



Oviposition patterns of an eruptive butterfly, *Aporia crataegi* L. (Lepidoptera: Pieridae), in an outbreak population

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Abstract

Patterns of egg distribution in eruptive phytophagous insects represent an important, yet understudied, component of their population dynamics. This study investigates oviposition strategies in an eruptive lepidopteran species, the black-veined white (*Aporia crataegi*), during the peak phase of an outbreak cycle. We analysed the number and size of egg clutches in relation to the characteristics of host plants. Additionally, we examined the colonisation dynamics of these host plants during the outbreak. Our findings demonstrate that *A. crataegi* exhibits selective oviposition. Females most frequently lay eggs on *P. padus*, with *M. baccata* and *S. aucuparia* being selected less frequently. Less preferred host plants are colonised with a greater selectivity; thus, most trees remain uncolonised, while individual trees exhibit a high density of egg clutches. Females preferentially oviposit on taller plants and do not avoid those defoliated within the current growing season, although depositing smaller clutches on such hosts. During the outbreak, colonisation rates increase on less preferred host plant species—*M. baccata* and *S. aucuparia*. We found no evidence of conspecific clutch avoidance, since clutch distribution across all host plants was aggregated. The highest degree of aggregation was observed on the least preferred host plant—*S. aucuparia*. The implications of clutch aggregation for offspring fitness and population dynamics are discussed.

Keywords Oviposition site selection · Host plant · Clutch size · Preference-performance hypothesis · Aggregation · Black-veined white

Introduction

Oviposition timing and site selection constitute the main form of parental care in most insects (Reznik 2005; Hilker et al. 2023). During the complex process of locating an optimal oviposition site, female phytophagous insects utilise tactile, chemical, and visual cues (Schoonhoven et al. 2005; Carrasco et al. 2015). Females are known to discriminate not only between plant species but also among conspecific plants based on water and nutrient content, secondary metabolite concentrations, and the quantity of food available for their offspring (e.g., Chew and Robbins 1984; Floater and Zalucki 2000; Talsma et al. 2008; Dunska et al. 2024). Furthermore, females may take into account host plant

abundance, microclimatic conditions, and the presence of predators and competitors (Tjørnløv et al. 2015; Jaumann and Snell-Rood 2017; Ghosh et al. 2022; Nardi et al. 2023; Johansson et al. 2024).

Some phytophagous insect species lay eggs individually on plants, while others lay them in clutches. An egg clutch represents the proportion of a female's realised fecundity allocated to specific environmental conditions (Stamp 1980; Fordyce 2005). The spatial distribution of offspring is determined not only by oviposition site selection but also by clutch size (Reznik 2005).

According to the widely discussed preference-performance hypothesis, females select plants that provide optimal conditions for their offspring's survival and development (Jaenike 1978; Thompson and Pellmyr 1991). This hypothesis is broadly supported for mono- and oligophagous species that develop on native host plant species (Gripenberg et al. 2010; Jones et al. 2019; Jones 2022). The outcomes of plant-phytophage interactions, as well as the resultant fitness of offspring, may vary depending on numerous factors. Notably, eruptive insect species face sudden shifts in host

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plant quality and availability due to significant fluctuations in population density.

To date, the patterns of egg clutch distribution in eruptive phytophagous species under high population density and the shifts in these patterns during outbreak cycles remain poorly understood. High population density in outbreak foci leads to reduced quantity and quality of food resources available for offspring, activation of latent viral infections, and increased pathogen prevalence, ultimately diminishing the insects' viability and fecundity (Isaev et al. 2001; Nykänen and Koricheva 2004; Elderd et al. 2013; Myers and Cory 2013; Pavlushin et al. 2021). According to the preference-performance hypothesis, under elevated population density, females are expected to mitigate the adverse effects of overcrowding by distributing clutches more uniformly, i.e., by prioritising unoccupied leaves or plants (Ellis 2008; Wetzel and Strong 2015; Nardi et al. 2023).

On the other hand, according to Price's hypothesis (1994), a key prerequisite for eruptive population dynamics is the weak or absent linkage between female oviposition preferences and larval performance. Consequently, females of eruptive species are hypothesised to exhibit relatively low selectivity in oviposition. Price's hypothesis appears to be supported for species whose females do not deposit eggs directly on the substrate their offspring will consume (Tamaru et al. 1995; Koricheva et al. 2012). However, it has not been directly tested for eruptive species with different life-history traits.

In this study, we examine the oviposition patterns by a phytophagous insect during the peak of a population outbreak, analysing both the distribution of egg clutches on host plants and clutch size. The black-veined white, *Aporia crataegi* (Linnaeus, 1758) (Lepidoptera: Pieridae), was selected as the model species. This eruptive butterfly is widely distributed across the Palaearctic region. While currently rare in Western and Central Europe (Todisco et al. 2020), it continues to exhibit outbreaks in Eastern Europe and Siberia, remaining a significant pest of orchards and plantations (Kuznetsova and Palnikova 2014; Ivonin et al. 2018; Kulakova and Tatarinov 2019; Gailis et al. 2023). Females of *A. crataegi* lay 2–4 clutches in their lifetime, containing between 3 and 285 eggs (Krasnyuk 1928; Blunck and Wilbert 1962; Babenko 1982). The host plant leaf selected by the female for oviposition, alongside adjacent foliage, serves as both food for early-instar larvae and construction material for overwintering nests. Throughout much of its range, *A. crataegi* larvae feed on the foliage of woody Rosaceae species, including genera such as *Prunus* L., *Malus* Mill., *Pyrus* L., *Amelanchier* Medik., *Crataegus* L., *Sorbus* L., and *Cotoneaster* Medik. (Kuznetsov et al. 1999; Clarke 2024). In the Central Urals, its primary host plants are bird cherry *Prunus padus* L., rowan *Sorbus aucuparia* L., and Siberian crab apple *Malus baccata* (L.) Borkh.

(Zakharova et al. 2020). Previous research has demonstrated that *A. crataegi* predominantly colonises *P. padus* and, at low population densities, is absent from other host plants. Furthermore, larvae developing on *P. padus* exhibit significantly higher survival rates, faster growth rates, and larger body sizes compared to those developing on *S. aucuparia* (Zakharova et al. 2020; Solonkin et al. 2024).

We propose the following hypotheses:

1. The females of *A. crataegi* selectively deposit egg clutches on host plants that may potentially provide improved survival and development for offspring;
2. Under high population density during an outbreak peak, females will prioritise unoccupied leaves and plants, which may result in a relatively uniform distribution of egg clutches and a subsequent shift towards oviposition on less preferred host plant species.

Materials and methods

Study site

The research was conducted near the village of Fomino (Sverdlovsk Oblast, Sysertsky District, 56° 36' N, 61° 03' E). The study site is located in the taiga biome, specifically within the pre-forest-steppe pine-birch forest subzone (Kulikov et al. 2013). The landscape is dominated by pine forests intersected by paths and clearings and bordered by floodplain and upland meadows with diverse herbaceous vegetation.

Population dynamics

In order to assess the population density of *A. crataegi* near the village of Fomino in 2015–2024, adults were counted using the Pollard transect method (Pollard and Yates 1993). From 2019 onwards, overwintering nests were also recorded (Supplementary Table S1). The Pollard method involves counting individuals observed within an imaginary cube of defined dimensions in front of a researcher moving along a fixed route (transect). Adult counts were conducted along a 1.6 km × 10 m transect following a power line clearing through a pine forest (Fig. 1). The counts were performed during the peak flight period and only in dry weather, with a shade temperature of or above 14 °C.

The overwintering nests of *A. crataegi* consist of bundles of skeletonised leaves, tightly rolled together and secured to branches of host plants with silk thread. They are exposed and clearly visible (Supplementary Fig. S1a). Nests were counted annually in autumn on the same preselected trees of *P. padus*, *M. baccata*, and *S. aucuparia* in the pine forest understorey, with the total number on each plant recorded.

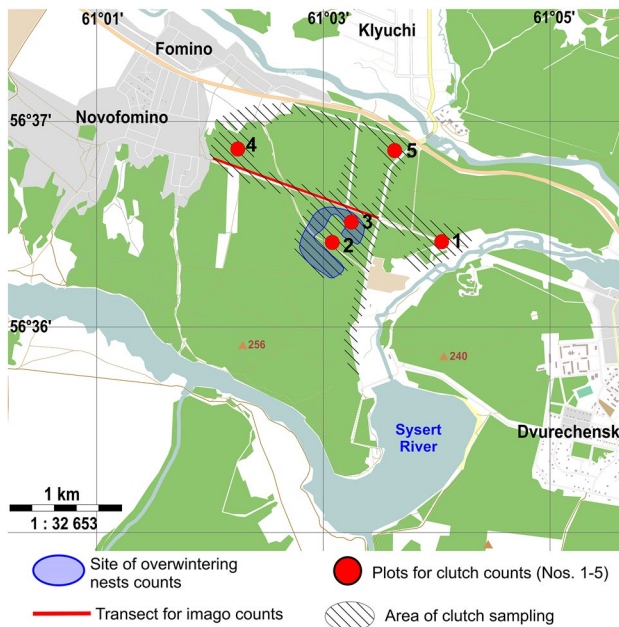


Fig. 1 Map of the study site near the village of Fomino

Based on these data, the proportion of host plants bearing overwintering nests relative to the total number surveyed was calculated. Some of the adult and nest count results have been published previously (Solonkin et al. 2024).

Egg clutch distribution

Egg clutch counts were carried out at the end of *A. crataegi* adult flight period (late June–early July 2024) across five study plots (Fig. 1). The distance between plots varied from 0.3 to 2 km, which falls within the typical dispersal range of adults (Watanabe 1978; Jugovic et al. 2017). Plot No. 1 was established in an open habitat beneath a power line clearing. It comprises two thickets: one of *P. padus* with *S. aucuparia* and the other of *M. baccata*, situated 25 m apart from each other. Plots Nos. 2–5 are squares with sides ranging from 10 to 20 m, located in a pine forest. The understorey of these forest plots was dominated by woody Rosaceae species: *S. aucuparia* and *P. padus*, with occasional presence of *M. baccata*, spiked serviceberry *Amelanchier spicata* (Lam.) K. Koch, 1869, and Peking cotoneaster *Cotoneaster acutifolius* Turcz., 1832. Plots Nos. 2 and 3 were established in sites where host plants exhibited low defoliation levels during the preceding study year (2023). In contrast, Plots Nos. 4 and 5 were positioned in sites that experienced localised outbreaks of *A. crataegi* in 2023, leading to near-total defoliation of host plants.

Egg clutches were counted on all woody Rosaceae plants taller than 0.6 m within the study plots. For each plant, we determined its growth form (tree or shrub), counted the

number of stems, visually estimated defoliation in 5% increments, measured height (as the length of the longest stem), and recorded minimum and maximum crown diameters (Table 1). Dead or dry stems and branches were excluded during measurements of plant height and crown dimensions. Plants retaining only post-defoliation regrowth leaves were scored as fully defoliated. Following this, we counted the total number of leaves and egg clutches on each plant. Small plants were surveyed in their entirety. For large plants, a single large first-order branch (on trees) or a large stem (on shrubs) was chosen for leaf and clutch counts. Crown projection area was calculated from the minimum and maximum crown diameters, assuming an oval crown shape.

Egg clutch size

Egg clutch sampling was carried out in 2023 and 2024 throughout the adult flight period. The collection day of each egg clutch was recorded, expressed as the number of days since the onset of adult flight. At the beginning of the generation's flight period, early-emerging females lay their first clutches. Subsequently, the proportion of repeat clutches from these females increases progressively, while clutches from later-emerging females also appear. Therefore, the day of egg clutch collection can serve as a proxy for the actual oviposition date. Clutches were collected from randomly chosen plants of *P. padus*, *S. aucuparia*, *M. baccata*, *A. spicata*, and *C. acutifolius*, growing both under the canopy of pine forests and in open habitats (Fig. 1; Table 2). Host plants were carefully inspected for the presence of clutches. On large, mature trees, only the lower canopy was examined. Young trees and shrubs, both small (< 2 m height) and large (2–4 m height), were inspected in their entirety. For each plant where clutches were found, its height was recorded and defoliation assessed (Table 2). Among branches with clutches, those measuring 40–70 cm in length were selected, cut, and transported to the laboratory followed by placement in water-filled containers. Discovered clutches (often multiple per branch) were labelled directly on the leaf using a permanent marker. The collected egg clutches were photographed on the host-plant leaf under a LOMO MSP-TM binocular microscope at 10× magnification using a TouPCam UCMOS05100KPA camera (Supplementary Fig. S1b). The resulting images were used to count the number of eggs per clutch in ImageJ software (Rasband 2014).

Data analysis

Statistical analysis was implemented in the R software environment (R Core Team 2024). The analysis of the proportion of host plants with overwintering nests was conducted using a binomial generalised linear mixed model. Host plant species and year were included as fixed effects; plant was

Table 1 Characteristics of host plants of *A. crataegi* examined in the study plots near the village of Fomino

Study plot, No	Host plant	N	Height, m (median; 25–75% quantiles)	Crown projection area, m ² (median; 25–75% quantiles)	Defoliation, % (median; 25–75% quantiles)
1	<i>P. padus</i>	18	1.48; 1.02–2.01	0.43; 0.31–1.15	0; 0–5
	<i>M. baccata</i>	27	1.32; 1.10–1.58	0.35; 0.18–0.56	0; 0–5
	<i>S. aucuparia</i>	2	1.85; 1.70–2.00	0.70; 0.62–0.78	0; 0–0
2	<i>P. padus</i>	3	0.80; 0.75–1.13	0.28; 0.19–1.01	40; 25–60
	<i>S. aucuparia</i>	65	1.90; 1.40–3.00	0.31; 0.11–1.10	15; 5–60
	<i>A. spicata</i>	10	2.12; 1.68–3.85	0.55; 0.28–1.54	5; 0–5
3	<i>P. padus</i>	12	1.65; 0.90–2.23	0.82; 0.46–1.59	25; 10–65
	<i>M. baccata</i>	2	2.35; 1.73–2.98	2.04; 1.04–3.05	50; 25–75
	<i>S. aucuparia</i>	20	1.54; 1.14–2.54	0.23; 0.13–1.01	0; 0–6.25
4	<i>P. padus</i>	53	1.20; 0.90–1.65	0.14; 0.06–0.33	0; 0–5
	<i>M. baccata</i>	2	2.25; 2.03–2.48	1.00; 0.64–1.35	2.5; 1.25–3.75
	<i>S. aucuparia</i>	78	1.55; 1.20–2.48	0.20; 0.11–0.49	0; 0–0
5	<i>P. padus</i>	118	1.55; 1.20–2.92	0.66; 0.19–1.89	10; 5–20
	<i>M. baccata</i>	71	1.60; 1.23–3.43	0.47; 0.12–1.40	5; 5–20
	<i>S. aucuparia</i>	40	1.49; 1.14–2.93	0.37; 0.13–2.34	2.5; 0–10
	<i>A. spicata</i>	7	2.10; 1.29–2.53	1.18; 0.51–1.24	5; 5–5
	<i>C. acutifolius</i>	2	1.08; 1.06–1.09	0.56; 0.52–0.60	2.5; 1.25–3.75

Table 2 Sample sizes of *A. crataegi* egg clutches collected near the village of Fomino in 2023–2024

Year	Sampling dates	Host plant	Number of plants	Height, m (median; 25–75% quantiles)	Defoliation, % (median; 25–75% quantiles)	Number of egg clutches
2023	11.06.–20.07	<i>P. padus</i>	47	1.8; 0.55–2.5	50; 2.5–100	167
	11.06.–13.07	<i>S. aucuparia</i>	33	2.0; 1.5–2.0	20; 0–100	78
	11.06.–29.06	<i>M. baccata</i>	24	2.0; 1.3–2.75	0; 0–8	49
	14.06.–26.06	<i>A. spicata</i>	8	1.1; 0.65–1.5	0; 0–0	8
2024	15.06.–15.07	<i>P. padus</i>	120	2.0; 1.0–3.5	17.5; 0–100	439
	15.06.–17.07	<i>S. aucuparia</i>	94	2.25; 1.5–3.0	0; 0–0	191
	15.06.–17.07	<i>M. baccata</i>	59	2.0; 1.45–4.0	0; 0–0	168
	16.06.–11.07	<i>A. spicata</i>	17	2.0; 1.5–3.0	0; 0–0	24
	23.06.–05.07	<i>C. acutifolius</i>	4	1.55; 0.95–2.0	0; 0–0	8

treated as a random factor. No predictor interactions were included.

Egg clutch density (mean number of clutches per leaf) was analysed in relation to host plant species, plant height, crown projection area, and defoliation level, with the study plot being included as a random factor. A Tweedie distribution was used to model the dependent variable. A significant correlation was found between plant height and crown projection area ($r=0.73$; $df=1$; $p<0.001$), resulting in moderate collinearity between the predictors (Supplementary Table S2). Nevertheless, we retained both predictors in the model, since the Akaike information criterion (AIC) provided support for their inclusion: the model containing both plant height and crown projection area was substantially better than the model excluding crown projection area

($\Delta AIC=11.1$) and the model using their product (i.e., crown volume) as a combined predictor ($\Delta AIC=27.6$).

Clutch size was analysed in relation to host plant species, plant height, defoliation level, study year, and clutch sampling day, with plant being included as a random factor. A negative binomial distribution with a linear variance-mean relationship was used to model the dependent variable. The full models for both clutch density and clutch size included all analysed predictors and their second-order interactions. Results of the full models are presented in Supplementary Tables S3 and S4. Then, we performed the procedure of model selection to establish the best models by evaluating all possible predictor combinations using the ‘dredge’ function in the ‘MuMin’ package (Bartoń, 2024). Models with the lowest AIC value were considered the best. The parameters

of competing models were estimated by maximum likelihood. The final model for clutch density exhibited a substantially reduced collinearity among the predictors compared to the full model (Supplementary Table S2).

For building models and estimating regression coefficients, we employed the `glmmTMB` package (Brooks et al. 2017). When modelling random effects, we assumed their influence on the mean values of the analysed variables (random intercept) but not on the regression coefficients (random slope). All predictors were standardised prior to analysis, following recommendations (Schielzeth 2010). As the distributions of continuous predictors deviated significantly from normality, the median and median absolute deviation were used for standardisation instead of the mean and standard deviation. Model diagnostics were performed by analysing randomised quantile residuals using the `DHARMA` (Hartig 2022) and `performance` (Lüdtke et al. 2021) packages.

The parameters of the full and final models were estimated by restricted maximum likelihood. Confidence intervals and significance of regression coefficients were computed using the Wald method. Degrees of freedom were determined via the Between-Within approximation method (Li and Redden 2015) in the `parameters` package (Lüdtke et al. 2020). To assess the significance of random effects, models with and without random effects were compared using likelihood ratio tests.

Confidence intervals for proportions were determined by Wilson's method (Brown et al. 2001), and those for sample means were calculated via the non-parametric BCa bootstrap method (DiCiccio and Efron 1996) with the `DescTools` package (Signorell 2024).

To assess the aggregation of egg clutch distribution, Morisita's index (I_M) (Morisita 1962) was computed using the `vegan` package (Oksanen et al. 2024). The value of this index is indicative of the factor by which the probability of two randomly selected clutches co-occurring on the same plant exceeds that which would be expected under a random distribution (Hurlbert 1990). Consequently, the Morisita index quantifies the degree of selectivity exhibited by females when choosing host plants. The calculated index values were compared to one (the expected value under random distribution) using the χ^2 test. For multiple comparisons, the Benjamini–Hochberg correction was applied.

Results

Population dynamics

The population of *A. crataegi* near Fomino village remained at low density between 2015 and 2020: mean adult abundance did not exceed 50 individuals per 1 km of transect, and the proportion of *P. padus* with overwintering nests,

the primary host plant, ranged from 25 to 35% (Supplementary Fig. S2; Fig. 2). In 2021, a population increase was observed, followed by an outbreak phase in 2022: adult abundance along the transect increased approximately ten-fold compared to the 2015–2020 period, with the colonisation rate of *P. padus* reaching 100%. The adult counts indicated continued population growth during 2023–2024 (Supplementary Fig. S2).

Dynamics of host plant colonisation over the outbreak cycle

The proportion of host plants with overwintering nests differed significantly depending on the host plant species (Wald $\chi^2 = 67.5$, $df = 2$, $p < 0.001$) and across years (Wald $\chi^2 = 159.9$, $df = 5$, $p < 0.001$). The proportion of plants with overwintering nests was highest in *P. padus*, with lower proportions observed in *M. baccata* and *S. aucuparia*. During the low-density phase (2015–2021), the frequency of *S. aucuparia* ($\leq 10\%$) and *M. baccata* (virtually absent) with overwintering nests remained minimal. During the outbreak (2022–2024), the proportion of plants with overwintering nests increased sharply for both *M. baccata* (up to 100%) and *S. aucuparia* (up to 88%; Fig. 2).

Egg clutch distribution

In 2024, the egg clutches of *A. crataegi* were recorded on *P. padus*, *M. baccata*, *S. aucuparia*, and *A. spicata*. Since *A. spicata* is scarce in the understorey and was not present across all study plots (Table 1), it was excluded from the subsequent analysis. The number of egg clutches per host plant ranged from 0 to 28 (median = 0, lower quartile = 0, upper quartile = 1.5). Clutch density differed among host plant species (Table 3), both in mean values and distribution shape

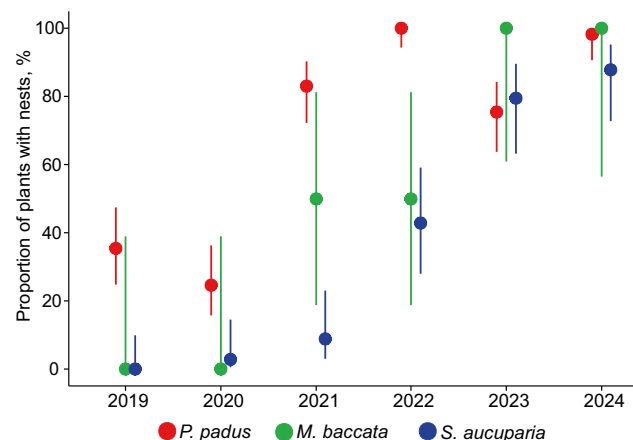


Fig. 2 Proportion of host plants (mean \pm 95% Wilson confidence intervals) with overwintering nests of *A. crataegi* in 2019–2024

Table 3 Results of the final generalised linear mixed model analysing the density of *A. crataegi* egg clutches

Predictor	Coefficient estimate \pm SE	95% CI, under–upper	z Value	df	p Value
Intercept	-4.34 ± 0.24	-4.81 to -3.88	-18.4	491	<0.001
Host plant (<i>M. baccata</i>)	-0.39 ± 0.17	-0.73 to -0.06	-2.3	491	0.022
Host plant (<i>P. padus</i>)	1.06 ± 0.12	0.83 – 1.29	9.0	491	<0.001
Defoliation	0.08 ± 0.09	-0.10 to 0.25	0.8	491	0.404
Height	0.37 ± 0.12	0.14 – 0.60	3.2	491	0.002
Crown projection area	0.15 ± 0.15	-0.14 to 0.45	1.0	491	0.305
Host plant (<i>M. baccata</i>) \times Height	0.08 ± 0.14	-0.20 to 0.36	0.6	491	0.571
Host plant (<i>P. padus</i>) \times Height	-0.32 ± 0.10	-0.52 to -0.12	-3.1	491	0.002
Host plant (<i>M. baccata</i>) \times Defoliation	0.13 ± 0.15	-0.16 to 0.42	0.9	491	0.367
Host plant (<i>P. padus</i>) \times Defoliation	-0.19 ± 0.10	-0.40 to 0.01	-1.9	491	0.059
Height \times Crown projection area	-0.12 ± 0.05	-0.22 to -0.03	-2.7	491	0.008
Height \times Defoliation	0.35 ± 0.12	0.12 – 0.57	3.0	491	0.003
Defoliation \times Crown projection area	-0.62 ± 0.17	-0.96 to -0.28	-3.6	491	<0.001

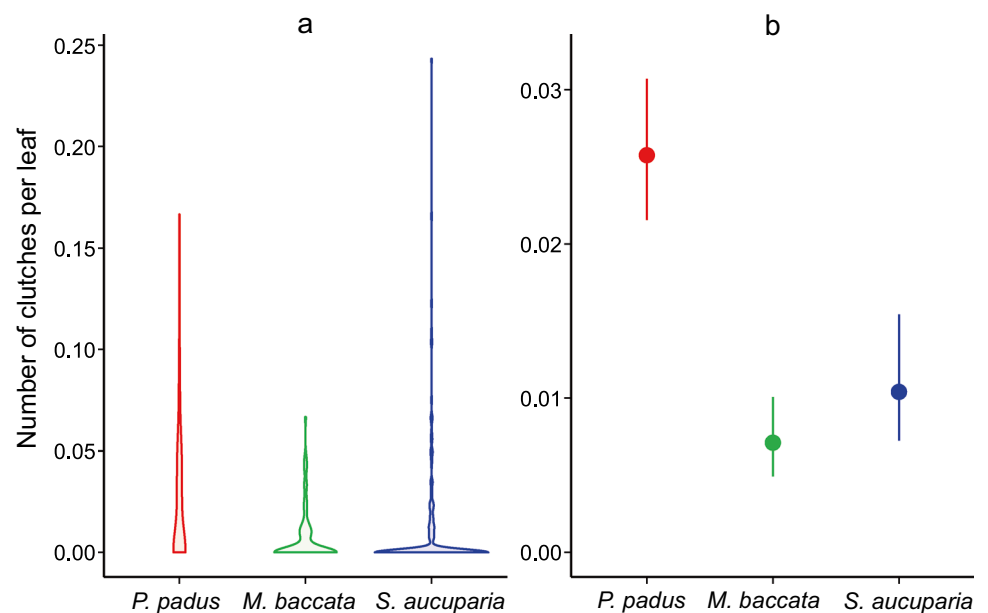
(Fig. 3). On *P. padus*, clutch density was significantly higher than that on *M. baccata* and *S. aucuparia*, exhibiting the flattest distribution (skewness = 1.7, excess kurtosis = 3.2). At least one clutch was found on 55% of the surveyed *P. padus* plants. Clutch density showed comparable values between *M. baccata* and *S. aucuparia* (Fig. 3b). However, distributions on *S. aucuparia* were markedly more skewed and fat-tailed (skewness = 4.6, excess kurtosis = 27.6) than those on *M. baccata* (skewness = 2.3, excess kurtosis = 5.2). Most *S. aucuparia* individuals (74%) contained no clutches, while their minority exhibited extremely high clutch densities (Fig. 3a).

Clutch density was also influenced by plant height, with females ovipositing more frequently on taller trees and shrubs. This pattern was evident in *M. baccata* and *S.*

aucuparia, rather than in *P. padus* (Fig. 4a) Furthermore, the effect of plant height depended on the area of crown projection and the degree of defoliation (Table 3). Along with an increase in the crown projection area, the influence of plant height is diminishing (Fig. 4b). It appears that a short plant height may be partially compensated for by a large crown area, and conversely. However, upon increasing defoliation, the effect of plant height is becoming more pronounced (Fig. 4c). Thus, the highest egg clutch density occurred on tall and partially defoliated plants.

Egg clutch density differed significantly across the study plots (LR $\chi^2 = 14.2$; df = 1; $p < 0.001$). It was at the highest level in Plots 2 and 3, situated in the pine forest understory with a low defoliation level from the previous year, with a slightly lower density in the open habitat (Plot 1). The lowest

Fig. 3 *A. crataegi* clutch density (a—distribution, b—mean \pm 95% confidence intervals) across host plant species



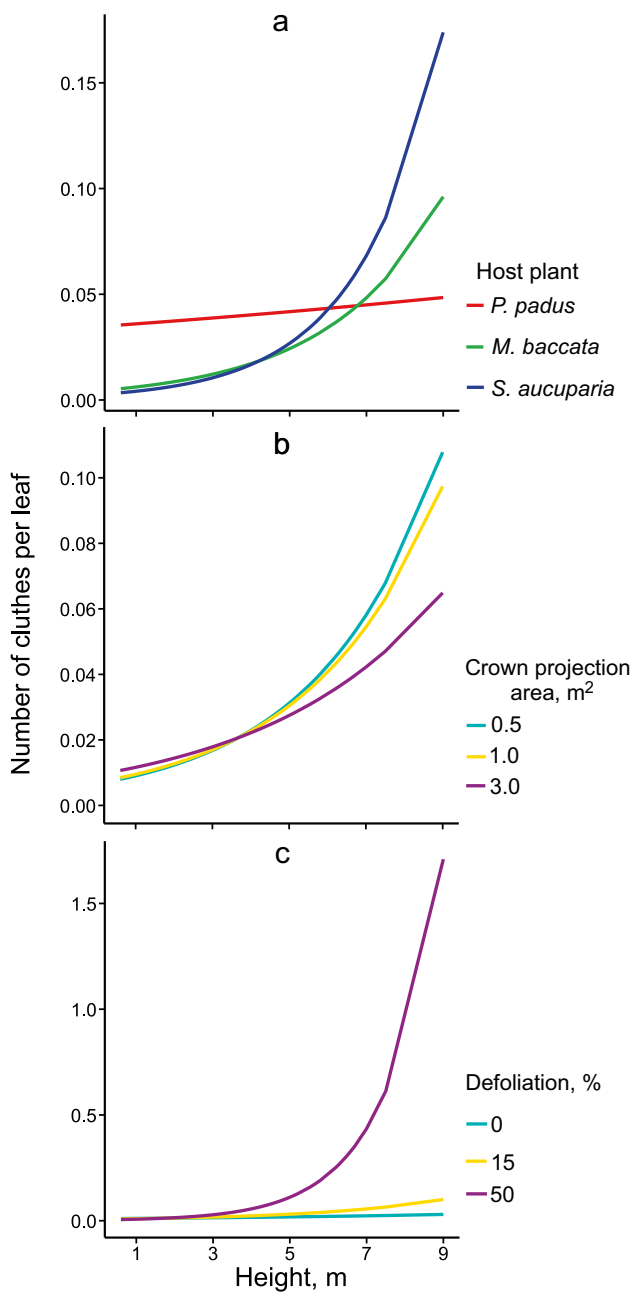


Fig. 4 Model predictions of *A. crataegi* clutch density against host plant height depending on the host plant species (a), crown projection area (b), and defoliation (c)

egg clutch density was observed in Plots 4 and 5, which experienced severe understory defoliation in 2023 (Supplementary Fig. S3).

Aggregation of clutch distribution

We calculated the values of Morisita's index to quantify the degree of selectivity exhibited by females when choosing specific plants of *P. padus*, *M. baccata*, and *S. aucuparia*.

Clutch distribution across all host plants was aggregated and significantly differed from random ($I_M > 1$, $p < 0.001$). The aggregation of egg clutches was lowest on *P. padus* ($I_M = 2.75$), slightly higher on *M. baccata* ($I_M = 3.65$), and highest on *S. aucuparia* ($I_M = 10.17$).

The number of egg clutches on individual leaves ranged from zero to five. We assessed the aggregation of clutch distribution within individual host plants by calculating Morisita's index for plants with at least four clutches. On most host plants, egg clutches were randomly distributed (index values did not differ significantly from one). However, on some plants, egg clutches were aggregated—females repeatedly laid eggs on the same leaves more frequently than expected under random leaf selection (Supplementary Table S5). Cases of aggregated clutch distribution were significantly more frequent on *S. aucuparia* than on *P. padus* ($\chi^2 = 4.3$; $df = 1$; $p = 0.038$). The proportion of *M. baccata* plants with aggregated clutches did not differ from that of *P. padus* ($\chi^2 = 0.2$; $df = 1$; $p = 0.67$) or *S. aucuparia* ($\chi^2 = 0.6$; $df = 1$; $p = 0.46$).

Egg clutch size

The number of eggs per clutch varied widely—from 11 to 191 (median = 76; lower quartile = 59; upper quartile = 95; Fig. 5a). Clutch size depended on host plant species and defoliation (Table 4). Overall, females deposited larger clutches on plants with lower defoliation levels. The influence of host plant species on clutch size varied significantly between the years (Wald $\chi^2 = 6.1$; $df = 2$; $p = 0.047$). In 2023, egg clutches on *S. aucuparia* were significantly smaller than those on *P. padus* and *M. baccata*. In 2024, the number of eggs per clutch became nearly identical across *P. padus*, *M. baccata*, and *S. aucuparia* (Fig. 5b). As the flight period progressed, females laid progressively smaller clutches, although this trend remained statistically non-significant ($p = 0.07$; Table 4). The influence of defoliation and plant height on clutch size differed between early and late clutches. The number of eggs in clutches collected early in the adult flight period varied independently of host plant defoliation and height. In contrast, late clutches were larger on taller and less defoliated plants (Fig. 6).

Discussion

Oviposition selectivity

We investigated the oviposition patterns of an eruptive Lepidopteran species during an outbreak peak. Our findings indicate that *A. crataegi* exhibits high selectivity when depositing egg clutches. Females make their choice depending on the host plant species (favouring *P. padus*), its size

Fig. 5 *A. crataegi* clutch size (a—distribution, b—mean \pm 95% confidence intervals) across host plant species in 2023 and 2024

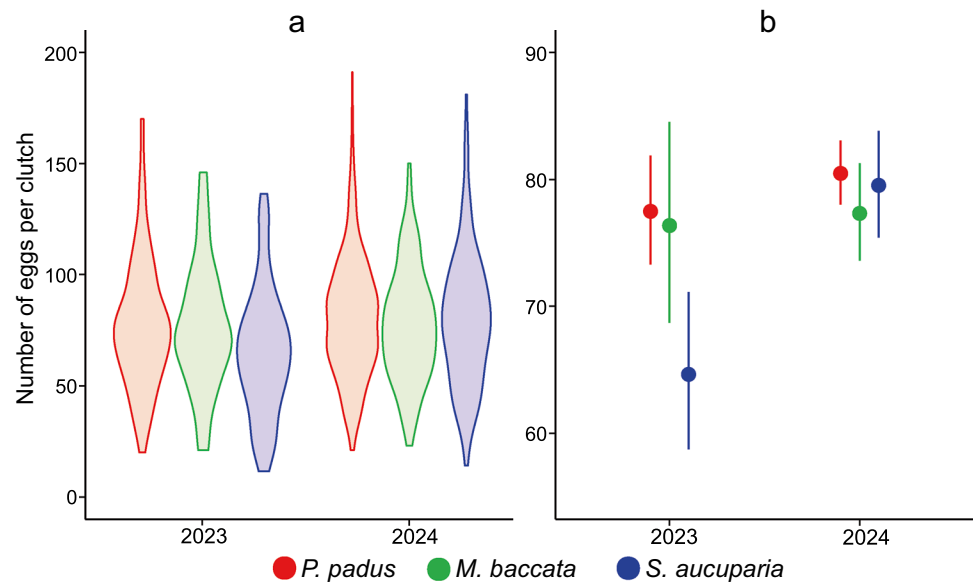
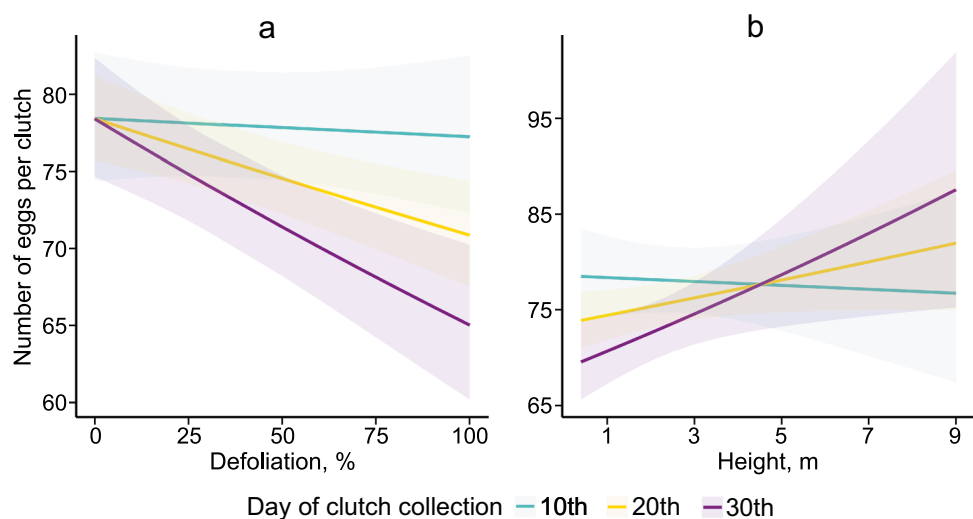


Table 4 Results of the final generalised linear mixed model analysing the egg clutch size of *A. crataegi*

Fixed factor	Coefficient estimate \pm SE	95% CI, under–upper	z Value	df	p Value
Intercept	4.33 \pm 0.02	4.30–4.36	284.21	909	<0.001
Host plant (<i>M. baccata</i>)	0.00 \pm 0.02	– 0.05 to 0.04	– 0.2	909	0.838
Host plant (<i>P. padus</i>)	0.06 \pm 0.02	0.03–0.10	3.56	909	<0.001
Year (2023)	– 0.03 \pm 0.02	– 0.06 to 0.01	– 1.65	909	0.098
Height	0.02 \pm 0.01	0.00–0.04	1.74	909	0.082
Defoliation	– 0.04 \pm 0.01	– 0.07 to – 0.02	– 3.39	909	<0.001
Clutch sampling day	– 0.02 \pm 0.01	– 0.05 to 0.00	– 1.82	909	0.069
Host plant (<i>M. baccata</i>) \times Year (2023)	0.02 \pm 0.02	– 0.02 to 0.06	0.84	909	0.399
Host plant (<i>P. padus</i>) \times Year (2023)	0.03 \pm 0.02	0.00–0.07	1.99	909	0.047
Height \times Clutch sampling day	0.02 \pm 0.01	0.00–0.04	1.8	909	0.072
Defoliation \times Clutch sampling day	– 0.03 \pm 0.01	– 0.05 to – 0.01	– 2.59	909	0.010

Fig. 6 Model predictions (regression lines \pm 95% confidence intervals) of *A. crataegi* clutch size in relation to host plant defoliation (a) and height (b) depending on the clutch collection day (days since the onset of imago flight)



(preferring taller plants), and degree of defoliation (depositing smaller clutches on severely defoliated plants). Notably, this selectivity extends beyond the choice of an oviposition site to include clutch size regulation. Similar to other Lepidoptera species (Leather and Burnand 1987; Fordyce 2005), *A. crataegi* appears to adjust egg number per clutch, allocating a greater proportion of offspring to potentially more favourable conditions.

The adaptive value of these female preferences remains unclear. However, previous studies have demonstrated that fifth-instar larvae and pupae of *A. crataegi* sampled from the preferred host plant (*P. padus*) attained larger sizes and exhibited lower mortality compared to those sampled from *S. aucuparia* (Zakharova et al. 2020; Solonkin et al. 2024). The selection of larger plants is typical among Lepidoptera and is likely aimed at enhancing offspring performance by ensuring a greater food supply for larvae (Zangerl and Berenbaum 1992; Floater and Zalucki 2000; Talsma et al. 2008; Johansson et al. 2024; Dunsakis et al. 2024).

Female *A. crataegi* exhibit an increased oviposition selectivity on less preferred host plants—*M. baccata* and *S. aucuparia*—compared to *P. padus*, which is colonised relatively uniformly. Among *M. baccata* and *S. aucuparia* individuals, females prefer specific plants with a greater height and, possibly, other unassessed characteristics. Notably, the least preferred (and presumably least suitable) host plant, *S. aucuparia*, experiences the most selective colonisation, resulting in pronounced clutch aggregation. Evidence suggests that the larval group size may be particularly critical when exploiting suboptimal host substrates (Kawasaki et al. 2009; Fiorentino et al. 2014). It is plausible that elevated clutch aggregation on *S. aucuparia* facilitates a more successful larval feeding and development on this host plant.

Oviposition selectivity in *A. crataegi* females regarding clutch size regulation increases towards the end of the adult flight period. Early in the flight season, females deposit similar-sized clutches on plants irrespective of their defoliation. Later in the season, however, larger clutches predominate on low-defoliation plants, while smaller clutches are deposited on severely defoliated plants. As demonstrated for various Lepidoptera, including another pierid species, female egg deposition declines with ageing (Kimura and Tsubaki 1986; Boggs 1997). *A. crataegi* females emerging later from pupae typically exhibit smaller body size (Shkurikhin et al. 2018) and consequently possess lower potential fecundity (Tarasova et al. 2015). Thus, towards the end of the flight season, *A. crataegi* females harbour fewer mature eggs available for deposition on average. A trade-off between female fecundity and oviposition selectivity is predicted by the life-history theory and has been observed in several insect species, including another pierid (Jaumann and Snell-Rood 2017). This inverse relationship may well be characteristic of *A. crataegi*.

Defoliation of host plants by the previous generation of phytophagous insects reduces food availability for offspring and typically induces rapid or delayed resistance (Nykänen and Koricheva 2004). It has been shown that defoliation of *P. padus* by larvae of the ermine moth *Yponomeuta evonymella* (Linnaeus, 1758) leads to decreased nutrient levels and increased concentrations of toxic compounds in its foliage (Uusitalo 2004). Therefore, we hypothesised that *A. crataegi* would lay eggs more frequently and in larger numbers on non-defoliated or minimally defoliated plants. This assumption was supported only for clutch size, while the clutch density on host plants was generally independent of their defoliation degree. However, the clutch density was lower on study plots with severe previous-year defoliation. Thus, *A. crataegi* does not avoid defoliated plants when laying eggs but prefers forest sites that were not severely defoliated in the previous year. It is known that rapid induced resistance is typically weaker than delayed induced resistance and often does not significantly impair insect fitness (Nykänen and Koricheva 2004). Moreover, defoliation can stimulate photosynthesis and increase nitrogen concentration in foliage (Nykänen and Koricheva 2004), a phenomenon also observed in *P. padus* (Leather 1995). It is possible that *P. padus* develops delayed induced resistance, which becomes apparent in the following year. Additionally, severe defoliation of *P. padus* reduces the number of foliated plants in the understory the subsequent year. *A. crataegi* may, as shown for other Lepidoptera (Tjørnløv et al. 2015; Dunsakis et al. 2024), assess the abundance of suitable host plants for oviposition and select sites with their higher density.

According to P. Price's hypothesis (1994), low oviposition selectivity constitutes a key prerequisite for eruptive population dynamics. Indeed, females of numerous eruptive Lepidoptera species exhibit low oviposition selectivity (Tammaru et al. 1995; Koricheva et al. 2012). However, there exist counterexamples (Floater and Zalucki 2000). The degree of oviposition selectivity appears to depend primarily on whether larvae both feed upon and develop within the microenvironment selected by the female, as originally envisioned by Price (1994). Dissociation between oviposition substrates and substrates for larval feeding and development may arise through egg-stage overwintering or dispersal of first-instar larvae using silk threads (ballooning). Both traits are indeed associated with low oviposition selectivity and eruptive population dynamics (Price 1994; Hunter 1995; Tammaru et al. 1995; Koricheva et al. 2012). Nevertheless, a significant proportion of eruptive Lepidoptera species in Europe and North America overwinter as larvae or pupae (Hunter 1995), and at least some exhibit no dispersal of first-instar larvae.

The larvae of *A. crataegi* feed on the host plant leaf, where the clutch was laid, and adjacent leaves, which also serve as material for constructing overwintering nests.

Fourth-instar larvae continue feeding on the same plant after emerging from diapause, and only fifth-instar larvae abandon the overwintering nest and may disperse to neighbouring trees and shrubs (Krasnyuk 1928; Blunck and Wilbert 1962; Kuznetsov et al. 1999). Thus, the performance of larvae (at least until the fifth instar) directly depends on the female's oviposition site choice. This dependence conclusively drives the observed high oviposition selectivity of *A. crataegi*.

A. crataegi may be considered a non-canonical eruptive species due to its taxonomic position: among Papilionoidea, few species exhibit outbreak dynamics. Nevertheless, our findings demonstrate that females of an eruptive lepidopteran species can display high oviposition selectivity. Consequently, such selectivity does not preclude population outbreaks. It is plausible that high oviposition selectivity also characterises other eruptive Lepidoptera with similar life-history traits (notably early-instar larval consumption of foliage selected by females). Should this prove valid, the role of non-selective oviposition in facilitating eruptive dynamics has likely been overemphasised by P. Price, with a greater significance potentially attributable to other traits, such as clutch aggregation and larval gregariousness.

Clutch aggregation

Eruptive species tend to aggregate eggs and clutches (Hanski 1987; Hunter 1995; Koricheva et al. 2012; Battisti et al. 2023). It is suggested that aggregated offspring distribution leads to an uneven allocation of risks and facilitates eruptive population dynamics (Hanski 1987; Floater and Zalucki 2000; Bruzzone et al. 2024). However, clutch aggregation during outbreaks should potentially result in local overcrowding and associated negative consequences. For instance, under high population density, the females of the pine processionary moth *Thaumetopoea pityocampa* (Denis & Schiffermüller, 1775) lay clutches aggregately, which increases larval mortality and suppresses outbreak (Pimentel et al. 2017). Therefore, we hypothesised that during outbreaks and under high population density, the females of *A. crataegi* would prefer plants and leaves without conspecific clutches. Contrary to expectations, we found no avoidance of conspecific clutches. In contrast, *A. crataegi* exhibit aggregated clutch distribution: a subset of host plants remains uncolonised, while others harbour multiple clutches. In most cases, the number of clutches on leaves within an individual plant varies randomly, with single clutches per leaf being the most frequent. However, pronounced clutch aggregation was observed on the leaves of certain plants. This suggests that the females of *A. crataegi* select specific, favoured plants and leaves irrespective of the presence of conspecific clutches. It is also plausible that conspecific clutches act as attractive cues for females, as demonstrated in some other Lepidoptera (Ulmer et al. 2003; Raitanen et al. 2014). Experimental

studies are required to elucidate the underlying mechanisms of egg clutch aggregation.

It is well established that gregarious development enhances larval survival and growth rates through more efficient defence against predators, thermoregulation, food consumption, and overcoming the induced resistance of host plants (e.g., Stamp 1980; Fordyce 2003; Qian et al. 2024). Clutch aggregation may lead to the merging of offspring from different females, thereby increasing group size. Some studies have demonstrated enhanced embryonic survival and more successful larval development under aggregated clutch distribution (Desurmont and Weston 2011; Griese et al. 2020). The positive effects of aggregation are typically more pronounced for early-instar larvae and diminish as they develop (Reader and Hochuli 2003; Inouye and Johnson 2005). According to our observations, the early-instar larvae of *A. crataegi* do not completely defoliate host plants and thus avoid food shortages, even under high local population density. The negative effects of overcrowding (e.g., food scarcity and increased incidence of nuclear polyhedrosis virus) primarily affect late-instar larvae, which are capable of migrating between host plants. Consequently, their performance is far less dependent on female oviposition choices. It is plausible that clutch aggregation serves to maximise the fitness of early-instar larvae.

Dynamics of host plant colonization

We established that an increase in the population density leads to an increase in the colonisation rate of less preferred host plant species—*S. aucuparia* and *M. baccata*. The shift in females to oviposition on less preferred species, as well as the expansion of the realised host repertoire during outbreaks, has been described for some eruptive Lepidoptera species (Ezzine et al. 2015; Castagneyrol et al. 2016). Selection of suboptimal host plants by females may be driven by a shortage of oviposition sites on the primary host. Furthermore, along with an increase in the population density, the suitability of the primary host plant may decline due to overcrowding and high larval competition (Wetzel and Strong 2015), increased offspring mortality from parasitoids, predators, and pathogens (e.g., Singer et al. 2004; Ghosh et al. 2022), as well as the development of induced resistance (Nykänen and Koricheva 2004; Underwood 2010). In our study system, the preference of *A. crataegi* females for *S. aucuparia* or *M. baccata* is unlikely to be linked to a shortage of available leaves or *P. padus* plants, since a substantial proportion of *P. padus* remained uncolonised, and we found no evidence of conspecific clutch avoidance. It is also improbable that *S. aucuparia* serves as an enemy-free space, as under high population density, mortality of later-instar caterpillars and pupae from parasitoids was higher on *S. aucuparia* than on *P. padus* (Solonkin et al. 2024). Thus,

the drivers behind increased colonisation of less preferred host plants during the outbreak remain unclear. This phenomenon may result merely from a rising population density, with oviposition preference for *S. aucuparia* and *M. baccata* remaining unchanged.

Conclusions

In this study, we demonstrate that an eruptive lepidopteran species can exhibit high oviposition selectivity. This selectivity of *A. crataegi* is likely to stem from early-instar larvae consuming foliage selected by the female during oviposition. Such selectivity may also characterise other eruptive species with comparable life-history traits. This challenges the view that low oviposition selectivity constitutes a key enabling factor for eruptive population dynamics.

We found no evidence of avoidance of conspecific clutches under high population density. Akin to other eruptive Lepidoptera species previously studied in this context (Floater and Zalucki 2000; Pimentel et al. 2017; Battisti et al. 2023), *A. crataegi* exhibits aggregated clutch distribution. It is plausible that clutch aggregation enhances fitness in early-instar larvae, even under outbreak conditions. Conversely, it may reduce fitness in later-instar larvae due to overcrowding, potentially contributing to the decline of population outbreaks.

During the outbreak cycle of *A. crataegi*, the realised repertoire of host plants undergoes changes: it narrows to a single most preferred species at low population densities (Zakharova et al. 2020) and expands during outbreak events. It remains unclear whether other aspects of oviposition site selection—particularly the degree of clutch aggregation—shift concurrently. The patterns of change in oviposition strategies among eruptive species during outbreak cycles remain largely unstudied and necessitate further detailed investigation.

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Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors of this work declare that they have no conflicts of interest.

Ethical approval Sampling and analysis of invertebrates was subject to approval of the Bioethics Committee of the Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences (Yekaterinburg), protocol No. 14 dated May 12, 2023.

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