* in early September. Despite *Ligustrum* retaining leaves until late autumn (until early November of 2017), *E. quadricollis* did not feed on it, suggesting overwintering is tied to the leaf fall of *Fraxinus*.

Mean annual temperatures at *E. quadricollis* sites in central Korea remained consistent over 30 years (1983–1988: 11.6°C ± 0.15°C, $n = 11$; 2017–2018: 11.5°C ± 0.13°C, $n = 4$). Other sites outside the phenology survey area averaged 11.78°C ± 1.36°C ($n = 6$), showing no significant difference (Table 1), suggesting that temperature is closely linked to habitat preference. Temperature is a critical abiotic factor affecting insect populations, impacting development rate, survival, fecundity, and dispersal (Bohannon et al. 2022; Lee and Elliott 1998; Rankin and Singer 1984; Ratte 1984).

The inland distribution of *E. quadricollis* in both North Korea (Kitano and Han 2014) and South Korea (Jeong et al. 2011; Korea Forest Service and National Park Research Institute 2014; Lim et al. 2011; Park 2008) has been found in several reports, yet this study is the first to report its presence on islands far distant from the mainland. On Ulleungdo, it was found exclusively on *L. foliosum* Nakai. The 2nd to 4th instar larvae were observed feeding on the host plant until the end of September, which is about a month later than on the mainland. Due to the limited duration and area of data collection on Ulleungdo, long-term research is required to better understand how its unique habitat affects the life cycle and ecology of the *E. quadricollis* population compared to the mainland. Whether this isolated population arose through natural dispersion or artificial introduction remains unclear.

Measurements of immature stages and development periods

The results of this study confirmed that head capsule width significantly differs between instars, making it a useful morphological marker for distinguishing larval stages. In contrast, overall body size excluding spines may, in general, temporarily decrease after molting, as the unsclerotized cuticle has not yet expanded (Nijhout 1981). During the intermolt period, the cuticle gradually unfolds as the larvae feed and grow, resulting in volumetric growth (Nijhout et al. 2014; Wolfgang and Riddiford 1981).

The developmental period from 1st to late 3rd instar (new 4th instar larva) for *E. quadricollis* was 36.9 days at 25°C ± 1°C, similar to that of *E. admirabilis* in northern Japan, which overwinters as larvae (Takeuchi et al. 2005). It was reported that the developmental period of *E. admirabilis* took 42.5 days on *T. cucumeroides* at 24°C from the 1st instar to the late 3rd instar. In contrast, *Henosepilachna vigintioctomaculata*, a contribal species that utilizes annual herbaceous plants (e.g., Solanaceae), undergoes 2–3 generations per year and exhibits rapid larval development (9.7 days from 1st to 3rd instar at 25°C; Kwon et al. 2010), typical of multivoltine species. On the other hand, both *E. quadricollis* and *E. admirabilis* show univoltine life cycles and extended developmental periods. Despite differences in host plant growth form—woody for *E. quadricollis* and herbaceous for *E. admirabilis* (Imai 2004; Katakura 1976; Takeuchi et al. 2005)—they both utilize long-lived, seasonally predictable host. These shared ecological traits may underlie the similarity in their developmental strategies, distinguishing them from species like *H. vigintioctomaculata* that exploit ephemeral, fast-turnover resources.

Reproductive schedule: adult longevity, fecundity, oviposition periods

Epilachna admirabilis and *E. quadricollis* coexist in Taiwan and China, but there are no reports of their presence together in Korea or Japan (Borowski 2020; Jadwiszczak and Węgrzynowicz 2003; Kurosawa et al. 1985). These species can be considered ecological homologues due to their similar life history traits, such as life cycle and reproductive characteristics. Imai (2004) reports that in mid-latitudes, photoperiod induces reproductive diapause in adult

E. admirabilis, which corresponds to the pre-oviposition period. Considering that species belonging to the tribe Epilachnini commonly exhibit reproductive diapause in response to photoperiod (Imai 2004), it is presumed that the extended pre-oviposition period in *E. quadricollis* is also influenced by photoperiod. However, the characteristic response, such as reduced feeding activity, observed in the diapause state of *E. admirabilis*, was not seen in *E. quadricollis*. In laboratory conditions, feeding begins within several days post-eclosion and continues until oviposition ceases, without typical signs of summer diapause.

Conclusions

This study provides comprehensive insights into the phenology, distribution, life cycle, developmental characteristics, and reproductive traits of *E. quadricollis* in Korea. Both field and laboratory data confirm that the species is univoltine and overwinters as a mature larva, with its development and reproduction closely synchronized with the phenology of *F. rhynchophylla*.

Morphological traits, including significant differences in head capsule size, serve as reliable indicators for larval stage differentiation.

The extended preoviposition period of approximately 40 days suggests a potential photoperiodic response, similar to that reported in the congeneric species *E. admirabilis* from northern Japan, indicating phylogenetic relatedness.

The relatively stable annual mean temperature (~11.6°C) at collection sites suggests that climate plays a significant role in limiting the species' geographical distribution and influencing its seasonal life cycle. In addition to known host plants (*Fraxinus* spp. and *L. obtusifolium*), *L. foliosum* was newly recorded as a host on Ulleungdo. The presence of *E. quadricollis* on isolated islands such as Ulleungdo raises questions about the mechanism by which the species' distribution has expanded, as well as the possibility of population differentiation.

Abbreviations

ANOVA: Analysis of variance
ARS: Agricultural Research Service
CI: Confidence interval
DIV: Division
MASL: Meters above sea level
RH: Relative humidity
SE: Standard error
USDA: United States Department of Agriculture

Acknowledgements

I am deeply grateful to Drs. R.W. Carlson, D.K. Reed, H.Y. Han, and J.H. Kim (formerly with USDA-ARS, Seoul) for their invaluable assistance with the field and laboratory studies on *E. quadricollis*. Special thanks are extended to Dr. R.W. Pemberton for his insightful suggestions and guidance on the manuscript.

Funding

This research in 2017–2018 was supported by a grant from 2016R1D-1A1B03932911.

Availability of data and materials

Not applicable.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The author declares that they have no competing interests.

References

Bielawski R. Die Marienkäfer (Coleoptera: Coccinellidae) der Koreanischen Volksdemokratischen Republik. Fragmenta Faunistica. 1980; 25:221-54.

Bohannon GR, Johnson CL, Jetton RM, Oten KLF. Phenology and voltinism of emerald ash borer (Coleoptera: Buprestidae) in central North Carolina. Environ Entomol. 2022;51(6):1077-85. https://doi.org/10.1093/ee/nvac088.

Borowski T. World inventory of beetles of the Subfamily Epilachninae Mulsant, 1846 (Coleoptera: Coccinellidae). Check list from 1758 to 2003. World News Nat Sci. 2020;30(1):1-74.

Chûjô M. Einige Coccinelliden aus Korea (Col.). Mushi. 1940;13(1):56-7.

Duan JJ, Bauer LS, Van Driesche RG, Gould JR. Progress and challenges of protecting North American ash trees from the emerald ash borer using biological control. Forests. 2018;9(3):142. https://doi.org/10.3390/f9030142.

Gaytán Á, Gotthard K, Tack AJM. Strong impact of temperature and resource specialisation on patterns of voltinism within an oak-associated insect community. Ecol Entomol. 2022;47(4):544-52. https://doi.org/10.1111/een.13139.

Google Earth LLC. Google Earth. 2024. https://earth.google.com/. Accessed 15 Apr 2024.

Han SS, Sim JS. Characteristics of photosynthesis and respiration in Fraxinus rhynchophylla Hance and Fraxinus mandshurica Rupr. leaves. J Korean For Soc. 1989;78(3):280-86.

Imai C. Photoperiodic induction and termination of summer diapause in adult *Epilachna admirabilis* (Coleoptera: Coccinellidae) from a warm temperate region. Eur J Entomol. 2004;101(4):523-9. https://doi.org/10.14411/eje.2004.074.

Jadwiszczak AS, Węgrzynowicz P. World catalogue of *Coccinellidae*. Part I – *Epilachninae*. Olsztyn: Mantis; 2003.

Jeong JC, Cha JY, Kwon JM, Choi JK, Nam SH, Choi M, et al. Historical review of the insect fauna and protected species in Byunsanbando National Park. J Natl Park Res. 2011;2(2):85-128.

Katakura H. On the life cycle of *Epilachna admirabilis* (Coleoptera: Coccinellidae) in Sapporo, Northern Japan, with special reference to its hibernation by adult stage. Kontyû. 1976;44(3):334-6.

Keenan TF, Richardson AD. The timing of autumn senescence Is affected by the timing of spring phenology: implications for predictive models. Global Change Biol. 2015;21(7):2634-41. https://doi: 10.1111/gcb.12890.

Kitano T, Han CD. Some results of field surveys in Democratic People's Republic of Korea (Coleoptera: Byrrhidae, Dermestidae and Coccinellidae). Arq Entomol. 2014;10:57-64.

Korea Forest Service and National Park Research Institute, Korea National Park Service. Insect stories of National Parks: Gyeongju Edition. 1st ed., Human Culture Arirang; 2014. in Korean.

Korea Meteorological Administration. Meteorological Data Open Portal. 2015. https://data.kma.go.kr/cmmn/main.do. Accessed 15 Apr 2024.

Kurosawa Y, Hisamatsu S, Sasaji H. Colored illustrations of the coleoptera of Japan. Osaka: Hoikusha; 1985.

Kwon M, Kim JI, Kim JS. Ecological characteristics of 28-spotted larger lady beetle, Henosepilachna vigintioctomaculata (Motschulsky) (Coleoptera: Coccinellidae) and its seasonal fluctuation in Gangneung, Korea. Korean J Appl Entomol. 2010;49(3):199-204. https://doi.org/10.5656/KSAE.2010.49.3.199.

Lee JH, Elliott NC. Temperature effects on development in *Aphelinus albipodus* (Hymenoptera: Aphelinidae) from two geographic regions. The Great Lakes Entomologist. 1998;3:173-9. https://doi.org/10.22543/0090-0222.1963.

Lee MJ. Systematic study of the Family Coccinellidae (Coleoptera) from Korea [PhD dissertation]. Andong: Andong National University; 2015.

Lim JS, Lee BW, Park SY, Jo DG. Insect Fauna of Maebongsan Mountain, Hongcheon-gun, Gangwon-do. J Korean Nat. 2011;4(4):293-307. https://doi.org/10.7229/jkn.2011.4.4.293.

Nijhout HF. Physiological control of molting in insects. Am Zool. 1981;21(3):631-40. https://doi.org/10.1093/icb/21.3.631.

Nijhout HF, Riddiford LM, Mirth C, Shingleton AW, Suzuki Y, Callier V. The developmental control of size in insects. WIREs Dev Biol. 2014;3(1):113-34. https://doi.org/10.1002/wdev.124.

Park HC, Yoon IB. A taxonomic revision of subfamily Epilachninae in Korea (Coleoptera: Coccinellidae). Entomol Res Bull (Korea). 1991;17:81-92.

Park JS. A study on the establishment of an inventory of insects inhabiting Jirisan and the derivation of detailed exhibition themes. Sejong: Ministry of Environment; 2008.

Rankin MA, Singer MC. Insect movement: mechanisms and effects. In: Huffaker CB, Rabb RL, editors. Ecological entomology. New York: Wiley; 1984. p. 185-216.

Ratte HT. Temperature and insect development. In: Hoffmann KH, editor. Environmental physiology and biochemistry of insects. Berlin: Springer Verlag; 1984. p. 33-65.

SAS Institute Inc. SAS/STAT® 9.4 User's Guide. Cary, NC; SAS Institute Inc; 2012.

Takeuchi M, Kishikawa H, Tamura M. Host use in relation to food availability and larval development in the specialist herbivore *Epilachna admirabilis* (Coleoptera: Coccinellidae). Jpn J Appl Entomol Zool. 2005;40(1):177-84. https://doi.org/10.1303/aez.2005.177.

Wolfgang WJ, Riddiford LM. Cuticular morphogenesis during continuous growth of the final instar larva of a moth. Tissue Cell. 1981;13(4):757-72. https://doi.org/10.1016/S0040-8166(81)80012-2.

Zhang S, Dai J, Ge Q. Responses of autumn phenology to climate change and the correlations of plant hormone regulation. Sci Rep. 2020;10:9039. https://doi.org/10.1038/s41598-020-65704-8.