Partial biennialism in alpine *Lycaena hippothoe* (Lycaenidae: Lycaenini)?

Klaus Fischer* & Konrad Fiedler**

* Institute of Evolutionary and Ecological Sciences, Leiden University, P. O. Box 9516 NL–2300 R A Leiden, The Netherlands, e-mail: Fischer@rulsfb.leidenuniv.nl

** Department of Animal Ecology I, University of Bayreuth, D-95440 Bayreuth, Germany, e-mail: konrad.fiedler@uni-bayreuth.de

Summary. Two growth strategies were found in caterpillars of alpine *Lycaena hippothoe eurydame* (Hoffmansegg, 1806). Laboratory experiments show that, following an obligatory winter diapause, most larvae develop into adults in the year after oviposition, whereas a minor proportion enters a second diapause. This fraction is higher at lower temperatures. We conclude to have found a temperature-triggered facultative biennialism, evolved as a bet-hedging strategy to cope with the unfavourable and unpredictable alpine environment.

Zusammenfassung. Bei Raupen des alpinen Tagfalters *Lycaena hippothoe eurydame* (Hoffmansegg, 1806)wurden zwei Wachstumsstrategien gefunden. Laborexperimente zeigten, daß sich im Anschluß an eine obligatorische Winter-Diapause zwar die meisten Raupen ohne weitere Verzögerung zu Imagines entwickelten, ein geringerer Teil jedoch nach einigen Tagen Fraßaktivität in eine zweite Diapause eintrat. Der Anteil der Individuen mit zweifacher Diapause war höher bei niedrigerer Temperatur. Hieraus wird auf einen temperaturabhängigen, fakultativ zweijährigen Entwicklungszyklus geschlossen, welcher als Strategie zur Risikostreuung unter den unwirtlichen und unvorhersagbaren Bedingungen des alpinen Lebensraumes verstanden werden kann.

Résumé. Deux stratégies de croissance ont été observées auprès de chenilles appartenant au taxon alpin *Lycaena hippothoe eurydame* (Hoffmansegg, 1806). Des expériences en laboratoire ont démontré que, suite à une diapause hivernale obligatoire, la plupart des larves se développent jusqu'à l'état adulte pendant l'année qui suit la ponte des œufs, alors qu'une proportion minoritaire entre en une seconde diapause. Celle-ci est plus élevée à des températures inférieures. Nous concluons à la découverte d'un cycle biennal facultatif conditionné par la température, qui a évoluée comme réponse aux conditions défavorables et imprévisibles d'un environnement alpin.

Key words. *Lycaena hippothoe*, larval growth, life cycle, bet hedging, alpine environment.

Introduction

Several (but overall few) insect species show the ecologically and evolutionarily fascinating phenomenon of delayed development with juvenile periods lasting for more than one year (e.g. Danks 1992; Stearns 1992; Wipking & Mengelkoch 1994). Within the Lepidoptera, many Ringlets (*Erebia* spp.) and Burnet moths (*Zygaena* spp.) comprise well-known examples (cf. Scott 1986; SBN 1987; Wipking & Mengelkoch 1994). An especially important factor promoting prolonged larval development is a short growing season, often combined with low average temperatures, as is the case in high-alpine environments or at higher latitudes (cf. Downes 1965; Butler 1982; Wipking & Mengelkoch 1994).

However, the coexistence of annual and biennial individuals within the same population is a decidedly rare phenomenon in the animal kingdom. The few examples include

salmonid fish (Gross 1985), Burnet moths (Wipking & Mengelkoch 1994), and some myrmecophilous insects (Thomas et al. 1998; Schönrogge et al. 2000). The latter two studies contain the first detailed descriptions of partial biennialism within the Lycaenidae (but see also Beuret 1956). However, the species referred to (*Maculinea rebeli*, *M. alcon*, *M. arion*) do not possess any trait previously related to prolonged growth. Here, a mixture of two growth strategies seems to be the most efficient way to exploit the limited, but steady, daily supply of food available to the cuckoo-feeding parasites (*M. rebeli, M. alcon*) of long-lived *Myrmica* ant colonies (Thomas et al. 1998), or, in case of predacious *M. arion*, an adaptation to the migratory behaviour of host ants (Schönrogge et al. 2000).

In this paper we describe a possible further example of a facultatively biennial life-cycle in a (myrmecoxenous) lycaenid butterfly, found in an alpine population of *Lycaena hippothoe* L.

Methods

Study organism. *L. hippothoe* is a widespread temperate zone butterfly ranging from northern Spain in the west throughout much of the northern Palaearctic region eastwards to the easternmost parts of Siberia and China (Ebert & Rennwald 1991; Lukhtanov & Lukhtanov 1994). The animals for this study belonged to the alpine subspecies *L. hippothoe eurydame* Hoffmannsegg, 1806. Ten freshly emerged females were caught in the summer of 1998 (20.–26.7.) in the central Alps (Senales valley, northern Italy) at an altitude of about 1800 m and transferred to Bayreuth University. As in almost the whole range of *L. hippothoe* (cf. Lukhtanov & Lukhtanov 1994; Tolman & Lewington 1998), this population is monovoltine with adults being on the wing from mid-July to late August (Scheuringer 1972). Usually, *L. h. eurydame* larvae exhibit an obligatory dormancy hibernating in a rather early developmental stage (Fischer 2000; see below).

Experimental arrangement. For oviposition captured females were maintained in an environmental cabinet at a constant temperature (25°C) and a photoperiod of L18:D6. They were placed individually in glass jars (1 litre) lined with moistened filter paper and the jars covered with gauze. Each jar contained a bunch of the larval food-plant *Rumex acetosa* L. (in H_2O) as oviposition substrate as well as highly concentrated sucrose solution for adult feeding. Eggs were removed each day and pooled. Hatchlings were placed individually in transparent plastic boxes (125 ml) containing moistened filter paper and fresh cuttings of *R. acetosa* in ample supply. The boxes were checked daily and supplied with new food when needed. Dormant third instar larvae were transferred to another cabinet (T 4°C, photoperiod L8:D16) for hibernation. After a diapause of about five months larvae were randomly divided among four temperatures of 15, 20, 25, and 30°C, respectively (photoperiod L18:D6 throughout), and reared in the way described above until adult eclosion or until they had stopped feeding for at least two weeks. The latter were assigned to hibernation conditions again and observed for the following three months.

Results and discussion

Following diapause, all *L. h. eurydame* larvae started to feed on *R. acetosa* leaves and moulted at least once. The majority of caterpillars developed without any further delay into adults. However, within each temperature group a certain proportion stopped feeding after a couple of days, obviously to enter a second diapause (Tab. 1). All of those survived, after being transferred to hibernation conditions again, for at least three additional months without feeding (after this period caterpillars were not observed any longer). The proportion of animals eventually denying further food intake was significantly higher at lower temperatures of 15 and 20°C (28.0%, n = 186) as compared to higher ones of 25 and 30°C (9.6%, n = 157; $\chi^2_{1df} = 18.3$, $p<0.0001$).

Tab. 1. Partially biennial life cycle in *L. h. eurydame*. Following diapause, larvae were randomly divided among four temperatures. In every group, some caterpillars stopped feeding after having moulted at least once. This proportion was significantly higher at low temperatures (15, 20°C) than at higher ones (25, 30°C). Given are absolute numbers and percentages of row totals (in parentheses).

[°C]	Number of larvae	
	developing into adults	entering second diapause
15	63 (77.8%)	18 (22.2%)
20	71 (67.6%)	34 (32.4%)
25	66 (91.7%)	6 (8.3%)
30	76 (89.4%)	9 (10.6%)

We therefore conclude to have found a temperature-modulated facultative biennialism in *L. h. eurydame*, where low temperatures, indicating unfavourable conditions for growth and development, seem to induce a higher rate of two-year developers. We suggest that adults producing a mixture of annual and biennial offspring gain bet-hedging benefits in case of particularly bad growing seasons (preventing offspring from reaching maturity and leading to death before onset of reproduction) or occasional catastrophes (cf. Thomas et al. 1998). The latter include years with occurrence of extremely early frost or snow cover. Hence, partial biennialism appears to be a strategy selected to cope with the unfavourable and unpredictable alpine environment (cf. Takahashi 1977; Hanski 1988; Danks 1992; Wipking & Mengelkoch 1994). In line with this reasoning, Beuret (1956) found incidental evidence for a comparable strategy in alpine *L. alciphron gordius* Sulzer 1776, but no evidence for a second larval diapause was ever found during own rearings with individuals of two other subspecies of *L. hippothoe*, viz. *L. h. hippothoe* and *L. h. sumadiensis* Szabó, 1956, originating from regions with more favourable climatic conditions (Fischer 2000).

About the instar which usually enters into (first) diapause there is some controversy in the literature. While SBN (1987) (and also Hesselbarth et al. (1995) for the related *L. candens* Herrich-Schäffer, 1844) claim that the second instar hibernates, Malicky (1970) noted that hibernation may occur in any larval stage. More recently, Bink (1992) explic-

itly stated that diapause occurs in the third instar. In large-scale rearings under controlled environmental conditions (Fischer 2000) the third instar indeed emerged as the dominant diapause stage, yet also diapausing fourth instars or subitaneous development were observed at variable rates depending on rearing temperatures. None of more than 1800 larvae from three different *L. hippothoe* populations ever went into diapause as second instar.

Acknowledgements

We are indebted to E. Scheuringer (Rosenheim) for sharing his knowledge on the occurrence of *L. hippothoe* in the central Alps. This study was supported by grants from the Friedrich-Ebert-Foundation to K. Fischer.

References

Beuret, H. 1956. Zur Diskrepanz im Entwicklungstempo der Raupen verschiedener Rassen von *Chrysophanus alciphron* Rott. (Lep., Lycaenidae). – Mitt. ent. Ges. Basel NF 6: 4–6.

Bink, F. A. 1992. Ecologische Atlas van de Dagvlinders van Noordwest-Europa. – Schuyt & Co., Haarlem. 512 pp.

Butler, M. G. 1982. A 7-year life cycle for two *Chironomus* species in arctic Alaskan tundra ponds. – Can. J. Zool. 60: 58–60.

Danks, H. V. 1992. Long life cycles in insects. – Can. Ent. 124: 167–187.

Downes, J. A. 1965. Adaptations of insects in the arctic. – Annu. Rev. Ent. 10: 257–274.

Ebert, G. & E. Rennwald 1991. Die Schmetterlinge Baden-Württembergs, vol. 2. – Ulmer, Stuttgart. 535

Fischer, K., 2000. Life-history-Plastizität in den Lebenszyklen der Feuerfalter *Lycaena hippothoe* und *Lycaena tityrus*. – PhD thesis, Univ. of Bayreuth, 313 p.

Gross, M. R. 1985. Disruptive selection for alternative life histories in salmon. – Nature 313: 47–48.

Hanski, I. 1988. Four kinds of extra long diapause in insects: a review of theory and observations. – Annls. Zool. Fenn. 25: 37-52.

Hesselbarth, G., H. v. Oorschot & S. Wagener 1995. Die Tagfalter der Türkei. – S. Wagener, Bocholt. 3 vols., 1354 + 847 p.

Lukhtanov, V. & A. Lukhtanov 1994. Die Tagfalter Nordwestasiens. Herbipoliana 3. – U. Eitschberger, Marktleuthen. 440 p.

Malicky, H. 1970. Untersuchungen über die Beziehungen zwischen Lebensraum, Wirtspflanze, Überwinterungsstadium, Einwanderungsalter und Herkunft mitteleuropäischer Lycaeniden. – Ent. Abh. Mus. Tierk. Dresden 36: 341–360.

SBN (Schweizerischer Bund für Naturschutz, ed.) 1987. Tagfalter und ihre Lebensräume. – Schweizerischer Bund für Naturschutz, Basel. xi + 516 p.

Scheuringer, E. 1972. Die Macrolepidopteren-Fauna des Schnalstales. – Studi trent. Sci. nat. 49: 229–448.

Schönrogge, K., J. C. Wardlaw, J. A. Thomas & G. W. Elmes 2000. Polymorphic growth rates in myrmecophilous insects. – Proc. R. Soc. Lond. B 267: 771–777.

Scott, J. A. 1986. The butterflies of North America. – Stanford University Press, Stanford. xii + 583 p., 64 pls.

Stearns, S. C. 1992. The evolution of life histories. – Oxford University Press, Oxford. xii + 249 p.

Takahashi, F. 1977. Generation carryover of a fraction of population members as an adaptation to unstable environmental conditions. – Res. Pop. Ecol. 18: 235–242.

Thomas, J. A., G. W. Elmes & J. C. Wardlaw 1998. Polymorphic growth in larvae of the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. – Proc. R. Soc. Lond. B 265: 1895–1901.

Tolman, T. & R. Lewington 1998. Die Tagfalter Europas und Nordwestafrikas (German ed. by M. Nuß). – Franckh-Kosmos, Stuttgart. 319 p, 104 pls.

Wipking, W. & C. Mengelkoch 1994. Control of alternate-year flight activities in high-alpine butterflies (*Erebia*, Satyridae) and Burnet moths (*Zygaena*, Zygaenidae) from temperate environments. – *In:* Danks, H. V. (ed.). Insect life-cycle polymorphism, p. 313–347. – Kluwer, Dordrecht.