

Biology and habitat requirements of the highly endangered butterfly *Tomares nogelii* (Lepidoptera, Lycaenidae) in southeastern Romania

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Research Article

Keywords: *Tomares nogelii*, host-plant interactions, phenology, larval ecology, butterfly conservation

Posted Date: February 5th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-8733985/v1>

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Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Journal of Insect Conservation on July 2nd, 2026. See the published version at <https://doi.org/10.1007/s10841-026-00791-y>.

Abstract

Understanding the ecological mechanisms limiting population persistence is essential for the conservation of highly specialised and endangered insects. *Tomares nogelii dobrogensis* is one of the rarest butterflies in the European Union and is strictly monophagous on *Astragalus ponticus* in Romania. Despite its high conservation relevance, quantitative data on its ecology and life history have been largely lacking.

During the 2025 flight season, an extensive field study in northern Dobrogea, Romania, investigated phenology, imaginal lifespan, behaviour, habitat characteristics and host-plant synchrony across six colonies. Patch-level analyses were used to assess how habitat structure, light availability and host-plant phenology influenced imaginal abundance. Oviposition patterns and preimaginal stages were documented.

Imaginal flight activity closely overlapped with the reproductive phenology of *A. ponticus*, with peak butterfly abundance coinciding with bud formation and flowering. Observed imaginal lifespan was short, resulting in a narrow reproductive window. At the patch scale, imago abundance increased strongly with host-plant patch area and light availability, while host-plant density alone was not a significant predictor. Oviposition was highly aggregated among host plants, occasionally leading to high larval densities and cannibalism.

Implications for insect conservation

Our results indicate that population performance of *T. n. dobrogensis* is primarily constrained by the spatial and temporal availability of suitable host-plant stages. Conservation management should therefore prioritise the maintenance of large, open *A. ponticus* patches and prevent disturbances by livestock during flight time and the larval feeding period which was shown during the study to significantly reduce reproductive success.

Introduction

Tomares nogelii (Nogel's Hairstreak) is one of the rarest butterflies in Europe and occurs only in southeastern Romania, Ukraine, Moldavia and Crimea, with additional populations in Anatolia, Azerbaijan, Lebanon and Syria (Rákosy et al. 2024). In Romania, the species was first recorded in 1866 near Tulcea (Mann 1866) later described as *T. n. dobrogensis* (Caradja 1895).

By the 1980s, *Tomares nogelii* had disappeared from all known Romanian sites, likely due to oversampling by collectors, the loss of its larval host plant *Astragalus ponticus* through overgrazing and increasing human disturbance such as recreational use of forest clearings and pesticide application (Rákosy 2024; Rákosy et al. 2024).

In the 2010 European Red List, the species was classified as Regionally Extinct in the EU-27 and Vulnerable at the pan-European level (Van Swaay et al. 2010). In 2014, the species was rediscovered at a different locality, but also in Dobrogea, Romania (Rákosy and Craioveanu 2015). In the 2025 assessment, *T. nogelii* is listed as Vulnerable in the EU-27 and Near Threatened in Europe (Van Swaay et al. 2025). In the Romanian Red List (Rákosy et al. 2021), the species is considered Extinct in Moldavia, Critically Endangered in Dobrogea and therefore Critically Endangered nationally. It is also included in Romania's List of Lepidoptera Species Protected by Law (OUG 57/2007, Annex 4B), which covers species of national interest requiring strict protection.

Since its rediscovery in 2014, several small subpopulations have been found in an area of about 5x10 km size in northern Dobrogea. Monitoring showed one subpopulation to remain stable, whereas the originally rediscovered subpopulation declined sharply and was not recorded after 2017 (Rákosy et al. 2024; Rákosy and Craioveanu 2015).

Despite its high conservation relevance, detailed information on the ecology and life history of *Tomares nogelii dobrogensis* remains scarce. Most available knowledge is limited to distributional records, taxonomic treatments and isolated biological observations, while quantitative data on phenology, lifespan, behaviour and reproductive biology are largely lacking (Bury and Savchuk 2015; Hesselbarth and Schurian 1984; Rákósy et al. 2024; Rákósy and Craioveanu 2015; Tolman and Lewington 2009).

In Romania, the subspecies shows a strict dependence on the larval host plant *Astragalus ponticus*, with eggs deposited on flower buds and larvae feeding on buds, flowers and immature fruits (Bury and Savchuk 2015; Hesselbarth and Schurian 1984; Rákósy et al. 2024). This high degree of specialization suggests that synchrony between butterfly phenology and host-plant flowering is a key prerequisite for successful reproduction and larval development. In herbivorous insects, mismatches between insect phenology and host-plant development have been shown to reduce larval performance and survival, thereby affecting population viability (Kharouba et al. 2018; Singer and Parmesan 2010; Visser and Gienapp 2019). Climate driven advances in insect phenology often exceed those observed in plants, potentially increasing the risk of phenological mismatch in specialized butterfly-host-plant systems (Forrest 2016; Parmesan 2007).

Beyond phenological synchrony, key aspects of the adult and preimaginal ecology of *T. nogelii dobrogensis* remain largely undocumented. Here, we present the results of an extensive field study conducted between May and July 2025 in northern Dobrogea, Romania. This study documents phenology, observed lifespan, daily activity patterns, nectar plant use, habitat characteristics and variation in upper wing coloration. In addition, we analyse the synchrony between butterfly emergence and *Astragalus ponticus* flowering and provide observations on oviposition behaviour, larval occurrence, pupation and rare events such as predation and larval cannibalism. By focusing on life-history traits directly linked to reproduction and population persistence, this study aims to provide a robust ecological basis for monitoring and conservation of *T. nogelii dobrogensis*.

A companion study (von der Wense Gonçalves et al., submitted), based on the same dataset, applies capture-mark-recapture methods to estimate population size, dynamics, connectivity, dispersal and modelled lifetime expectancy.

Methods

Study species

Tomares nogelii (Lycaenidae, Theclinae) is a butterfly species showing pronounced geographic variation in larval host-plant use. In Romania, the subspecies *T. n. dobrogensis* is strictly monophagous and closely associated with the Fabaceae *Astragalus ponticus*. Populations in Turkey and Crimea use *Astragalus macrocephalus* and *Astragalus dasyanthus* as additional *host plants* (Bury and Savchuk 2015; Seven Çalışkan 2014). Females oviposit primarily on floral buds and occasionally on young leaves, and larval development takes place inside buds, flowers and immature fruits of the host plant (Hesselbarth and Schurian 1984; Rákósy 2024; Rákósy et al. 2024; Fig. 1). After hatching, larvae feed on floral tissues and are frequently attended by ants, although there is no evidence that larval development depends on obligate myrmecophily (Rákósy et al. 2024).

According to Rákósy et al. (2024), pupation has been reported to occur in July at the base of the host plant, typically in a loosely woven cocoon on or just below the soil surface. The species overwinters in the pupal stage. The short flight period of approximately 15–20 days usually peaks in early June in Dobrogea. Wing pattern and coloration are highly variable, both among subspecies and within individual populations. Upperwing coloration ranges from almost entirely brown to largely orange, with intermediate forms being common (van Oorschot and Wagener 2000). Detailed descriptions from Anatolian populations indicate that females tend to display a higher proportion of orange coloration

than males, although orange may be entirely absent in both sexes (van Oorschot and Wagener 2000). Only a single aberrant individual has been documented, representing a case of reduced orange pigmentation reported from Romania (Cuvelier 2022).

Imagines have been reported to use *Astragalus ponticus* as a nectar source but have also been observed visiting flowers of *Salvia*, *Ajuga*, *Potentilla*, *Veronica* and *Euphorbia* species (Rákosy et al. 2024). Egg development is rapid. Published data from Turkey indicate hatching after approximately 4–6 days (Hesselbarth and Schurian 1984).

Astragalus ponticus is a long-living perennial hemicryptophyte, characteristic of steppe and forest-steppe habitats. It occurs in clearings and at margins of thermophilous oak forests, steppe grasslands and limestone slopes, where it typically forms small groups of scattered, but persistent individuals (Sirenko 2016). Plants can reach considerable age, developing thick multi-branched caudices over time. Flowering takes place from May to June and reproduction is exclusively by seed (Izverscaia and Ghendov 2025; Sirenko 2016).

Astragalus ponticus is native to Romania, Bulgaria, Greece, Turkey, Iran, Ukraine, Crimea, the NW Balkan Peninsula, southern European Russia, the northern Caucasus and Transcaucasia (Izverscaia and Ghendov 2025). Within Romania, it is characteristic of dry silvo-steppe systems, including northern Dobrogea. *Astragalus ponticus* is considered vulnerable or declining in several parts of its range (Izverscaia and Ghendov 2025; Sirenko 2016) and because it is the sole larval host plant of *Tomares nogelii* in Romania, its local abundance and flowering phenology are essential components of the butterfly's ecology and conservation.

Study area

Fieldwork was conducted from 12th of May to 7th of July in a forest-steppe transition zone in south-eastern Romania. Intensive searches by the fourth author from 2022 to 2025 in the Tulcea and Moldava districts revealed several colonies. At the studied location, there are 10 colonies known. Of these, four large (Colonies 1–4) and two small colonies (Colonies 5 and 6) were studied. At respective distances of 30 and 45 km of the studied area, some other colonies exist. All colonies are relatively small and extremely vulnerable to several threats. At the start of the season, only two large and one small colonies were known by the first two authors to host *Tomares nogelii*. About one week after the beginning of the flight period, two additional large colonies and another small colony were discovered.

All colonies were located in a silvo-steppic landscape characterised by the presence of *A. ponticus* (Fig. 2). Colony sizes ranged from several hundred to several thousand square metres. Colonies 1–5 form a near linear system, with Colony 4 located 2.3 km from the others and the remaining colonies separated by 500–1300 m. Colony 6 was situated further within the forest, forming a triangle with Colonies 1 and 2. For conservation reasons, the exact locations of the localities are kept strictly confidential and not reported here.

Habitat characterisation

Habitat types were assigned to EUNIS categories based on vegetation composition recorded in each colony. Vascular plant species were documented and grouped into grassland, shrubland and forest-associated taxa to characterise habitat structure and openness. This vegetation-based classification was then compared with the official Romanian EUNIS habitat descriptions to assign habitat types (Bodescu et al. 2017).

To quantify microhabitat conditions, temperature and relative humidity were recorded using data loggers installed across several colonies. Loggers measured air temperature and humidity hourly at approximately 1 m height. All logger locations were georeferenced, and local light conditions were noted.

Colonies were further subdivided into *A. ponticus* clusters, defined as groups of plants with a maximum distance of 3 m between neighbouring individuals. In total, 71 clusters were identified, ranging from 1 m² to nearly 600 m². All clusters were mapped as polygons in QField (v4.14.1; QField Development Team 2025).

For vegetation and larval habitat assessment, only the 45 clusters larger than 10 m² were surveyed. Within these polygons, random sampling points were generated in numbers proportional to the polygon area based on predefined size classes. Among the surveyed clusters, 18 measured 10–20 m² (one point), 14 measured 20–70 m² (two points), 6 measured 70–150 m² (three points), 5 measured 150–300 m² (four points) and 2 exceeded 450 m² (eight points).

At each sampling point, a 1 × 1 m quadrat was placed, resulting in a total of 100 quadrats sampled once during the study. Quadrats were not permanently installed; instead, a rope frame was positioned at each sampling point, measurements were taken and the frame was then moved to the next location.

Within each quadrat, the following variables were recorded: host plant abundance, number of reproductive host plants, host plant height, surrounding vegetation height, dominant *A. ponticus* flowering stage, larval abundance, number of plants with caterpillar feeding marks, habitat type (shrubland, forest, grassland, mixed), light condition (full sun, partial shade, full shade) and bare soil cover in 25% classes.

Host plant monitoring

At the start of the fieldwork, 35 *A. ponticus* plants were randomly selected across the sites: 15 in Colony 1, 10 in Colony 3, 5 in Colony 5 and 5 in Colony 6. In this study, a “plant” was defined as a single stem, since *A. ponticus* can develop from one to several stems (sometimes up to 10–20 with age), which would otherwise have complicated monitoring.

The selected stems covered a range of sizes and microhabitats, including isolated and clustered individuals and plants growing in sun exposed or shaded conditions. Each stem received a unique ID, was marked with a red string, photographed, measured and mapped in QField.

The plants were revisited every 4 to 7 days, with height and flowering stage (vegetative, bud formation, start of flowering, full flowering, end of flowering, fruit development, seed ripening, damaged) recorded during each visit.

Butterfly monitoring

The imagines of *Tomares nogelii* were monitored as part of a capture-mark-recapture (CMR) study (von der Wense Gonçalves et al., submitted). All individuals encountered were marked on the hindwings using a black STAEDTLER Lumocolor permanent pen (size S) and recorded with the QField mobile app. For each butterfly, sex, wing condition, behaviour, capture status and upper-wing colour were documented. Sex was determined by gently everting the genitalia through slight pressure on the abdomen.

Wing condition was categorised into four classes: fresh, slight wing wear, moderate wing wear and severe wing wear. Behaviour was classified as resting on host plant, resting on other vegetation, ovipositing, nectaring (including the plant species if observed), or flying. Upperwing colour was categorised as brown, partially orange, or strongly orange.

Linear transects were established within each colony by connecting all accessible *A. ponticus* patches to a continuous walking route. This resulted in transects of 1,025 m (Colony 1), 565 m (Colony 2), 746 m (Colony 3), 229 m (Colony 4), 138 m (Colony 5) and 210 m (Colony 6). The routes followed the natural distribution of host plants and therefore

occasionally included short stretches of unsuitable habitat (e.g. forested sections) that had to be crossed to reach the next patch. Transects were surveyed repeatedly under favourable weather conditions and walked at an effective pace of approximately 500 m per hour across colonies. Each colony was surveyed 7 to 18 times (mean interval 2 to 4 days).

Ovipositing females and butterflies in active copulae were not captured, but left undisturbed for reasons of conservation. Previously marked individuals were recorded without handling. All copulae were additionally logged, ensuring that mating pairs were documented even if neither individual had been marked previously.

Adult lifespan was estimated from capture-mark-recapture data as the number of days from first to last capture (inclusive) for each recaptured individual. Lifespan estimates represent minimum values, as emergence and death could not be observed directly.

Preimaginal stages

During host plant and butterfly monitoring, eggs and larvae encountered by chance were logged in QField, particularly in areas without previous records. For larvae, body length, probable instar and (when possible) the associated plant ID were recorded. Eggs were counted per stem and their position on the plant was noted when possible.

Between 15th and 18th of June, targeted egg surveys were carried out in each colony, covering about ten plants in large colonies and five in small ones. For each plant, egg count, plant height and the dominant egg stage (green, black, white or mixed) were recorded.

On 1st July, two last-instar larvae were collected and transferred to a pupation box containing soil, wood, plant debris and *A. ponticus* to mimic natural conditions. The box was kept in a light room, but not directly in the sun. It was lightly watered daily and checked regularly for larval behaviour.

Data analysis

All field data were collected in QField with predefined and controlled categories. After fieldwork, data were cleaned and processed in R version 4.4.2 (R Core Team 2024) using the packages *dplyr* and *tidyr*. Visualisations were produced with *ggplot2* and summary tables with *flextable*. For quadrat surveys, random points within host plant polygons were generated in QGIS version 3.40.7 (QGIS Development Team 2025) using the Random Points tool and patch areas and transect lengths were measured in QGIS.

To account for the hierarchical sampling design, quadrat level habitat variables were aggregated to the patch scale prior to statistical analyses. Patch level predictors were calculated as proportions or means, depending on variable type. Light conditions were summarized as the proportion of quadrats exposed to full sun to represent patch-level microclimatic conditions. Host plant phenology was aggregated in an ecologically meaningful manner, with bud forming and flowering stages considered reproductively relevant, reflecting oviposition and habitat use by imagines. Imago abundance was determined per patch by spatially joining georeferenced capture records with host plant patch polygons in QGIS.

Patch level relationships between imago abundance and habitat predictors were analysed using negative binomial generalized linear models (*glm.nb*, MASS) to account for overdispersion in count data. Patch area was log-transformed and included as a covariate to control for differences in patch size. Candidate predictors included patch area, light availability, host plant phenology, host plant density, habitat type and structural vegetation variables. Predictors without statistical support were excluded from final models to improve parsimony. P-values were derived from Wald z-tests.

For butterfly daily activity analyses, observation effort was recorded in ten-minute bins and behavioural counts were standardised by dividing raw counts by observation effort per bin. For the imago-plant synchrony analysis, host plant observations were aggregated to weekly values using a last observation carried forward procedure and butterfly observations were aggregated to weekly counts.

Results

Habitat characteristics

The vegetation across all colonies consists of a mosaic of dry calcareous grasslands (EUNIS: E1.26), calcareous scrubs (F3.2) and thermophilous oak forests (G1.7A), with the proportions of these habitats varying among sites (Fig. 2). Colony 1 is characterised by a parcel-like structure, with elongated grassland patches extending from a central path into the surrounding oak forest and interspersed with numerous shrubs. The forest here was lower and less dense than in the other colonies. Colony 2 is the most open site, dominated by typical dry grassland with sparse shrub encroachment and scattered dead *Fraxinus ornus* plantations. Colony 3 consists of several open forest clearings, many of which originated from declining *F. ornus* stands that had transitioned into grassland and shrub patches. Colony 4 is also situated within the forest, but represents a naturally open clearing, not associated with *F. ornus* plantations and remains more exposed and less shrub dominated than Colony 3. Colony 5 follows a narrow forest road with predominantly ruderal vegetation, whereas Colony 6 is located deeper within the forest and is the darkest and most shaded of all colonies.

Quadrat surveys (n = 100) summarised in Tables 1 and 2 highlight these differences. Bare soil cover typically ranges between 1–25%. It is lowest in Colony 2 and highest in Colony 5. Most *Astragalus ponticus* individuals occur in a vegetative state (49%), but flowering stages vary between colonies. Only Colony 4 is dominated by plants in late flowering stages (43%). Habitat composition across all quadrats reflects a mixture of shrubland (36%), mixed/transition habitat (31%) and grassland (23%), with Colony 6 consisting entirely of forest. Host plant height is usually 30–60 cm (57%) but exceeds 60 cm more often in Colonies 4 and 6, where overall vegetation is also taller. Light conditions are dominated by partial shade (66%), followed by full sun (24%) and full shade (10%), with Colony 4 being the brightest and Colony 1 the most shaded site.

Table 1

Summary of quadrat-based habitat characteristics across the six colonies. Values represent the percentage of sampled quadrats per colony and overall (Total) falling into each category for bare soil cover, host-plant flowering state, habitat type, host-plant height, light condition and surrounding vegetation height. Flowering states reflect the phenological condition of host plants recorded at the time of quadrat surveys and represent the proportion of quadrats in each state. Quadrat surveys were conducted once per sampling point ($n = 100$ quadrats in total)

Variable	Category	Colony 1	Colony 2	Colony 3	Colony 4	Colony 5	Colony 6	Total
Bare soil cover	0%	11.8%	11.8%	11.8%	25.0%	0.0%	50.0%	13.3%
	1–25%	55.9%	88.2%	64.7%	50.0%	33.3%	0.0%	62.2%
	25–50%	26.5%	0.0%	17.6%	12.5%	0.0%	50.0%	17.3%
	50–75%	0.0%	0.0%	2.9%	12.5%	33.3%	0.0%	3.1%
	> 75%	5.9%	0.0%	2.9%	0.0%	33.3%	0.0%	4.1%
Flowering state	Vegetative	52.8%	82.4%	35.3%	14.3%	66.7%	0.0%	48.5%
	Bud Formation	16.7%	0.0%	8.8%	0.0%	0.0%	0.0%	9.1%
	Start of Flowering	2.8%	5.9%	2.9%	14.3%	0.0%	0.0%	4.0%
	Full Flowering	13.9%	0.0%	8.8%	14.3%	0.0%	50.0%	10.1%
	End of Flowering	11.1%	11.8%	23.5%	42.9%	33.3%	50.0%	19.2%
	Fruit Development	2.8%	0.0%	20.6%	14.3%	0.0%	0.0%	9.1%
Habitat type	Grassland	8.3%	0.0%	38.2%	87.5%	0.0%	0.0%	23.0%
	Shrubland	33.3%	35.3%	47.1%	12.5%	33.3%	0.0%	36.0%
	Forest	5.6%	35.3%	0.0%	0.0%	0.0%	100.0%	10.0%
	Mixed/Transition	52.8%	29.4%	14.7%	0.0%	66.7%	0.0%	31.0%
Host plant height	10–30 cm	8.3%	17.6%	17.6%	14.3%	0.0%	0.0%	13.1%
	30–60 cm	66.7%	58.8%	50.0%	42.9%	66.7%	0.0%	56.6%
	60–100 cm	25.0%	23.5%	23.5%	42.9%	33.3%	100.0%	27.3%
	> 100 cm	0.0%	0.0%	8.8%	0.0%	0.0%	0.0%	3.0%
Light condition	Full sun	8.3%	5.9%	41.2%	75.0%	0.0%	0.0%	24.0%
	Partial shade	66.7%	94.1%	55.9%	25.0%	100.0%	100.0%	66.0%
	Full shade	25.0%	0.0%	2.9%	0.0%	0.0%	0.0%	10.0%
Vegetation height	10–30 cm	0.0%	0.0%	11.8%	25.0%	0.0%	0.0%	6.0%
	30–60 cm	61.1%	58.8%	88.2%	50.0%	33.3%	0.0%	67.0%
	60–100 cm	38.9%	35.3%	0.0%	25.0%	66.7%	100.0%	26.0%
	> 100 cm	0.0%	5.9%	0.0%	0.0%	0.0%	0.0%	1.0%

Host plant abundance varies strongly among colonies, with an overall mean of 9.7 ± 5.8 plants per m^2 (range 0–28). Densities peak in Colony 3 (12.2 ± 6.7) and Colony 6 (11.5 ± 4.9), whereas Colony 5 has the lowest values (4.3 ± 1.5).

Reproductive plant density averages 2.4 ± 3.6 per m^2 , highest in Colonies 4 and 6 (4.2 and 4.5 per m^2). Feeding marks were recorded on 1.9 ± 3.4 plants per m^2 , again most frequent in Colony 3 (3.6 ± 4.7).

Table 2

Numerical summary of host-plant patch characteristics and butterfly abundance by colony. Values are given for each colony and overall (Total). Host-plant variables are reported per quadrat and imago abundance per host-plant patch as mean $\pm$ SD with ranges in brackets. Empty patches indicate the number and proportion of host-plant patches without recorded imagines

Col.	Patches (n)	Area (m^2)	Quadrats (n)	Host plants / quad	Reprod. plants / quad	Feedings marks / quad	Imago / patch	Empty n/N (%)
1	22	1,552	36	9.1 ± 5.0 [1–18]	1.4 ± 2.2 [0–8]	0.9 ± 1.7 [0–7]	7.2 ± 14.6 [0–54]	10/22 (45%)
2	18	474	17	8.7 ± 4.4 [4–17]	0.6 ± 1.7 [0–7]	0.4 ± 0.9 [0–3]	0.7 ± 1.4 [0–4]	13/18 (72%)
3	17	1,612	34	12.2 ± 6.7 [3–28]	4.0 ± 4.8 [0–20]	3.6 ± 4.7 [0–20]	4.6 ± 9.8 [0–34]	9/17 (53%)
4	7	235	8	6.1 ± 5.0 [0–14]	4.2 ± 4.1 [0–11]	3.2 ± 3.1 [0–8]	4.4 ± 4.3 [0–13]	1/7 (14%)
5	4	78	3	4.3 ± 1.5 [3–6]	1.3 ± 2.3 [0–4]	1.3 ± 2.3 [0–4]	0.2 ± 0.5 [0–1]	3/4 (75%)
6	3	43	2	11.5 ± 4.9 [8–15]	4.5 ± 2.1 [3–6]	1.5 ± 2.1 [0–3]	0.3 ± 0.6 [0–1]	2/3 (67%)
Total	71	3,994	100	9.7 ± 5.8 [0–28]	2.4 ± 3.6 [0–20]	1.9 ± 3.4 [0–20]	4.0 ± 9.8 [0–54]	38/71 (54%)

At the patch level, imago abundance varied strongly among host plant patches (Table 2) and is primarily explained by patch area and light availability. Imago numbers increased significantly with patch size ($p < 0.001$) with substantially higher abundances in larger patches. Light availability further influenced imago abundance, with patches containing a higher proportion of sun exposed quadrats supporting significantly more imagines than shaded patches ($p = 0.047$). Host plant phenology showed a weaker positive effect, as patches with a higher proportion of host plants in reproductively active stages (bud formation to flowering) tended to host more imagines ($p = 0.060$). Neither host plant density nor habitat type or structural vegetation variables (host plant height, surrounding vegetation height and bare soil cover) showed a significant effect on imago abundance when tested in separate patch level models.

Microclimatic conditions recorded by the data loggers were broadly similar across colonies. Mean daily temperatures ranged from 19.7°C in Colony 1 to 22.9°C in Colony 4, while mean relative humidity varied between 53% (Colony 4) and 68% (Colony 1). Daily temperature fluctuations were moderate overall, with Colony 3 showing the most stable conditions (mean daily range 16.1°C) and Colony 1 and Colony 4 exhibiting the largest ranges (22.0°C and 20.4°C , respectively). The comparatively warm and dry values in Colony 4 are likely influenced by the later installation date of its logger, which captured only the warmer part of the flight period.

In Colony 2, intense grazing activity was observed during the study period. On 22nd of June, goats were recorded moving through parts of the Colony 2 while most *Astragalus ponticus* plants still carried intact inflorescences. During the subsequent visit on 2nd of July, nearly all flower buds and inflorescences in the area had been eaten up by the goats and only three larvae were recorded on that day.

Phenology and lifespan

Across all colonies, 638 imagines of *Tomares nogelii* were caught and marked between 24th of May and 24th of June, resulting in 194 recaptures and a total of 832 capture events as shown in Table 3. Colony 1 yielded the highest number of individuals (n = 331), followed by Colony 4 (n = 127) and Colony 3 (n = 109). Slightly more males than females were recorded among first captures (312 versus 289). Colony 1 also exhibited the longest continuous flight period, lasting 31 days. Peak flight dates differed among colonies, ranging from 31st of May in Colony 4 (the easternmost site) to 6th of June in Colony 1 (the westernmost site). Colony 6 was excluded from trend analyses due to its extremely low sample size (three individuals in total).

Colony 2 lacked a distinct peak and instead showed a wave-like abundance pattern with daily counts reaching up to 14 individuals (Fig. 3). Colony 4 was incorporated later into the survey area, and the first monitoring visit probably coincided with its flight peak, with 57 individuals recorded on that day (Fig. 3).

Table 3

Summary of imago observations of *Tomares nogelii* by colony. For each colony, the table shows the first and last observation date, duration of the flight period (days), numbers of first captures, males, females and individuals of unknown sex (based on first captures only), recaptures, total observations, and the date and abundance of the peak count

Col.	First date	Last date	Days	First cap.	♂	♀	Unk.	Recap.	Total obs.	Peak (date, n)
1	25.05.2025	24.06.2025	31	331	175	134	22	114	445	06.06.2025 (n = 69)
2	30.05.2025	17.06.2025	19	55	31	20	4	10	65	02.06.2025 (n = 14)
3	24.05.2025	17.06.2025	25	109	50	56	3	38	147	03.06.2025 (n = 31)
4	31.05.2025	15.06.2025	16	127	52	70	5	22	149	31.05.2025 (n = 57)
5	25.05.2025	16.06.2025	23	13	4	7	2	10	23	06.06.2025 (n = 7)
6	13.06.2025	18.06.2025	6	3	0	2	1	0	3	18.06.2025 (n = 2)
Total	24.05.2025	24.06.2025	32	638	312	289	37	194	832	

Observed imaginal lifespan, measured as the number of days from first to last capture, was generally short (Fig. 4). Median lifespan was 3 days in females (n = 61) and 4 days in males (n = 83), while mean lifespan amounted to 4.28 days in females and 4.71 days in males. Maximum observed lifespan reached 14 days in females and 13 days in males. These values represent minimum estimates of imaginal lifespan, as individuals may have emerged before first capture or survived beyond their last observation.

Daily activity and behaviour

Activity patterns showed two daily peaks (Fig. 5). Raw observations (Panel a) increased shortly after 08:00, peaked around 10:00–10:30, declined towards midday and rose again around 14:00–15:00. After standardising for unequal survey effort (Panel b), this bimodal structure remained: the strongest activity occurred between 09:30 – 10:30 and again around 14:00–15:00. Oviposition was almost entirely restricted to the morning, nectaring peaked before noon and flying increased during the afternoon.

Survey effort during the flight period was highest between 08:30 and 12:00 and declined sharply after 14:00 (Panel c). Late afternoon time bins (17:30 – 19:00) are shown in grey, as they are based on less than four pooled survey days and should therefore be interpreted with caution.

Across all observations, resting was the most common behaviour (32.5% on *A. ponticus*, 29.1% on other plants), followed by flying (26.6%). Nectaring (9.3%) and ovipositing (2.6%) were comparatively rarely observed. The most frequently used nectar plant was *Allium rotundum* (n = 30), followed by *Orlaya grandiflora* (19), *Salvia nemorosa* (10), *Salvia nutans* (9) and *Ligustrum vulgare* (3).

A total of 11 copulae were observed between 29th of May and 9th of June and recorded between 14:30 and 18:45.

Predation events

Observed predators of *T. nogelii* included lynx spiders (*Oxyopes heterophthalmus*, Fig. 6b), crab spiders (*Thomisus onustus*) and robber flies (Asilidae, Fig. 6c). In addition, green bush-cricket nymphs (*Tettigonia* sp.) were very common throughout all colonies and were frequently found sitting on *A. ponticus* stems in a characteristic ambush posture (Fig. 6a). Although their exact species identity could not be determined, their behaviour strongly suggested predatory tendencies: the nymphs regularly remained motionless on the host plants; on one occasion, a nymph was observed feeding on an imago of *T. nogelii*. Large dragonflies (Anisoptera) were also regularly present in the area and likely represent additional potential predators, although no predation event was recorded.

Wing colour variation

Figure 7 Upperwing colour categories of *Tomares nogelii* by sex based on first captures only. Individuals were classified as brown, partially orange or strongly orange. Bars show absolute numbers of individuals per category, with percentages indicating the proportion of each colour category within sexes

Some butterflies stood out because they lacked the typical orange pigment; instead, the underside of their wings showed a pale-yellow pattern. All but one of these individuals were brown on the upper side, while one showed a “strong orange” appearance (Fig. 8d), which in this case meant an intense pale yellow. In total, nine such aberrant individuals were observed (1,4% of the total number of observations), six females and three males. Most were found in Colony 1 (n = 6), the remaining three in Colony 4.

Synchrony with host plant phenology

Figure 9 shows the synchrony between butterfly abundance and *A. ponticus* phenology binned in weeks. Bud formation began during the week of 18th to 24th of May, coinciding with the onset of the flight period. The first butterflies were recorded on 24th of May in Colony 3; the first marked plants exhibiting bud formation appeared on 22nd of May in the same colony.

As shown in Table 4, more than half of the monitored plants (54%, n = 19) remained vegetative or were damaged before flowering. Flowering activity (from bud formation to full flowering) peaked during the first week of June and coincided with the highest weekly butterfly count (294 individuals). Only six of the 35 monitored plants (17%) progressed beyond reproductive onset after the start of flowering; all remaining plants either remained vegetative or were damaged prior to flowering.

Inflorescence damage increased steadily over time, reaching 49% overall, mainly due to larval feeding inside buds and developing inflorescences. Plant performance varied strongly among colonies: none of the marked plants in Colonies

1 and 5 progressed beyond reproductive onset, whereas three of five plants in Colony 6 and three of ten in Colony 3 reached this stage. Plant height ranged from 12–108 cm (mean 55 cm).

Table 4

Summary of *Astragalus ponticus* host-plant phenology by colony. Shown are the numbers and proportions of monitored plants that remained vegetative, reached reproductive onset (bud formation or later), or progressed to advanced reproductive stages (flowering to fruit development) at any time during the study period, as well as the number of damaged plants and the mean of individual maximum plant heights with ranges in brackets

Col.	Plants (n)	Veg. n (%)	Rep. on. n (%)	Rep. prog. n (%)	Dam. n (%)	Height
1	15	9 (60)	6 (40)	0 (0)	10 (67)	39.3 (14–59)
3	10	4 (40)	6 (60)	3 (30)	4 (40)	67.2 (12–100)
5	5	5 (100)	0 (0)	0 (0)	2 (40)	48.0 (38–72)
6	5	1 (20)	4 (80)	3 (60)	1 (20)	86.2 (48–108)
Total	35	19 (54)	16 (46)	6 (17)	17 (49)	55.2 (12–108)

Oviposition and larval occurrence

Oviposition occurred predominantly before midday (Fig. 5). Females deposited their eggs on unopened flower buds of *A. ponticus* and less frequently on fresh leaves positioned directly adjacent to the inflorescences (Fig. 1c). A total of 58 plants with eggs were examined, as summarised in Table 5. Egg numbers averaged approximately eight per stem (ranging from one to 45). Stems typically carried around six to seven buds. The highest egg loads occurred in Colony 4 (mean 11.8, range 1–21) and Colony 1 (mean 10.6, range 1–45), which also showed the highest imago abundances. The first oviposition was recorded on the 31st of May in Colony 4. Eggs were found on plants measuring 40 to 113 cm in height (mean 79 cm).

Larval development comprised four larval instars, based on observed size classes and the absence of intermediate forms. Although individual moulting events were not directly observed, the number of four larval instars is typical of Theclini and Eumaeini in Europe (Markl and Wagner, in press.). The earliest larvae were observed on 7th of June in Colony 4. Mature larvae were up to 20 mm large. Small larvae fed concealed within flower buds, whereas larger larvae became increasingly visible and frequently wandered openly shortly before pupation (Fig. 1e). In addition, some last-instar larvae showed a distinct change in body coloration to pink.

Table 5

Summary of oviposition and larval observations of *Tomares nogelii* by colony and for all colonies combined. Shown are the number of host plants with eggs, total egg counts, egg load per occupied plant, oviposition height, the timing of earliest oviposition and larval occurrence, and larval size ranges recorded during the study period. Egg load per observation, oviposition height, and larval length are reported as mean values with ranges in brackets

Col.	Obs. with eggs	Total eggs	Eggs / obs.	Earliest oviposition	Oviposition height	Total larvae	Earliest larval obs.	Larval length
1	18	191	10.6 (1–45)	01.06.2025	73 (40–112)	14	08.06.2025	12 (7–18)
2	10	48	4.8 (1–8)	02.06.2025	78 (59–109)	4	17.06.2025	18 (16–20)
3	16	55	3.4 (1–12)	01.06.2025	75 (46–113)	3	13.06.2025	9 (9–9)
4	11	130	11.8 (1–21)	31.05.2025	91 (64–112)	6	07.06.2025	11 (3–14)
5	3	24	8.0 (3–13)	03.06.2025	92 (85–98)	0		
Total	58	448	7.7 (1–45)	31.05.2025	79 (40–113)	27	07.06.2025	12 (3–20)

On 24th of June in Colony 1, cannibalistic behaviour was documented. As shown in Fig. 10, within approximately 30 minutes a larger larva (probably L4) consumed a smaller one of its own species (probably L3) on a plant, whose flowers were basically eaten bare.

Ants were already commonly present on egg-bearing plants and their occurrence increased as soon as the larvae emerged. Larvae were almost invariably attended by one or more ant species, which frequently made contact with them to stimulate secretion. These ants had been collected in 2024 by the last author and were identified by B. Seifert, Görlitz (Senckenberginstitut für Biodiversitätsforschung). The ant species comprised *Plagiolepis pygmaea*, *Lasius bombycina*, *Crematogaster sordidula*, *Camponotus atricolor* and *Camponotus aethiops*.

The two larvae collected in Colony 1 and put into a plastic container on the first of July were highly active and moved not only across the plant, but also over the soil surface and the container walls. On 5th of July, one larva burrowed into the soil and became inactive, while the other one disappeared. By 9th of July, both larvae had pupated and were buried approximately 5 cm deep in the soil, positioned in a small hole next to each other (Fig. 1f). The pupae measured approximately 1 cm in length and 0.5 cm in diameter.

Discussion

Phenology, climate and host-plant synchrony

In 2025, the flight period of *Tomares nogelii* was closely synchronised with the phenology of its larval host plant *Astragalus ponticus*. Bud formation coincided with the onset of imaginal flight activity and peak flowering corresponded with the highest butterfly abundances. In contrast, observations from 2023 indicate that some imagines emerged before *A. ponticus* had reached suitable reproductive stages, resulting in high larval mortality, likely due to the lack of suitable host-plant resources (Markl and Wagner, in press). These contrasting patterns suggest that the degree of phenological synchrony varies substantially between years and may be sensitive to interannual weather variation.

A high proportion of monitored host plants remained vegetative or did not progress to flowering. This pattern is likely related to the life-history characteristics of *Astragalus ponticus*, as plants were selected randomly across a wide range of sizes and developmental stages, many of which may not have been physiologically capable of flowering in the study year. Within patches, flowering stages were highly heterogeneous, forming a mosaic of vegetative, bud-forming, flowering and damaged plants. Such fine scale heterogeneity likely buffers the effects of both phenological mismatch and larval damage by ensuring that suitable host-plant stages remain available even when individual plants remain non-reproductive or are heavily exploited.

The temporal pattern of imaginal activity closely followed short-term temperature dynamics, with flight activity beginning only after a period of rising daily temperatures (Fig. 11). This pattern is consistent with the widely reported phenomenon of butterflies emerging in response to temperature (Dennis 1993; Shreeve 1984). However, the present data cannot be used to infer causal relationships. Taken together, these results suggest that imaginal emergence and flight phenology in *T. nogelii* are closely associated with temperature dynamics, whereas reproductive success depends more strongly on the availability and spatial distribution of suitable host-plant stages. Population persistence therefore appears to be shaped by the interaction between weather conditions and host-plant phenology rather than by either factor alone.

Flight period and lifespan

The observed flight period of *T. nogelii* was longer than expected. In Colony 1, imaginal activity extended over 31 days, exceeding the 15–20 days reported in the literature (Rákossy et al. 2024), although peak flight activity remained concentrated between 31st of May and 6th of June, broadly matching previous reports. The extended activity period may reflect relatively cool conditions during May, which likely delayed emergence and prolonged imaginal presence.

Observed imaginal lifespan was generally short, with most individuals living only 3–4 days. Nevertheless, a small number of exceptionally old imagines were recorded, reaching minimum lifespans of 10–14 days, indicating that adult longevity in this species may be more variable than previously assumed. Sex-specific differences in survival were difficult to interpret. Although females showed lower mean and median lifespans than males, the oldest individual was a female. Sex-specific differences in adult lifespan have also been reported in other lycaenid butterflies, including *Polyommatus daphnis*, *Phengaris teleius*, *P. nausithous* and *Pseudophilotes bavius*, and are commonly linked to higher energetic costs of mate searching and courtship in males (Crişan et al. 2014; Sielezniew et al. 2020; Timuş et al. 2017). In *T. nogelii*, the absence of a clear female longevity advantage may reflect behavioural and methodological factors rather than true survival differences. Females were generally more cryptic and were the only sex observed to disperse between colonies. Capture-mark-recapture data from the companion study (von der Wense Gonçalves et al., submitted) further indicate markedly shorter female residence times in Colony 1, the largest population, likely reducing the detectability of older females through emigration rather than increased mortality.

Daily activity patterns and behaviour

Imaginal activity followed a clearly bimodal daily pattern, with peaks in the morning and early afternoon. This structure persisted after standardising for unequal survey effort, indicating genuine behavioural rhythms rather than sampling artefacts. Comparable bimodal activity patterns are common in temperate butterflies and are often interpreted as responses to microclimatic constraints in open habitats (Dennis 1993; Shreeve 1984).

Behavioural activities were strongly partitioned across the day. Oviposition occurred almost exclusively during the morning, nectaring peaked before noon and copulations were restricted to the afternoon and early evening. Morning oviposition has been reported in several butterfly species and may reduce exposure to heat stress and predators,

while coinciding with favourable host-plant conditions (Dennis and Sparks 2006; Wiklund 1984). The concentration of mating activity in the afternoon likely reflects periods of increased flight activity and encounter probability (Rutowski 1991).

Across all observations, resting behaviour dominated, accounting for more than half of all recorded activities. High proportions of inactivity are typical of butterflies inhabiting warm, open landscapes and likely serve multiple functions, including energy conservation, thermoregulation and predator avoidance (Dennis 2012). In species with limited imaginal longevity, such as *T. nogelii*, resting may be particularly important for balancing energetic constraints with reproductive demands. The frequent use of *Astragalus ponticus* as a resting substrate further suggests that host plant patches function not only as larval resources, but also as key imaginal microhabitats providing suitable resting and refuge sites.

Nectar use and microhabitats

Nectar feeding was comparatively uncommon and involved a limited set of flowering plants, most notably *Allium rotundum* and *Orlaya grandiflora*. The low proportion of nectaring observations suggests that adult *T. nogelii* may prioritise reproductive activities over sustained energy intake, relying on brief and opportunistic nectar visits. Similar patterns have been reported for other Lycaenidae with short flight periods (Dennis 2012).

Notably, nectar feeding on *Astragalus ponticus*, described in the literature as an important nectar source (Rákosy et al. 2024; van Oorschot and Wagener 2000), was not observed. Several nectar plants reported previously (Rákosy et al. 2024), including *Potentilla*, *Veronica* and *Euphorbia* species, were likewise not recorded, whereas visits to *Salvia* species occurred occasionally. In 2023, *Salvia* were the most important nectar species observed by the last author. In general, nectaring was most frequent on locally abundant flowering plants, indicating that nectar use is strongly influenced by local floral composition rather than by strict species preferences.

Predation and mortality risks

Direct predation on *T. nogelii* by lynx spiders (*Oxyopes heterophthalmus*), crab spiders (*Thomisus onustus*) and robber flies (Asilidae) was documented, with multiple events photographically recorded. Bush-cricket nymphs (Tettigoniidae) were frequently observed on *A. ponticus* inflorescences, but direct predation was confirmed only once. Although predation rates could not be quantified, the repeated presence of predators on host plants suggests that predation risk likely influences adult behaviour and habitat use.

Preimaginal ecology and density-dependent interactions

As expected for a strictly monophagous species, reproductive habitat suitability in *Tomares nogelii* was primarily determined by the presence of *Astragalus ponticus* in suitable phenological stages. Eggs were consistently recorded, after bud formation had begun, indicating that host-plant availability and timing represent the primary constraints for reproduction, whereas oviposition occurred across a wide range of microhabitat conditions.

Rearing observations from 2023 showed that eggs hatched after five to six days. Field-based estimates suggested slightly longer development times, but these are likely conservative because early instar larvae (L1-L2) feed concealed within unopened buds and are difficult to detect. Taken together, egg development in *T. nogelii* is likely completed within one week under favourable conditions.

Larval development likely comprises four instars which is typical for several Theclinae, whereas many other butterfly species develop through five or more larval instars (Markl and Wagner, in press). In our study, mature larvae reached lengths of up to 20 mm, exceeding the maximum size of approximately 10 mm reported in earlier accounts

(Hesselbarth and Schurian 1984). This discrepancy may reflect underestimation in previous literature, local differences in growth conditions, or the fact that fully developed larvae are only briefly exposed and therefore rarely detected in the field.

Exceptionally high egg loads were recorded in Colonies 1 and 4, with maxima of up to 45 eggs per stem in Colony 1, which also supported the highest imago abundances. This aggregation of eggs and larvae likely increases intraspecific interactions at the host-plant level. This interpretation is supported by the observation of cannibalistic behaviour in Colony 1, where a late-instar larva (likely L4) was observed feeding on a smaller conspecific (likely L3). Cannibalism has been reported in several Lycaenidae species (Cottrell 1984) and has been also noted for *Tomares ballus* (Tolman and Lewington 2009). Most published accounts, including behavioural overviews such as Pierce et al. (2002), indicate that cannibalism in Lycaenidae typically occurs among eggs or early instars feeding within confined structures such as buds or seedpods. The observation of cannibalism involving later larval instars in *T. nogelii* therefore suggests that unusually high local densities may intensify competitive interactions beyond the earliest developmental stages. On the plant where this behaviour was observed, nearly all flower buds had already been consumed, suggesting that local depletion of food resources likely triggered cannibalistic behaviour.

Larval feeding caused extensive internal bud damage, particularly in Colony 1. Comparable florivory in *Tomares ballus* has been shown to substantially reduce host-plant (*Astragalus lusitanicus*) fecundity in patches with high egg loads (Jordano et al. 1990). However, the authors argued that these effects were spatially and temporally heterogeneous and largely confined to individual patches, as host plant populations varied strongly with succession, flowering phenology and patch structure. Consequently, seed predation did not lead to sustained negative effects at the population or landscape scale. A similar dynamic may apply to the *T. nogelii*-*A. ponticus* system, where high larval pressure appears locally intense, but is embedded within a spatially heterogeneous and temporally variable host plant population. Assessing whether repeated high levels of bud and seed damage lead to longer-term effects on host plant recruitment will require multi-year monitoring.

High levels of host-plant exploitation may also influence adult behaviour. Capture-mark-recapture data indicate that females in Colony 1 had comparatively short residence times (von der Wense Gonçalves et al., submitted), consistent with individuals moving away from heavily exploited patches to maximise feeding and oviposition success as host-plant suitability declines.

By collecting two late-instar larvae and rearing them under controlled conditions, aspects of the pupation process could be directly documented. Both larvae burrowed into narrow soil fissures at a depth of approximately 5 cm. From the onset of inactivity to completion of pupation, development took four days. Notably, both larvae pupated at the same location. While this may partly reflect the experimental setup, other suitable fissures were available, suggesting a possible preference for specific microstructures during pupation. Such behaviour is consistent with reports from other Theclinae, which typically pupate in the soil close to the host plant and exhibit limited dispersal prior to pupation (Tolman and Lewington 2009).

Habitat quality and colony-level differences

Although the study area comprised a mosaic of steppe grassland, shrub patches and forest edges with broadly similar habitat composition, the quality and stability of *Astragalus ponticus* patches varied markedly among colonies and strongly influenced local population performance of *Tomares nogelii*.

Colony 1 supported the highest butterfly densities, but also showed pronounced signs of resource pressure, including extensive bud damage and low flowering success among monitored host plants. As the only colony from which

individuals dispersed into adjacent areas (“wanderers”; von der Wense Gonçalves et al., submitted), high local density may already be pushing part of the population beyond the core habitat. Given its accessibility and status as the best-known site of the subspecies, Colony 1 may also face an elevated risk of future human disturbance or oversampling.

In contrast, Colony 3 combined high host-plant density with healthy flowering and stable butterfly numbers, suggesting favourable conditions for long-term persistence. Although this colony experienced a complete local extinction around 2017, possibly associated with insecticide application (Rákossy et al. 2024), it has since recovered and currently represents one of the most robust sites. If grazing pressure and chemical disturbance remain controlled, this colony may have the potential to support even higher abundances in the future.

Colony 2 was strongly affected by a late-season grazing event, which resulted in near-complete removal of inflorescences (Fig. 12) during larval development. Because larvae feed within flower buds, this grazing caused direct larval mortality and represents an acute bottleneck for population persistence, even in otherwise suitable habitats.

Peripheral colonies (5 and 6) supported only low butterfly numbers and likely function as marginal or satellite habitats. Together, these patterns indicate that local population performance is shaped not only by host-plant presence, but also by disturbance regimes and patch stability.

Although host plant abundance varied strongly among colonies, it was not a significant predictor of imago abundance at the patch scale. This indicates that host-plant density alone is insufficient to explain habitat suitability and that fine-scale habitat structure and light availability modulate the effective use of host plants by imagines. Despite broadly similar microclimatic conditions recorded across colonies, strong differences in butterfly abundance highlight the importance of patch openness over colony-level mean temperature or humidity values.

Wing colour variation and aberrations

Variation in upperwing coloration was quantified and broadly confirmed previous descriptions from Anatolian populations, which reported a higher proportion of orange coloration in females than in males (van Oorschot and Wagener 2000). In the Romanian population studied here, approximately half of the individuals of both sexes exhibited uniformly brown upperwings; the proportion of individuals with strong orange coloration was significantly higher in females (23%) than in males (10%).

Colour aberrations in *Tomares nogelii* have previously been reported only once, based on a single individual described as albino by Cuvelier (2022). That specimen showed an almost complete absence of the typical orange upperwing coloration, while the dark (melanic) wing pattern and venation were largely retained. However, given that melanic pigmentation was preserved, this phenotype more likely reflects a selective loss of orange pigmentation rather than true albinism, which would imply a general absence of melanin. In the present study, nine additional individuals showing a comparable aberrant colour pattern were recorded. These aberrant individuals accounted for 1.4% of all captured butterflies. This suggests, that reduced orange pigmentation may occur more regularly in this population than previously recognised.

Conservation implications

The results of this study underline the high vulnerability of *Tomares nogelii* resulting from its strict host-plant specialisation, short imaginal lifespan and narrow reproductive window. At the patch scale, imago abundance was mainly driven by patch area and light availability, indicating that conservation measures should prioritise the maintenance of large, open and sun-exposed *Astragalus ponticus* patches.

Reproductive success depended strongly on host-plant phenology and the degree of synchrony between butterfly flight period and flowering varied between years. This highlights the sensitivity of the species to climatic variability and emphasises the need for long-term monitoring to detect unfavourable shifts in phenological synchrony.

Grazing emerged as a critical, but timing-dependent factor. A single late season grazing event caused near complete removal of inflorescences during larval development and likely resulted in substantial larval mortality in one of the monitored colonies. Management should therefore prevent grazing during the larval feeding period, while allowing carefully timed grazing outside this window to prevent shrub encroachment.

Finally, the study area appears to function as a metapopulation of few high-quality core sites surrounded by low-density satellite patches. Conservation efforts should thus focus on protecting core habitats while maintaining connectivity among host-plant patches to support metapopulation persistence at the landscape scale.

Declarations

Author contributions

This study is based on the master's thesis of Inka Hahn, who did the field study, performed the data analysis and wrote the first draft of the manuscript. Field work and data collection were carried out by Inka Hahn and Paulo von der Wense Gonçalves. László Rákossy and Lieven Caekebeke contributed by identifying suitable study sites, providing methodological guidance and commenting on the manuscript. Gregor Markl invented and supervised the project, coordinated the study design and field work, discussed the data and revised the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Funding

No funding was received to assist with the preparation of this manuscript.

Data availability

The data supporting the findings of this study are not publicly available due to the sensitive nature of the study species and locations, but are available from the corresponding author upon reasonable request.

Ethics approval and animal welfare

All procedures involving live insects were conducted with care to minimise handling time and stress. Adult butterflies were captured, marked and released immediately. Two larvae were temporarily collected for observation and returned to their natural habitat after pupation.

Acknowledgements

We are grateful to Romeo Enescu, Director of the Forestry Division, for granting permission to access the study sites and conduct fieldwork. Our thanks also go to Dr. Bernhard Seifert (Department of Entomology, Senckenberg Museum

für Naturkunde, Görlitz, Germany) for identifying the ant species associated with the larval stages of *Tomares nogelii*. We also thank colleagues and collaborators who assisted with fieldwork and data collection.

References

1. Bodescu F, Nicoara R, Miu I, Comanescu M (2017) Habitats identification guide of EUNIS level 3 for Romania: an instrument for validating the distribution of ecosystems for the implementation of the MAES process in Romania. <https://doi.org/10.13140/RG.2.2.19180.87688>
2. Bury J, Savchuk V (2015) New data on the biology of ten lycaenid butterflies (Lepidoptera: Lycaenidae) of the genera *Tomares*, *Pseudophilotes*, *Polyommatus* and *Plebejus* from the Crimea and their attending ants (Hymenoptera: Formicidae). *Acta Entomologica Silesiana* 23:1–16
3. Caradja A (1895) Die grossschmetterlinge des Königreiches Rumänien. *Dtsch Entomol Z Iris* 8:1–102
4. Cottrell CB (1984) Aphytophagy in butterflies: its relationship to myrmecophily. *Zool J Linn Soc* 80(1):1–57. <https://doi.org/10.1111/j.1096-3642.1984.tb02318.x>
5. Crişan A, Sitar C, Craioveanu C, Vizauer T-C, Rákossy L (2014) Multiannual population size estimates and mobility of the endemic *Pseudophilotes bavius hungarica* (Lepidoptera: Lycaenidae) from Transylvania (Romania). *North-Western J Zool* 10:S115–S124
6. Cuvelier S (2022) La diversité entomologique de la Roumanie (voyage en juin 2022): quel avenir? (Lepidoptera, Papilionoidea). *Lépidoptères* 31(81):76–84
7. Dennis RLH (1993) Butterflies and climate change. Manchester University
8. Dennis RLH (2012) A resource-based habitat view for conservation: butterflies in the British landscape. Wiley-Blackwell. <https://doi.org/10.1002/9781444315257>
9. Dennis RLH, Sparks TH (2006) When is a habitat not a habitat? Dramatic resource use changes under differing weather conditions for the butterfly *Plebejus argus*. *Biol Conserv* 129(3):291–301. <https://doi.org/10.1016/j.biocon.2005.10.043>
10. Forrest JR (2016) Complex responses of insect phenology to climate change. *Curr Opin Insect Sci* 17:49–54. <https://doi.org/10.1016/j.cois.2016.07.002>
11. Hesselbarth G, Schurian KG (1984) Beitrag zur Taxonomie, Verbreitung und Biologie von *Tomares nogelii* (Herrich-Schäffer, 1851) in der Türkei (Lepidoptera: Lycaenidae). *Entomofauna* 5:243–250
12. Izverscaia T, Ghendov V (2025) Vulnerable species of the legume family (Fabaceae) for the Red Book of the Republic of Moldova. *Acta et Commentationes: Ştiinţe Exacte şi ale Naturii* 19(1):150–160. 4th edn. <https://doi.org/10.36120/2587-3644.v19i1.150-160>
13. Jordano D, Rodríguez J (1990) The effect of seed predation by *Tomares ballus* (Lepidoptera: Lycaenidae) on *Astragalus lusitanicus* (Fabaceae): determinants of differences among patches. *Oikos* 57(2):250–260. <https://doi.org/10.2307/3565947>
14. Kharouba HM, Ehrlén J, Gelman A, Bolmgren K, Allen JM, Travers SE, Wolkovich EM (2018) Global shifts in the phenological synchrony of species interactions over recent decades. *Proc Natl Acad Sci USA* 115(20):5211–5216. <https://doi.org/10.1073/pnas.1714511115>
15. Mann J (1866) Verzeichniss der im Jahre 1865 in der Dobrudscha gesammelten Lepidopteren. *Proceedings of the Zoological and Botanical Society in Vienna* 16:1–40
16. Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob Change Biol* 13(9):1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>

17. Pierce NE, Braby MF, Heath A, Lohman DJ, Mathew J, Rand DB, Travassos MA (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annu Rev Entomol* 47:733–771.
<https://doi.org/10.1146/annurev.ento.47.091201.145257>
18. QField Development Team (2025) QField for QGIS (Version 4.14.1). OPENGIS.ch. <https://qfield.org>
19. QGIS Development Team (2025) QGIS geographic information system (Version 3.40.7). Open Source Geospatial Foundation. <https://qgis.org>
20. R Core Team (2024) R: a language and environment for statistical computing (Version 4.4.2). R Foundation for Statistical Computing. <https://www.r-project.org>
21. Rákosy L (2024) A field guide to the butterflies of Romania. Pelagic Publishing
22. Rákosy L, Corduneanu C, Crişan A, Dincă V, Kovács S, Stănescu M, Székely L (2021) In: Rákosy L (ed) Romanian Red List of Lepidoptera. Presa Universitară Clujeană
23. Rákosy L, Craioveanu C (2015) Rediscovering *Tomares nogelii dobrogensis* Caradja, 1895 in Romania. *Entomologica Romanica* 19:13–16
24. Rákosy L, Mancic C, Covaciu C, Rákosy D (2024) Rediscovered only to be almost exterminated again: the story of *Tomares nogelii dobrogensis*, a charismatic butterfly endemic to Europe. *Ecol Conserv Sci* 4(3):5556366.
<https://doi.org/10.19080/EOCA.2024.04.555636>
25. Rutowski RL (1991) The evolution of male mate-locating behavior in butterflies. *Am Nat* 138(5):1121–1139.
<https://doi.org/10.1086/285273>
26. Seven Çalışkan S (2014) A new species of blue from Turkey, *Neolycaena soezen* Seven, sp. n. (Lepidoptera: Lycaenidae). *SHILAP* 42:311–317
27. Shreeve TG (1984) Habitat selection, mate location, and microclimatic constraints on the activity of the speckled wood butterfly *Pararge aegeria*. *Oikos* 42(3):371–377. <https://doi.org/10.2307/3544407>
28. Sielezniew M, Kostro-Ambroziak A, Kőrösi Á (2020) Sexual differences in age-dependent survival and life span of adults in a natural butterfly population. *Sci Rep* 10:10394. <https://doi.org/10.1038/s41598-020-66922-w>
29. Singer MC, Parmesan C (2010) Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? *Philos Trans R Soc B* 365(1555):3161–3176.
<https://doi.org/10.1098/rstb.2010.0144>
30. Sirenko TV (2016) Diagnostic signs of age states of *Astragalus ponticus* Pall. *Plant Introduction* 71:16–22.
<https://doi.org/10.5281/zenodo.2386729>
31. Timuş N, Czekes Z, Rakosy L, Nowicki P (2017) Conservation implications of source-sink dynamics within populations of endangered *Maculinea* butterflies. *J Insect Conserv* 21:369–378. <https://doi.org/10.1007/s10841-016-9906-6>
32. Tolman T, Lewington R (2009) Collins butterfly guide. HarperCollins
33. van Oorschot H, Wagener S (2000) Zu *Tomares* in der Türkei: Ergänzungen und Korrekturen zu Hesselbarth (1995). *Phegea* 28(3):87–117
34. van Swaay C, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M, Settele J, Verovnik R, Verstrael T, Warren M, Wiemers M, Wynhof I (2010) European Red List of Butterflies. Publications Office of the European Union
35. van Swaay CA, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M, Settele J, Verovnik R, Verstrael T, Warren M, Wiemers M, Wynhof I (2025) Measuring the pulse of European biodiversity: European Red List of Butterflies. Publications Office of the European Union / IUCN Red List
36. Visser ME, Gienapp P (2019) Evolutionary and demographic consequences of phenological mismatches. *Nat Ecol Evol* 3(6):879–885. <https://doi.org/10.1038/s41559-019-0880-8>

37. Wiklund C (1984) Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. *Oecologia* 63(1):23–29. <https://doi.org/10.1007/BF00379780>

Figures



Figure 1

Life stages and host-plant association of Tomares nogelii and Astragalus ponticus. a Imago nectaring on *Orlaya grandiflora*. *b* Copula on grass vegetation adjacent to host-plant patches. *c* Eggs deposited on unopened flower buds of

A. ponticus. d Early larval stages attended by ants and feeding concealed within developing buds. e Last instar larva attended by ants shortly before pupation. f Two pupae located in close proximity within the soil



Figure 2

Study sites (Colonies 1-6) of *Tomares nogelii* in northern Dobrogea, Romania. a Colony 1. b Colony 2. c Colony 3. d Colony 4. e Colony 5. f Colony 6

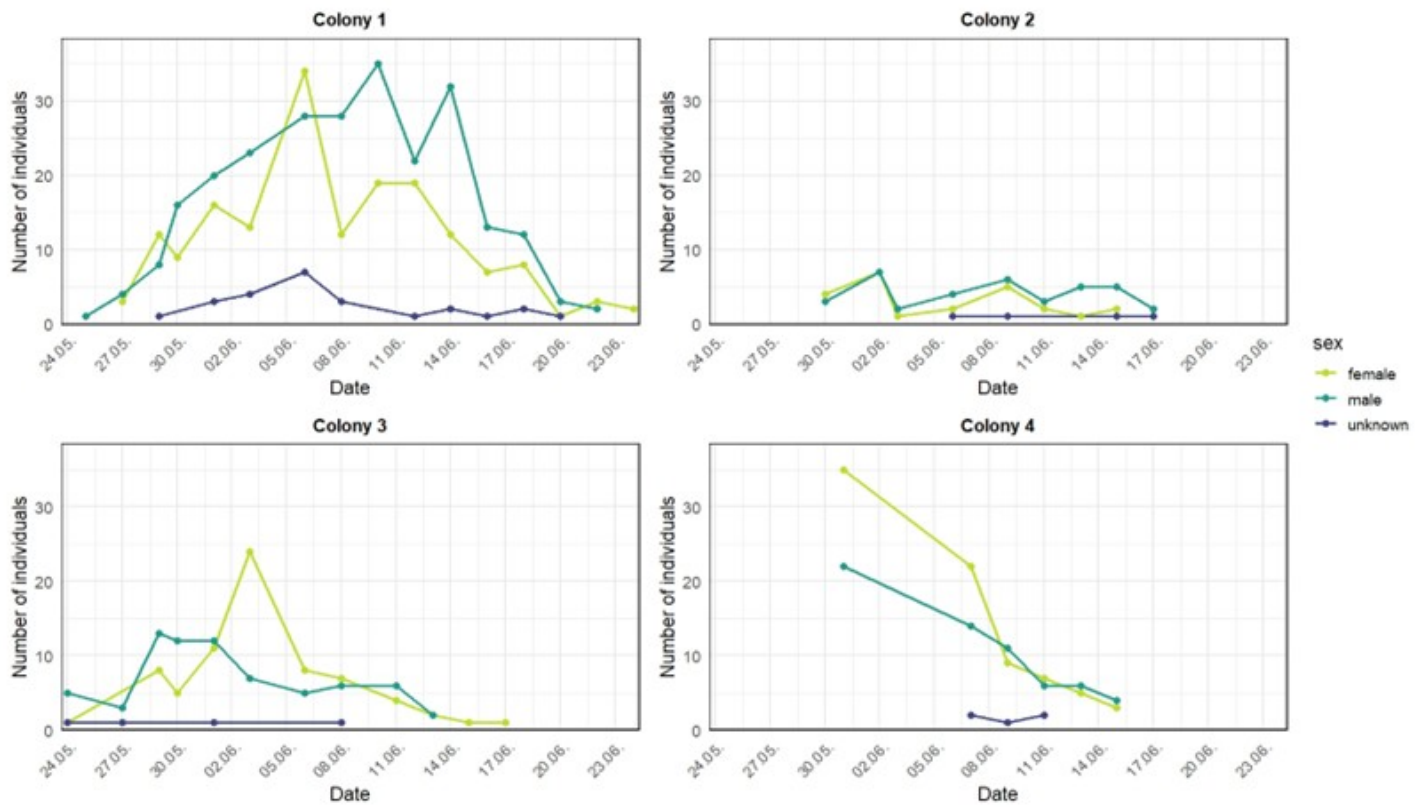


Figure 3

Daily numbers of *Tomares nogelii* imagines recorded in Colonies 1-4, shown separately for females, males and individuals of unknown sex. Values represent pooled counts per survey day

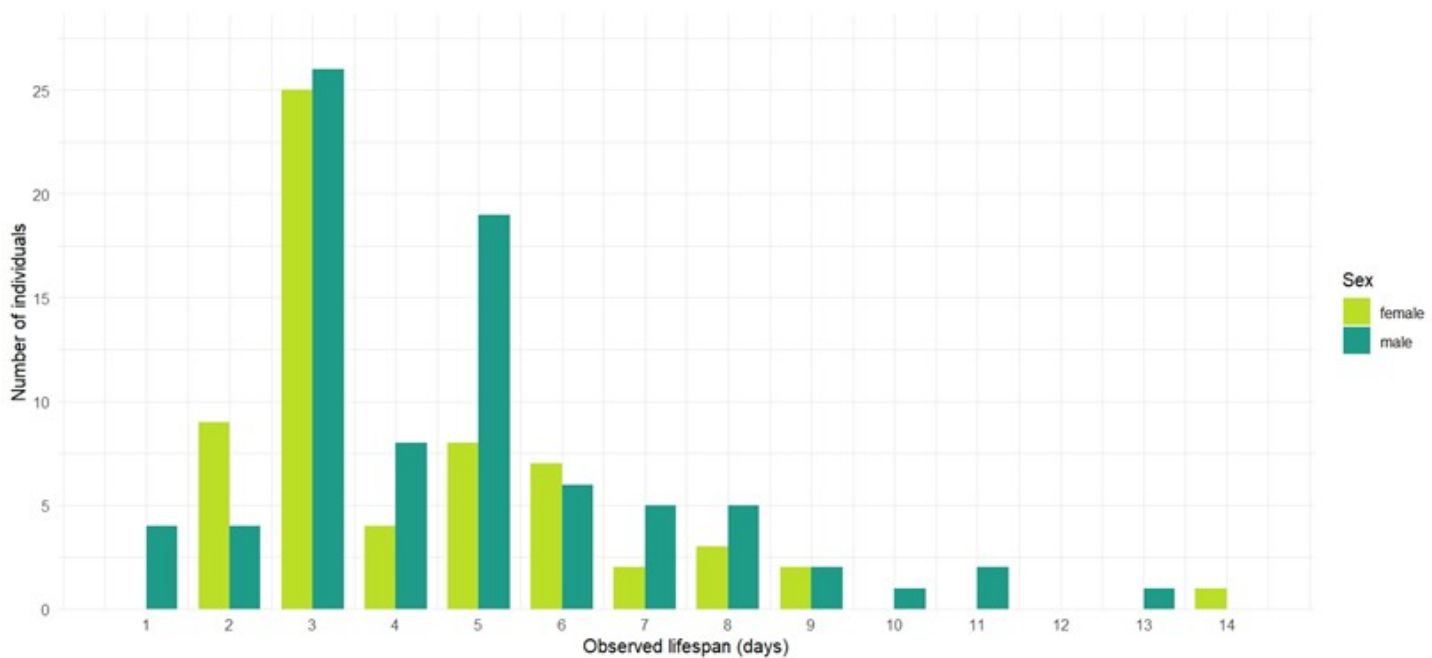


Figure 4

Frequency distribution of observed adult lifespans of *Tomares nogelii* based on recaptured individuals only, shown separately for females and males. Observed lifespan was calculated as the number of days between first and last capture

(inclusive)



Figure 5

Behavioural activity of *Tomares nogelii* across the day. a Raw behavioural counts per 10-minute bin. b Effort-standardised behavioural observations per 10-minute bin (faded bins indicate fewer than four survey days). c Survey effort per 10-minute bin



Figure 6

Upperwing colour categories of *Tomares nogelii* by sex based on first captures only. Individuals were classified as brown, partially orange or strongly orange. Bars show absolute numbers of individuals per category, with percentages indicating the proportion of each colour category within sexes

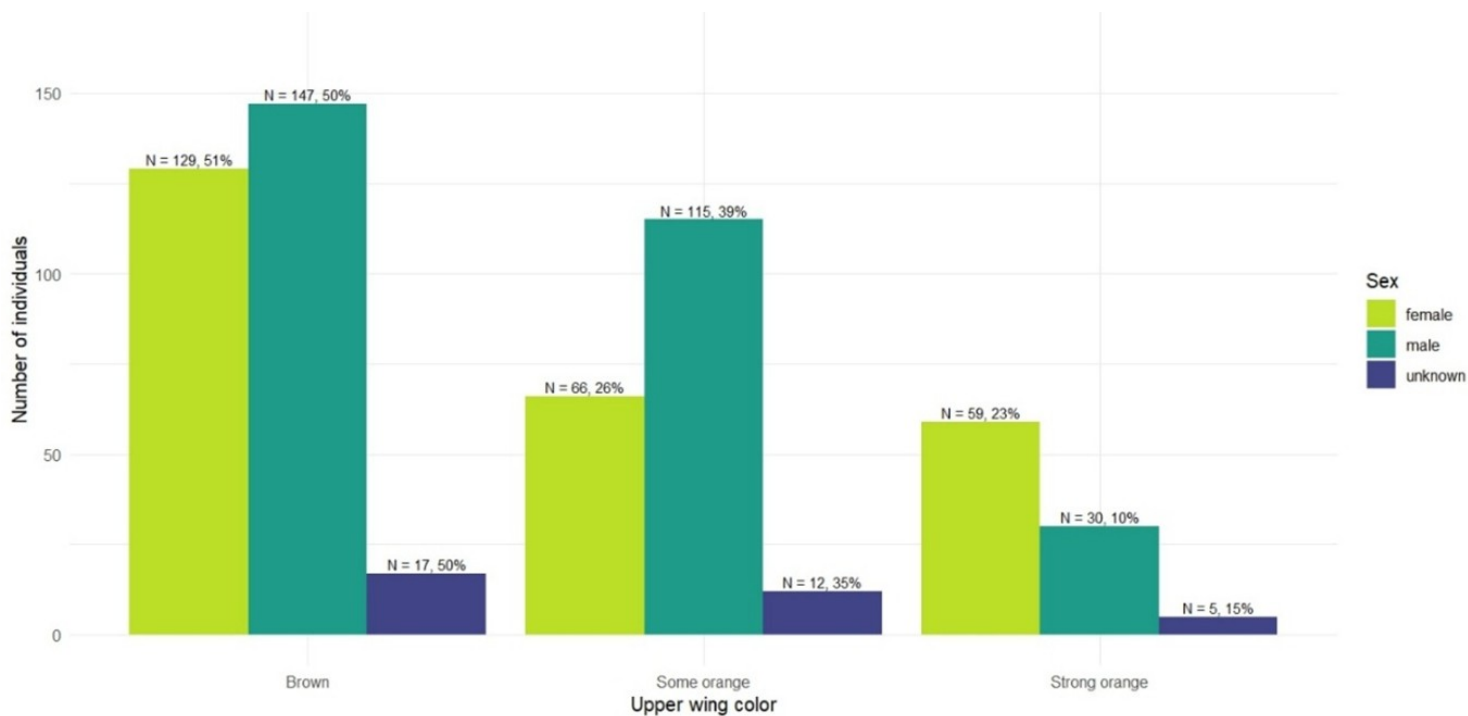


Figure 7

Upperwing colour categories of Tomares nogelii by sex based on first captures only. Individuals were classified as brown, partially orange or strongly orange. Bars show absolute numbers of individuals per category, with percentages indicating the proportion of each colour category within sexes



Figure 8

Upperwing colour variation in *Tomares nogelii*. a Uniformly brown upperwings. b Brown upperwings with limited orange scaling. c Strongly orange upperwing phenotype. d Aberrant individual with strongly reduced orange pigmentation (yellowish phenotype). e Aberrant (left) and normal imago on *Allium rotundum*

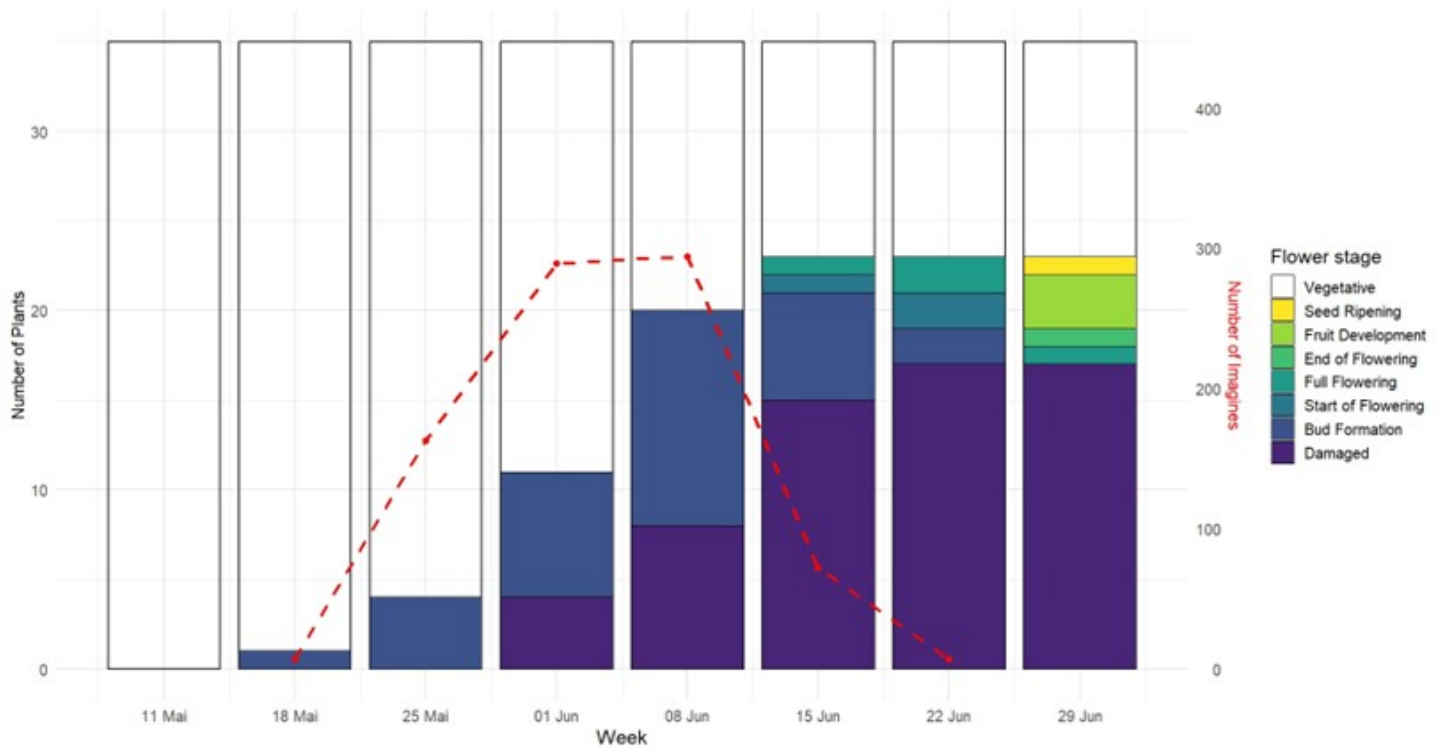


Figure 9

Temporal development of phenological stages of *Astragalus ponticus* and imago abundance of *Tomares nogelii* during the study period. Stacked bars show the number of monitored host plants per week in different phenological stages (left y-axis), while the dashed line indicates the weekly number of observed imagoes (right y-axis)



Figure 10

Cannibalistic behaviour in larvae of *Tomares nogelii* observed on *Astragalus ponticus*. a-b Early stage of the interaction at 09:00, showing a larger larva in contact with a smaller one. c Same interaction at 09:30, with the smaller larva largely consumed

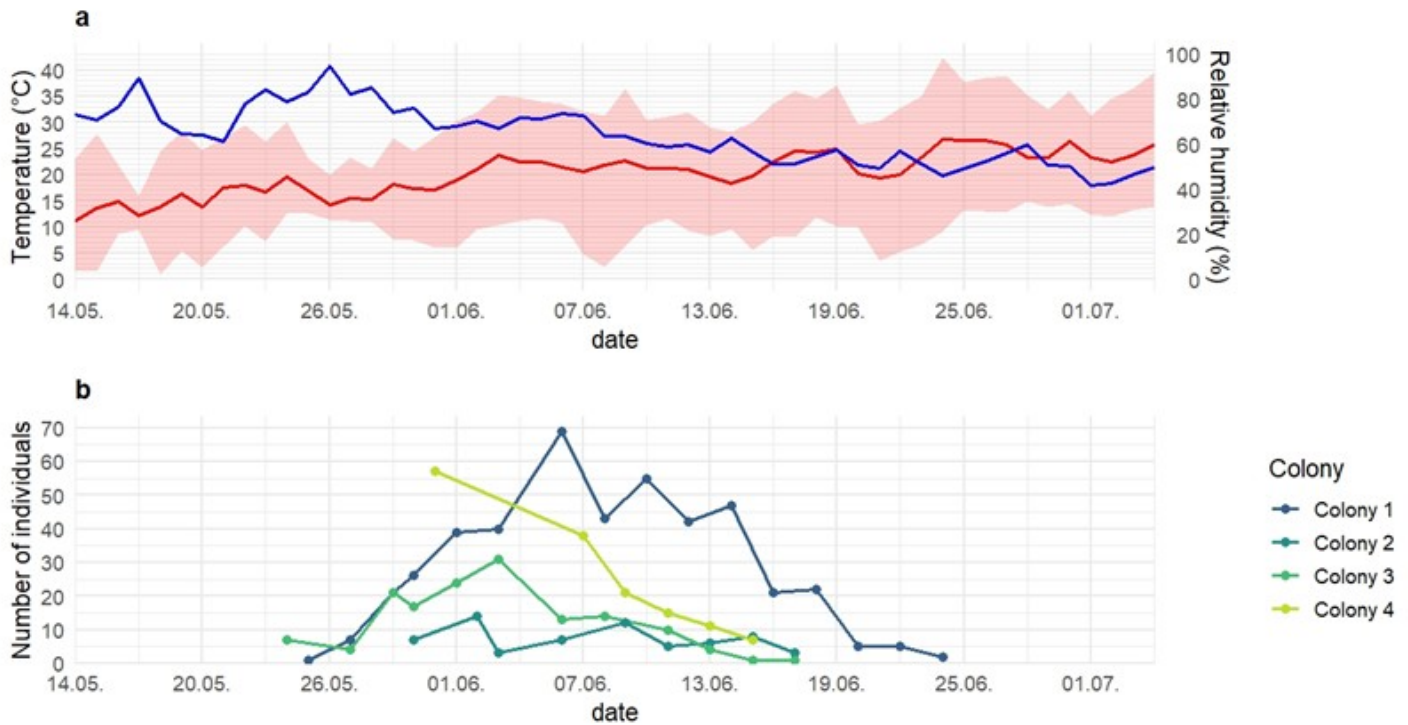


Figure 11

Temporal relationship between microclimatic conditions and imago activity of *Tomares nogelii*. The upper panel shows logger-derived temperature and humidity data, with a ribbon indicating daily minimum and maximum temperature, a line indicating daily mean temperature and a second line indicating mean relative humidity (right y-axis), while the lower panel shows daily numbers of observed imagines per colony (Colonies 1-4)



Figure 12

Astragalus ponticus in Colony 2 with inflorescences eaten up by goats during the study period

