Journal of Insect Conservation (2025) 29:30
https://doi.org/10.1007/s10841-025-00663-x

ORIGINAL PAPER

Oviposition preferences indicate a wide range of host plant species in two regionally declining butterfly species

Susanne Kurze[1] · Thilo Heinken[1] · Thomas Fartmann[2,3]

Received: 6 January 2025 / Accepted: 26 February 2025

Abstract
Different host plants may vary in their effects on butterfly larvae or adult performance, with possibly pervasive consequences for the viability of local populations. Understanding host plant preferences is therefore crucial for butterfly conservation. *Lycaena phlaeas* and *L. tityrus* are rather widespread butterflies in Central Europe. They though recently declined in several regions. Both *Lycaena* species use *Rumex* species as host plants, with so far unknown preferences within this genus. We investigated oviposition preferences of both butterfly species in a simultaneous choice experiment, considering five to six *Rumex* species (*R. acetosa,R. acetosella,R. crispus, R. obtusifolius, R. thyrsiflorus*, and in *L. phlaeas* additionally *R. sanguineus*). Oviposition proportions of both *Lycaena* species differed among *Rumex* species. *Rumex acetosella* was avoided, while all other species were utilized quite evenly. This finding suggests that all tested *Rumex* species are generally suitable host plants. The wide host plant range likely reflects a risk-spreading strategy, as females are limited in their ability to identify highly suitable plants for their larvae.

Implications for insect conservation
Since our study suggests that both *Lycaena* species utilize a wide range of *Rumex* species, further parameters than host-plant identity likely determine habitat suitability. The wide range of host plant species should facilitate the conservation of both butterfly species.

Keywords Habitat suitability · Host plant preference · *Lycaena phlaeas* · *Lycaena tityrus* · *Rumex* · Simultaneous-choice experiment

Introduction

Different host plants may vary in their effects on butterfly larvae or adult performance (Thompson and Pellmyr 1991; Gripenberg et al. 2010). Host plants can thus be ranked according to their suitability for a given species (Gripenberg et al. 2010). This host plant suitability has possibly pervasive consequences for the viability of local populations (e.g. Krämer et al. 2012; Scherer and Fartmann 2022). Understanding host plant suitability as a key component of habitat suitability is therefore crucial for the conservation of butterflies (Fartmann and Hermann 2006).

Butterfly eggs lack any opportunities for active movements and larvae are very limited in their mobility (Fartmann and Hermann 2006; García-Barros and Fartmann 2009). Therefore, oviposition site selection by females is critical for the development of immature stages and populations' reproductive success. Females should select the optimal microhabitat and host plant to ensure a good larvae performance, considering both abiotic (e.g. microclimate) and biotic factors (e.g. food quantity, food quality, competition, predators) (Jaenike 1990; Thompson and Pellmyr 1991). This positive relationship between oviposition site selection and larvae performance has been stated as

✉ Thomas Fartmann
t.fartmann@uos.de

[1] Institute of Biochemistry and Biology, General Botany, University of Potsdam, Maulbeerallee 3, 14469 Potsdam, Germany

[2] Department of Biodiversity and Landscape Ecology, Faculty of Biology and Chemistry, Osnabrück University, Barbarastraße 11, 49076 Osnabrück, Germany

[3] Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, D-48157 Münster, Germany

Published online: 03 April 2025

preference-performance hypothesis or mother-knows-best hypothesis (Thompson and Pellmyr 1991; Gripenberg et al. 2010). It has been confirmed in various insects, including butterflies, based on host plant selection, one aspect of oviposition site selection (e.g. Friberg et al. 2015; Meister et al. 2015; Gripenberg et al. 2010 for review). Females identify host plants by visual and chemical cues and select the most suitable ones for their offspring (Thompson and Pellmyr 1991; Renwick and Chew 1994).

Lycaena phlaeas (Linnaeus, 1761) and *Lycaena tityrus* (Poda, 1761) are rather widespread butterflies in Central Europe (Reinhardt et al. 2020; van Swaay et al. 2022). They though recently declined in several regions (Pöhler et al. 2019; León-Cortés et al. 2000; van Swaay et al. 2022; Fox et al. 2023). These declines are likely associated with increasing land-use intensity, often going along with a loss of nutrient-poor grasslands and habitat edges – the main habitats of both species (Bräu et al. 2013; Pöhler et al. 2019). Higher land-use intensity also affects the abundance of *Rumex* species, the host plants of both *Lycaena* species. *Rumex acetosella* and less pronounced *R. thyrsiflorus* prefer nutrient-poor conditions and disappear from more eutrophic habitats (Ellenberg and Leuschner 2010). By contrast, *R. acetosa* and *R. obtusifolius* are common in nutrient-rich grasslands, but they are often chemically controlled as weeds (Ellenberg and Leuschner 2010; Pöhler et al. 2019).

So far, the importance of single *Rumex* species for both *Lycaena* species remained unclear. *Lycaena phlaeas* is proposed to prefer *R. acetosella* over *R. acetosa*, while in *L. tityrus* it should be the other way around (Ebert and Rennwald 1991; Bräu et al. 2013). Furthermore, single observations in rearing experiments and under natural conditions suggest that both species use also further *Rumex* species as host plants. In *L. phlaeas*, oviposition and/or feeding behaviour of larvae have been observed on *R. crispus,R. obtusifolius,R. thyrsiflorus*, and *R. scutatus*. *Lycaena tityrus* has been shown to use *R. crispus,R. thyrsiflorus*, and *R. scutatus* (Fiedler 1989; Rose 2010; Bräu et al. 2013; Steffner et al. 2022). Comparative surveys on oviposition or feeding preferences are to our knowledge missing. However, understanding the relevance of single *Rumex* species for both *Lycaena* species is crucial for their conservation.

Here, we investigated oviposition preferences of both *Lycaena* species in a simultaneous choice experiment. We considered *R. acetosa,R. acetosella,R. crispus,R. obtusifolius*, and *R. thyrsiflorus* as potential host plants. In a smaller experiment, we investigated ovipositions of *L. phlaeas* on *R. acetosa* and *R. sanguineus*.

Materials and methods

Study species and species' origin

Lycaena phlaeas and *L. tityrus* exhibit similar habitats and host plants but differ in their distribution and voltinism. *Lycaena phlaeas* has a wide distribution across the Holarctic with strongholds in Europe and in the East of North America, while *L. tityrus* is mainly restricted to Europe (Ebert and Rennwald 1991; Bräu et al. 2013). Both species inhabit various open, oligo- to mesotrophic habitats on dry to moist soils, such as grasslands, ruderal habitats, clearings, or fringes (Ebert and Rennwald 1991; Bräu et al. 2013; Reinhardt et al. 2020). *Lycaena phlaeas* exhibits a slightly wider ecological amplitude and also occurs in gardens, urban green spaces, or quarries (Reinhardt et al. 2020). Both species lay their eggs singly on *Rumex* species (see details on host plant preferences above) and overwinter as larva (Ebert and Rennwald 1991; Bräu et al. 2013). *Lycaena phlaeas* is multivoltine with three to four generations per year. It is on the wing between April and October. *Lycaena tityrus* is usually bivoltine in Central Europe, with adults appearing from May to June and from July to August/September (Ebert and Rennwald 1991; Bräu et al. 2013).

Oviposition experiments were conducted with females of a F1 generation of field-collected individuals. We caught females in two to three habitats in Saxony (Germany) in spring/early summer 2014. Females of both species originated from sparse acidic grasslands near Bärwalde and species-rich mesic grasslands near Hoyerswerda in Upper Lusatia. A few females of *L. phlaeas* were also collected in heathlands near Weixdorf (near Dresden). For oviposition, the females were kept individually in cages containing leaves of *R. acetosella* and cotton balls prepared with sugar solution. Larvae were reared on *R. acetosella* in small groups in ventilated plastic boxes until adult emergence. For mating, a maximum of six individuals was kept in a cage (23 × 16 × 17 cm) with shoots of *R. acetosella* and cotton balls prepared with sugar solution. Individuals were exposed to almost natural conditions (no rain) during oviposition, larval development, and mating. Individuals of the lineages from the three habitats were separated during rearing and mating.

Oviposition experiments

Standard simultaneous choice tests (e.g. Nylin and Janz 1993) were used to investigate oviposition preferences in both *Lycaena* species. After observed matings or first ovipositions in mating cages, females were individually placed in cages (plastic boxes 23 × 16 × 17 cm, containing moist

cotton balls with sugar solution) under natural, shady conditions (except during night or rain). Each cage contained similar sized shoots of the five *Rumex* species (*R. acetosa,R. acetosella,R. crispus,R. obtusifolius,R. thyrsiflorus*) fixed as a bunch in a plastic jar with water in the middle of the cage. The shoots contained a stem with at least one fully developed, healthy, uncut leaf (minimum leaf area 4–5 cm^2). Due to differences in leaf size, usually several leaves of *R. acetosa* and *R. acetosella* and only one leaf of *R. crispus,R. obtusifolius*, and *R. thyrsiflorus* were provided. Touching or overlapping of leaves and with the cage were minimized. Shoots originated from plants (10–30 individuals per species) grown in pots under natural conditions. The plants were raised from seeds of commercial seed suppliers (except *R. obtusifolius*, grown from small plants dug out from a nearby meadow). Each female received shoots from different plants of a *Rumex* species during the experiment. Shoots were daily controlled for eggs and replaced. Eggs were separately counted for each *Rumex* species and summed up until the death of the female. Eggs on other material (e.g. cage, plastic jar, referred to as off-plant ovipositions) than *Rumex* shoots were also counted. Oviposition proportions were calculated for each female by dividing the number of eggs on a *Rumex* species by the total number of eggs (including off-plant ovipositions).

The oviposition experiments were conducted with 13 females of *L. phlaeas* and eight females of *L. tityrus* (see Table 1 for details). Four females (not included in Table 1) were excluded from the experiment due to early dead, almost without ovipositions. A smaller simultaneous choice test was conducted as described above with four females of *L. phlaeas* (Table 1) to compare ovipositions on *R. acetosa* and *R. sanguineus* (raised from seeds of a commercial seed supplier).

Statistical analysis

Differences in oviposition proportions among *Rumex* species were tested with *F* tests on linear mixed models (LMM) separately for both *Lycaena* species using the package nlme (Pinheiro et al. 2020) in R version 4.0.3 (R Core Team 2020). Oviposition proportion as response variable was arcsin square root transformed. *Rumex* species was considered as explanatory factor and female identity nested within habitat were included as random factors. In the smaller experiment with *L. phlaeas*, only female identity was considered as random factor. The proportion of variance explained by the fixed explanatory factor (marginal R^2,R^2m) and by both the fixed and random factors (conditional R^2,R^2c) was calculated by using the package MuMIN (Barton 2020). Pairwise differences between *Rumex* species were assessed with Tukey post-hoc tests using the package emmeans (Lenth 2022). We also tested differences in oviposition proportions between both *Lycaena* species on the five *Rumex* species (including off-plant ovipositions) using a Chi-squared test.

Table 1 Habitat origin of the lineages of the females of *Lycaena phlaeas* and *Lycaena tityrus* used in the experiments with five or two *Rumex* species

Female origin	Lycaena phlaeas		Lycaena tityrus
	5 Rumex species	2 Rumex species	5 Rumex species
Bärwalde	8	2	5
Hoyerswerda	3	2	3
Weixdorf	2	-	-
Total number females	13	4	8
Total number eggs	1,539	160	928

Results

Females of *L. phlaeas* laid between 24 and 174 eggs during their life time (118 ± 13, mean ± standard error; for total number see Table 1). They preferred the upper leaf surface (48% of all eggs). This preference was most strongly pronounced in *R. acetosella,R. obtusifolius*, and *R. thyrsiflorus* (55–66% of eggs on upper leaf side). *Lycaena tityrus* females laid between 68 and 149 eggs (116 ± 10; Table 1) that were almost evenly distributed on both leaf sides in all *Rumex* species (both sides 36%). Both *Lycaena* species hardly deposited eggs on stems (less than 4%).

Oviposition proportions of *L. phlaeas* differed among the five *Rumex* species (Fig. 1a). *L. phlaeas* tended to prefer the large-leaved *Rumex* species, especially *R. crispus* and *R. obtusifolius*, over *R. acetosella* and *R. acetosa*. In the smaller experiment, ovipositions of *L. phlaeas* did not differ between *R. acetosa* and *R. sanguineus* (Fig. 1b). *Lycaena tityrus* also differently distributed eggs on the five *Rumex* species, with the highest number of eggs on *R. thyrsiflorus* and the lowest on *R. acetosella* (Fig. 1c). In both species, female identity and habitat hardly influenced oviposition preferences (i.e. R^2m = R^2c). Oviposition preferences did not differ between both *Lycaena* species ($X^2 = 30$, $P = 0.22$).

Discussion

Both *Lycaena* species used all tested *Rumex* species for oviposition, i.e. no species was rejected. Oviposition proportions also slightly differed among *Rumex* species in both butterflies. *Rumex acetosella* was avoided, while all other species were utilized quite evenly. Accordingly, both *Lycaena* species use a wide range of host plants in the genus *Rumex* for oviposition.

The ovipositions on all tested *Rumex* species suggest that all are generally suitable host plants. This finding is

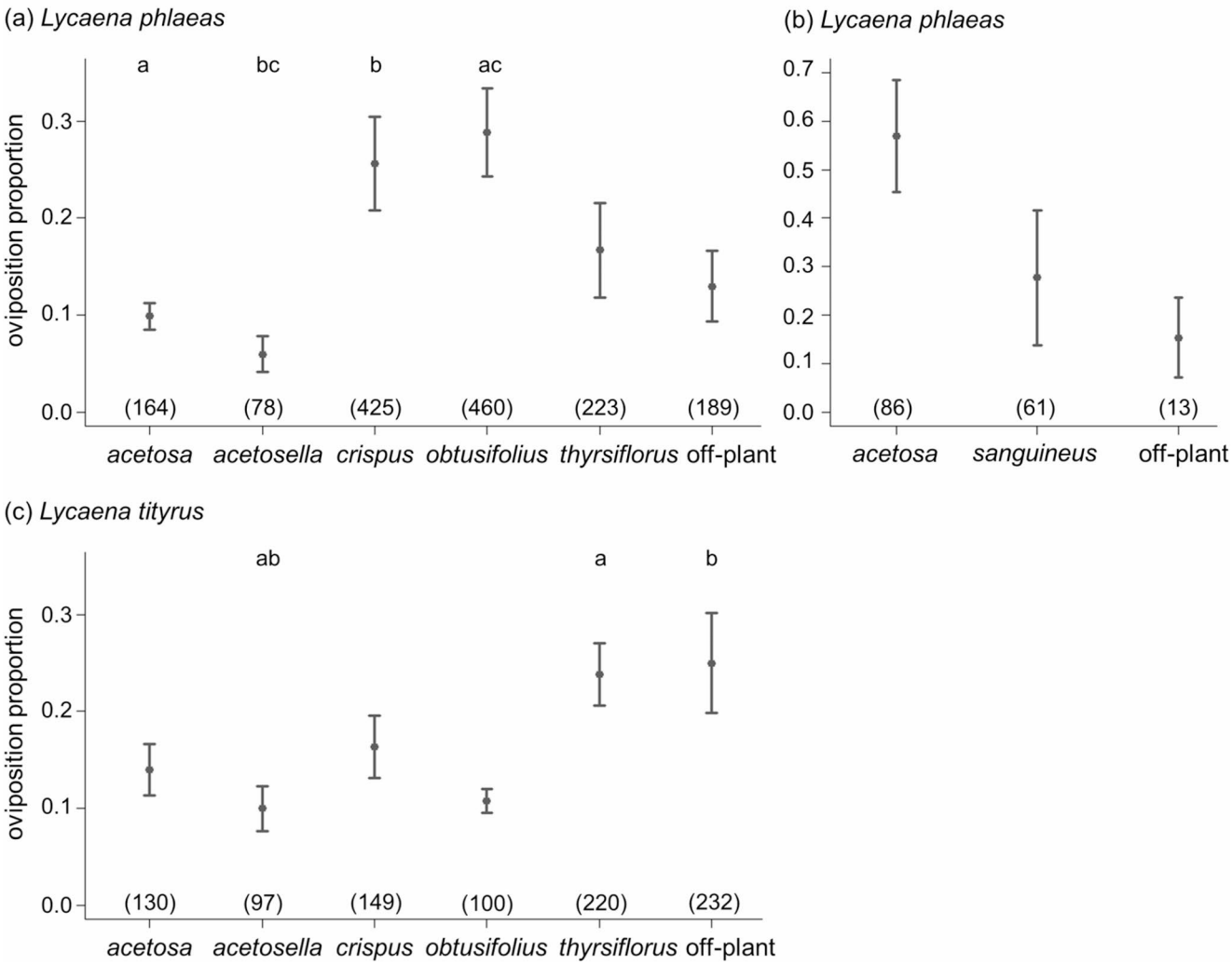

Fig. 1 Oviposition proportions (mean ± standard error) of (**a**) *Lycaena phlaeas* on five *Rumex* species (13 females) and (**b**) on two *Rumex* species (four females), and of (**c**) *Lycaena tityrus* on five *Rumex* species (eight females). Numbers in parenthesis give absolute egg number. Significant pairwise differences between *Rumex* species (including off-plant ovipositions) are indicated by the same letters above error bars ($P < 0.05$). LMM statistics: (**a**) $F_{5, 60} = 5.38$, $P < 0.001$, $R^2\text{m} = R^2\text{c} = 0.26$, (**b**) $F_{2, 6} = 2.66$, $P = 0.149$, (**c**) $F_{5, 35} = 3.51$, $P = 0.011$, $R^2\text{m} = R^2\text{c} = 0.27$

supported by the qualitative observation that larvae of both *Lycaena* species feed on all tested *Rumex* species and reach adulthood (personal observation; Rose 2010). The use of a wide range of host plants without clear preferences is rather uncommon in Lepidoptera feeding on dicotyledonous plants. Usually, Lepidoptera species exhibit clear preferences for one or a few species (e.g. Suwarno et al. 2010; Friberg et al. 2015; Meister et al. 2015). These preferences emerge as plant species mostly differ in their quality for herbivorous insects due to their secondary compounds and nutrient stoichiometry (Bernays and Graham 1988). Also, *Rumex* species differ in their secondary compounds, such as oxalates, tannins, and phenols (Cavers and Harper 1964; Costan et al. 2023).

However, the visual and chemical differences of *Rumex* species are may insufficient for discrimination by females (see Jaenike 1990). *Lycaena phlaeas* has been observed to erroneously deposit eggs on plants next to instead on *Rumex* individuals (Wiklund 1984; Ebert and Rennwald 1991). *Lycaena tityrus* females failed to prefer the plants that are most suitable for their larvae in an oviposition experiment with *R. acetosa* plants differing in nutritional quality (Rahavololoniaina et al. 2023). These observations together with the off-plant ovipositions in the present experiment suggest that *Lycaena* females are limited in their ability to identify the most suitable host plant for their larvae.

Rumex plants often grow singly (except *R. acetosella*) under natural conditions (Ellenberg and Leuschner 2010), i.e. females need to overcome distances to find host plants. Considering the single ovipositions of both *Lycaena* species as well as the energy cost and risk of flight and searching behaviour, it might be more efficient for females to deposit

eggs on basically suitable host plants than searching for more optimal plants (Jaenike 1990; Bernays 2001). If host plants of a species are rare, larvae should accept several species to reduce the risk and energy costs for females (Thompson and Pellmyr 1991). This oviposition pattern has indeed been observed in some butterflies with rare or unpredictable host plant abundance (Jaenike 1990; Wiklund and Friberg 2009; König et al. 2016). Both the deficiencies in discrimination behaviour and the occurrence pattern of *Rumex* plants thus likely weaken preference-performance relations in both *Lycaena* species. Females may rather follow a risk-spreading strategy and deposit eggs on various *Rumex* species to ensure that at least some larvae survive and reach adulthood (see Jaenike 1990; Wiklund and Friberg 2009).

The present finding on rather similar oviposition proportions on different *Rumex* species is in contrast to the commonly stated preferences of *R. acetosella* by *L. phlaeas* and *R. acetosa* by *L. tityrus*. These preferences have been mainly observed under natural conditions (Ebert and Rennwald 1991; Bräu et al. 2013). The differences thus likely emerge as simultaneous choice experiments cannot simulate all factors influencing oviposition behaviour under natural conditions. In dry to fresh habitats of both *Lycaena* species, *R. acetosella* and *R. acetosa* are often the most abundant *Rumex* species (León-Cortés et al. 2000; Bräu et al. 2013). Their high abundance can result in proportionally more ovipositions (Thompson and Pellmyr 1991; Sahoo and Kodandaramaiah 2018). Furthermore, both *Lycaena* species prefer warm microhabitats for oviposition (Pradel and Fischer 2011; Streitberger et al. 2014). Females deposit eggs on plants growing on sites with high cover of bare ground and low vegetation height (Pradel and Fischer 2011; Streitberger et al. 2014). Such microhabitats are characteristic for *R. acetosella,R. acetosa*, and *R. thyrsiflorus*, but hardly for *R. crispus* and *R. obtusifolius* (Ellenberg and Leuschner 2010). Microclimatic preferences by females thus likely contribute to the observed preferences for *R. acetosella* and *R. acetosa* under natural conditions. Also in *Lycaena dispar*, host plant preferences of females are more strongly determined by flooding risk and occurrence of predators and/or parasitoids in the microhabitat than by species identity (Martin and Pullin 2004a, b). However, oviposition preferences of both *Lycaena* species have so far mainly been investigated in dry to fresh habitats (see Bräu et al. 2013). In moister conditions with a different abundance pattern of *Rumex* species, the observed wide host plant range of both species may become more relevant.

Implications for conservation

Since our study suggests that both *Lycaena* species utilize a wide range of *Rumex* species, further parameters than host-plant identity should determine habitat suitability. The recent decline of both butterflies is thus hardly based on changing abundances of their host plants but other effects of increasing land-use intensity. Higher land-use intensity often goes along with nitrogen enrichment, reducing warm microhabitats with open vegetation that prefer both butterflies for oviposition (Pradel and Fischer 2011; Streitberger et al. 2014). Additionally, larvae show higher mortalities on fertilized host plants due to smaller carbon-nitrogen ratios (Kurze et al. 2018; Raharivololoniaina et al. 2023). Accordingly, conservation measures for both *Lycaena* species should focus on the maintenance of oligo- to mesotrophic habitats (Bräu et al. 2013; Pöhler et al. 2019). These should exhibit open microhabitats with *Rumex* species (see Streitberger et al. 2014), with the abundance or identity of single species being less important. Overall, the wide range of host plants should facilitate the conservation of both butterfly species.

Acknowledgements We are grateful to the Kurze family (Dresden) for contributing to the capture of females in different habitats and practical support during the conductance of the experiment. Moreover, we would like to thank two anonymous reviewers for helpful comments on an earlier version of the manuscript.

Author contributions S.K. conducted the study and wrote the main manuscript text. All authors reviewed the manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

References

Barton K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. https://CRAN.R-project.org/package=MuMIn

Bernays EA (2001) Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. Ann Rev Entomol 46:703–727. https://doi.org/10.1146/annurev.ento.46.1.703

Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecol 69:886–892. https://doi.org/10.2307/1941237

Bräu M, Bolz R, Kolbeck H, Nummer A, Voith J, Wolf W (2013) Tagfalter in Bayern. Eugen Ulmer, Stuttgart

Cavers PB, Harper JL (1964) *Rumex obtusifolius* L. and *R. crispus* L. J Ecol 52:737–766. https://doi.org/10.2307/2257859

R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Costan CA, Godsoe W, Bufford JL, Hulme PE (2023) Comparing the above and below-ground chemical defences of three *Rumex* species between their native and introduced provenances. J Chem Ecol 49:276–286. https://doi.org/10.1007/s10886-023-01427-0

Ebert G, Rennwald E (1991) Die Schmetterlinge Baden-Württembergs, vol 2. Ulmer, Stuttgart

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen. 3 eds. Ulmer, Stuttgart

Fartmann T, Hermann G (2006) Larvalökologie von Tagfaltern & Widderchen in Mitteleuropa – von den Anfängen bis heute. In: Fartmann T, Hermann G (ed). Larvalökologie von Tagfaltern & Widderchen in Mitteleuropa. Abhandlungen aus dem Westfälischen Museum für Naturkunde 68. pp 11–60

Fiedler K (1989) Die Zucht von *Lycaena phlaeas* und *Lycaena tityrus* (Lep., Lycaenidae) auf verschiedenen Polygonaceae. Nachr Ent Ver Apollo 4:299–300

Fox R, Dennis EB, Purdy KM, Middlebrook I, Roy DB, Noble DG, Botham MS, Bourn NAD (2023) The state of the UK's butterflies 2022. Butterfly Conservation, Wareham

Friberg M, Posledovich D, Wiklund C (2015) Decoupling of female host plant preference and offspring performance in relative specialist and generalist butterflies. Oecologia 178:1181–1192. https://doi.org/10.1007/s00442-015-3286-6

García-Barros E, Fartmann T (2009) Butterfly oviposition: sites, behaviour and modes. In: Settele J, Shreeve TG, Konvička M, van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, pp 29–42

Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference–performance relationships in phytophagous insects. Ecol Lett 13:383–393. https://doi.org/10.1111/j.1461-0248.2009.01433.x

Jaenike J (1990) Host specialization in phytophagous insects. Ann Rev Ecol Evol Syst 21:243–273. https://doi.org/10.1146/annurev.es.21.110190.001331

König MAE, Wiklund C, Ehrlén J (2016) Butterfly oviposition preference is not related to larval performance on a polyploid herb. Ecol Evol 6:2781–2789. https://doi.org/10.1002/ece3.2067

Krämer B, Kämpf I, Enderle J, Poniatowski D, Fartmann T (2012) Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. J Insect Conserv 16:857–865. https://doi.org/10.1007/s10841-012-9473-4

Kurze S, Heinken T, Fartmann T (2018) Nitrogen enrichment in host plants increases the mortality of common Lepidoptera species. Oecologia 188:1227–1237. https://doi.org/10.1007/s00442-018-4266-4

Lenth RV (2022) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.3. https://CRAN.R-project.org/package=emmeans

León-Cortés J, Cowley MJR, Thomas CD (2000) The distribution and decline of a widespread butterfly *Lycaena phlaeas* in a pastoral landscape. Ecol Entomol 25:285–294. https://doi.org/10.1046/j.1365-2311.2000.00271.x

Martin LA, Pullin AS (2004a) Host-plant specialisation and habitat restriction in an endangered insect, *Lycaena dispar batavus* (Lepidoptera: Lycaenidae) I. Larval feeding and oviposition preferences. Eur J Entomol 101:51–56. https://doi.org/10.14411/eje.2004.012

Martin LA, Pullin AS (2004b) Host-plant specialisation and habitat restriction in an endangered insect, *Lycaena dispar batavus* (Lepidoptera: Lycaenidae) II. Larval survival on alternative host plants in the field. Eur J Entomol 101:57–62. https://doi.org/10.14411/eje.2004.013

Meister H, Lindman L, Tammaru T (2015) Testing for local monophagy in the regionally oligophagous *Euphydryas aurinia* (Lepidoptera: Nymphalidae). J Insect Conserv 19:691–702. https://doi.org/10.1007/s10841-015-9792-3

Nylin S, Janz N (1993) Oviposition preference and larval performance in *Polygonia c-album* (Lepidoptera: Nymphalidae): the choice between bad and worse. Ecol Entomol 18:394–398. https://doi.org/10.1111/j.1365-2311.1993.tb01116.x

Pinheiro J, Bates D, DebRoy S, Sarkar D, Core Team R (2020) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–149. https://CRAN.R-project.org/package=nlme

Pöhler R, Dudler H, Hille A (2019) Das stille Sterben der Schmetterlinge. Eigenverlag

Pradel K, Fischer K (2011) Living on the edge: habitat and host-plant selection in the butterfly *Lycaena tityrus* (Lepidoptera: Lycaenidae) close to its Northern range limit. J Res Lepidoptera 44:35–41

Raharivololoniaina A, Moewert E, Fischer K (2023) Simulating effects of agricultural intensification and climate change: nitrogen fertilisation and drought stress decrease insect herbivore performance. Ecol Entomol 48:325–335. https://doi.org/10.1111/een.13224

Reinhardt R, Harpke A, Caspari S, Dolek M, Kühn E, Musche M, Trusch R, Wiemers M, Settele J (2020) Verbreitungsatlas der Tagfalter und Widderchen Deutschlands. Eugen Ulmer, Stuttgart

Renwick JAA, Chew FS (1994) Oviposition behavior in Lepidoptera. Ann Rev Entomol 39:377–400. https://doi.org/10.1146/annurev.en.39.010194.002113

Rose S (2010) Generalist vs Specialist? Egg laying and food plant preferences in two related lycaenid butterflies. Diploma Thesis. University of Münster

Sahoo RK, Kodandaramaiah U (2018) Local host plant abundance explains negative association between larval performance and female oviposition preference in a butterfly. Biol J Linn 125:333–343. https://doi.org/10.1093/biolinnean/bly111

Scherer G, Fartmann T (2022) Occurrence of an endangered grassland butterfly is mainly driven by habitat heterogeneity, food availability, and microclimate. Insect Sci 29:1211–1225. https://doi.org/10.1111/1744-7917.12975

Steffner C, Bräu M, Gros P, Wanninger O (2022) Die Tagfalter Deutschlands & Österreichs, 3rd eds. Bayerische Akademie für Naturschutz & Landschaftspflege

Streitberger M, Rose S, Hermann G, Fartmann T (2014) The role of a mound-building ecosystem engineer for a grassland butterfly. J Insect Conserv 18:745–751. https://doi.org/10.1007/s10841-014-9670-4

Suwarno C, Salmah MR, Ali A, Hassan AA (2010) Oviposition preference of swallowtail butterfly, *Papilio polytes* (Lepidoptera: Papilionidae) on four Rutaceae (Sapindales) host plant species. Insect Sci 17:369–378. https://doi.org/10.1111/j.1744-7917.2010.01330.x

Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. Ann Rev Entomol 36:65–89. https://doi.org/10.1146/annurev.en.36.010191.000433

Van Swaay CAM, Dennis EB, Schmucki R, Sevilleja CG, Åström S, Balalaikins M, Barea-Azcón JM, Bonelli S, Botham M, Cancela JP, Collins S, De Flores M, Dapporto L, Dopagne C, Dziekanska I, Escobés R, Faltynek Fric Z, Fernández-García JM, Fontaine

B, Glocovcan P, Gracianteparaluceta A et al (2022) European Grassland Butterfly Indicator 1990–2020 Technical report. VS2022.039. https://assets.vlinderstichting.nl

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

Wiklund C, Friberg M (2009) The evolutionary ecology of generalization: among-year variation in host plant use and offspring survival in a butterfly. Ecol 90:3406–3417. https://doi.org/10.1890/08-1138.1