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EFFECTS OF ADULT FEEDING AND TEMPERATURE REGIME ON FECUNDITY AND LONGEVITY IN THE BUTTERFLY *LYCAENA HIPPOTHOE* (LYCAENIDAE)

KLAUS FISCHER AND KONRAD FIEDLER
Department of Animal Ecology I, University of Bayreuth, D-95440 Bayreuth, Germany

ABSTRACT. When fed highly concentrated sucrose solution, adult females of the Purple-Edged Copper butterfly *Lycaena hippothoe* L. laid significantly more eggs (mean = 464) than those individuals given water only (mean = 65). Longevity was also three to five times greater, whereas hatching rate of the eggs was not affected by the mother's nutrient intake. Stored resources acquired during the larval stage supported realization of only 14% of the fecundity of the fed females. Hence, *L. hippothoe* butterflies depend far more on adult-derived resources than other nectar-feeding butterflies for which comparable data exist. These findings may be important for the population dynamics of the species, as reduced availability of nectar sources presumably constrains realized fecundity.

Additional key words: Adult diet, reproduction, nutritional ecology, population dynamics.

Oogenesis in insects is typically a nutrient-limited process, triggered only if sufficient nourishment is available (Wheeler 1996). The required resources can be acquired during the larval or adult stage (or both), depending on the insects' life cycle (Boggs 1997a). In the holometabolous Lepidoptera, resources for reproductive investment may stem from the herbivorous larval stage or from the adult stage, during which they collect liquid food such as nectar (Wheeler 1996). Although it is generally thought that butterflies and moths usually rely more on reserves accumulated during the larval stage to supply egg production (Wheeler 1996), there is broad variation with regard to the importance of adult feeding (Hill 1989, Murphy et al. 1983). Many adult moths do not feed at all and rely completely on reserves accumulated during the larval stages ("capital breeders" sensu Tammaru & Haukioja 1996). At the other extreme, female *Heliconius* butterflies collect protein-rich pollen which supports the laying of eggs through the adult life span of several months (Gilbert 1972, Dunlap-Pianka et al. 1977). Such species can be referred to as "income breeders" (Tammaru & Haukioja 1996), for which successful reproduction is essentially mediated by resources available to the adults.

In many temperate-zone nectar-feeding butterflies (cf. Boggs & Ross 1993, David & Gardiner 1962, Karlsson & Wickman 1990, Labine 1968, Murphy et al. 1983, Stern & Smith 1960) and at least some moths (Adler 1989, Cheng 1970, Leahy & Andow 1994, Leather 1984, Miller 1989), even though substantial protein is not acquired after adult eclosion, carbohydrate ingestion can profoundly affect longevity and fecundity. Certain tropical butterflies even appear to supplement their nitrogen budget by visiting protein-rich mud-puddles (Beck et al. 1999). The degree of dependence on nectar, however, varies between species (e.g., Boggs 1997b). The majority of previous studies are concerned with analyzing correlations between butterfly abundance and availability or diversity of potential nectar sources (e.g., Douwes 1975, Grossmueller & Lederhouse 1987, Hill 1992, Loertscher at al. 1996, Schultz & Dlugosch 1999). Controlled experimental studies, in contrast, are available only for a small range of taxa.

With far more than 5000 extant species, the Lycaenidae are the second-largest family of true butterflies in the world (Heppner 1991). However, hitherto almost no experimental data on the role of adult feeding in lycaenid butterflies are available (with exception of the Australian species *Jalmenus evagoras*; Hill & Pierce 1989). This paper reports the effects of different feeding and temperature regimes on fecundity, survival and hatching rate of the Purple-Edged Copper butterfly *Lycaena hippothoe*, in order to assess the relative importance of income vs. stored resources. Furthermore, we discuss the relevance of our results for the population dynamics of this species.

STUDY ORGANISM, MATERIAL AND METHODS

Lycaena hippothoe is a widespread 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). In Central Europe, adults fly in one generation from about mid-June through late July (Fischer 1998). The species inhabits different kinds of wetland as well as unimproved grassland. The principal larval hostplant is *Rumex acetosa* L. (Polygonaceae), a common and widespread perennial herb occurring in various types of grassland. Recent declines of *L. hippothoe* populations stimulated concern among nature conservation authorities and resulted in the inclusion of this species into "Red Data Lists" in various European countries (cf. Marttila et al. 1999, Pretscher 1998, SBN 1987, Tax 1989).

In June 1997 and 1998, respectively, freshly emerged females (not older than one or two days, judged by wing wear) of *L. hippothoe* were caught in the Westerwald area (western Germany; see Fischer

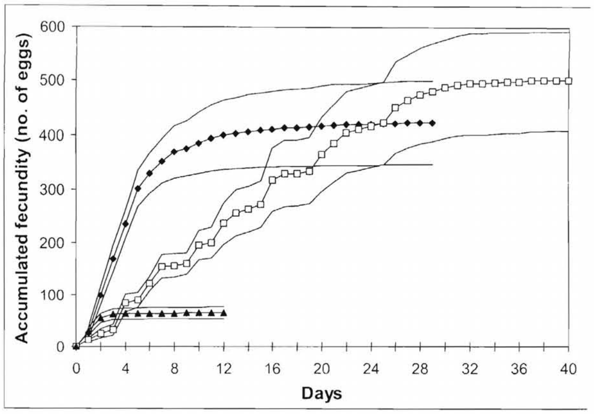

FIG. 1. Mean accumulated fecundity (solid lines without symbols: ±SE of respective means) of *Lycaena hippothoe* over time under different feeding and temperature regimes (rhombuses: "fed 25°C", squares: "fed", triangles "water").

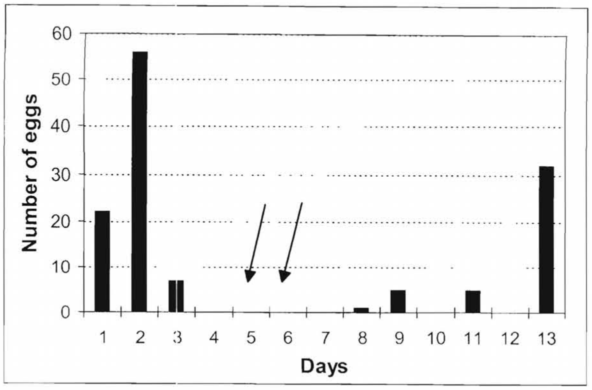

FIG. 2. Fecundity in a single female *Lycaena hippothoe* provided with water only. On two occasions (indicated by arrows) the female was allowed to feed on highly concentrated sucrose solution for about half an hour each time.

1998) for rearing experiments and to provide the foundation of a captive breeding stock. Females were placed individually in glass jars (1 L) containing moistened filter paper and the jars covered with gauze. Each jar contained a bunch of the larval foodplant *R. acetosa* (in H_2O) as oviposition substrate.

For measuring the effects of feeding and temperature regime three experimental treatments were used. (1) Ambient daylight and temperature conditions (from mid-June to mid-July 1997, wild-caught females), butterflies fed with a highly concentrated sucrose solution. (2) Conditions as before (from mid-June to mid-July 1998, wild-caught females), but butterflies were provided with water only. (3) In an environmental chamber at a constant temperature (25°C) and a photoperiod of L18:D6 (in 1998), fed with a highly concentrated sucrose solution (these females originated from captive breeding stock, F_1-generation). The three treatments are hereafter referred to as "fed" (1), "water" (2), and "fed 25°C" (3). For egg-laying under ambient conditions glass jars were put on a table outside in a sheltered area. The day-night regime during the periods was about L16.30:D7.30 (time between sunrise and sundown excluding civil twilight).

In the morning (i.e., before onset of oviposition activities) of each day eggs were removed and counted. Eggs were then exposed to a constant temperature of 20°C (photoperiod L18:D6) to assess hatching rate. Females were dissected after death occurred, and the number of mature oocytes remaining in their ovaries was determined under a stereomicroscope. Furthermore, 10 freshly emerged and unfed females from captive breeding stock were dissected to analyze the status of oogenesis at emergence. Only already yolked oocytes with a diameter of at least 0.5 mm were counted.

Differences in mean values were tested using the Mann-Whitney *U*-test and the Tukey-Kramer post-hoc comparison after the non-parametric Kruskal-Wallis H-test (Sachs 1997), since data distributions deviated strongly from normality. Throughout the text all means are given ±1 SD.

RESULTS

Egg production and hatching rate. Total lifetime egg production was strongly affected by access to nutrients, but not by temperature regime (see below). Females fed highly concentrated sucrose solution in both treatments laid significantly more eggs than those individuals given water only ($H_{2df} = 14.3$, $p = 0.0008$; Table 1). The latter achieved, on average, only 14.0 % of the fecundity of the fed individuals (64.9 ± 30.1 vs. 464.2 ± 207.1 eggs, data for "fed" and "fed 25°C" pooled). The number of eggs laid in the "water"-group coincides with the well developed oocytes at emergence (mean 60.9 ± 18.8, n = 10; *U*-test: z = 0.44, p = 0.66, n.s.). Likewise, total potential fecundity (measured as the total number of eggs laid plus mature oocytes remaining after death) was much reduced in the water-only treatment, but did not differ between the two sugar-feeding treatments.

In females with no access to carbohydrate sources, substantial oviposition occurred only during the first three days of the experiment (Fig. 1). One of those butterflies was provided with sucrose solution on two days, after which it resumed laying eggs again (Fig. 2). These eggs laid after sucrose feeding were excluded from further data analysis.

No significant difference in egg production was found between females fed at a constant temperature of 25°C compared to those fed under ambient tem-

Table 1. Fecundity, hatching rate and longevity (means ± SD) of female *Lycaena hippothoe* under different feeding and temperature regimes ("fed 25°C": in environmental chamber at a constant temperature of 25°C, fed with sucrose solution; "fed": ambient temperature conditions, fed with sucrose solution; "water": ambient temperature conditions, access to water only). Figures within one row followed by the same letter do not differ significantly (Tukey-Kramer post-hoc comparison after Kruskal-Wallis H-test, threshold for significance $p < 0.05$).

	Fed 25°C	Fed	Water
Number of females	6	7	8
Number of eggs laid	422.3 ± 187.9^{a}	500.1 ± 245.7^{a}	64.9 ± 32.1^{b}
Range (eggs laid)	165–690	126–808	9–102
Highest egg number/day	98	110	65
Number of oocytes	43.0 ± 41.0^{a}	26.9 ± 23.1^{a}	28.5 ± 22.8^{a}
Number of eggs and oocytes	465.3 ± 163.7^{a}	527.1 ± 240.4^{a}	93.4 ± 14.9^{b}
Relative realized fecundity [%]	88.1 ± 11.9^{a}	93.0 ± 6.4^{a}	66.6 ± 29.8^{a}
Hatching rate of eggs [%]	83.0 ± 11.9^{a}	81.3 ± 17.8^{a}	84.1 ± 11.8^{a}
Female longevity [days]	16.8 ± 7.8^{a}	31.7 ± 9.7^{b}	6.1 ± 3.6^{c}
Oviposition period [days]	10.8 ± 8.2^{a}	28.0 ± 10.1^{b}	4.0 ± 1.5^{c}

perature conditions (Table 1). However, under the ambient temperature regime it took the females far longer to reach saturation of the fecundity curve (about 30 compared to 10 days; Fig. 1). The "steps" in the fecundity curve of the individuals fed under an ambient temperature regime are caused by days with adverse weather conditions and hence no egg-laying.

Realized relative fecundity, expressed as the ratio of eggs laid relative to the total number of eggs laid plus remaining mature oocytes after death, was high in fed individuals and lower, though not significantly so, in the water-fed butterflies ($H_{2df} = 4.5$, $p = 0.1$; Table 1). In contrast, hatching rate of eggs was invariably high (80–85 %) and not affected by adult feeding ($H_{2df} = 0.1$, $p = 0.95$). As all females produced viable eggs, they obviously were mated.

Longevity. Feeding as well as temperature regime strongly influenced longevity (Table 1). Sucrose-fed females (both treatments) lived three to five times longer than water-fed individuals ($H_{2df} = 14.5$, $p = 0.0007$). Furthermore, sucrose-fed individuals under ambient climatic regime survived twice as long as the group fed at 25°C. Extended survival also distinctly increased the duration of an individual's oviposition period ($H_{2df} = 15.1$, $p = 0.0005$). Compared to females provided with water only, among sucrose-fed butterflies the period over which eggs were laid increased by a factor of 2 (at 25°C) to 7 (at ambient temperature conditions).

DISCUSSION

Our data demonstrate the exceptional importance of adult feeding for reproduction in female *L. hippothoe*. Overall, fecundity in our experiments was much higher than suggested for this species in the literature (Bink 1992), and sucrose-feeding increased total egg production, oviposition period as well as longevity. Therefore, nourishment from nectar sources is essential for maintenance of basic metabolic functions as well as for egg production.

Adult-derived resources seem to be even more important for egg production and longevity than in many other butterfly species. For example, in *Pararge aegeria* (Nymphalidae) egg number is approximately four times higher after sugar-feeding than after water-feeding (Karlsson & Wickman 1990). In the checkerspot butterfly, *Euphydryas editha* (Nymphalidae), as well as in *Jalmenus evagoras* (Lycaenidae), sugar-feeding roughly doubles egg production and longevity relative to individuals kept with no access to food or supplied with water only (Murphy et al. 1983, Hill & Pierce 1989). In *L. hippothoe*, in contrast, the increase in fecundity was seven-fold, and longevity was three to five times greater. Obviously, substantial egg production in *L. hippothoe* relies strongly on adult-derived rather than larval-derived carbohydrates. Thus, in the continuum between capital and income breeders the species is positioned far to the latter side. Until recently, carbohydrate intake was largely regarded as a means of acquiring flight fuel, and its importance for oogenesis was not clear (Wheeler 1996). But now the incorporation of carbohydrates into developing oocytes has been confirmed directly by radiotracer studies (Boggs 1997a), and our results further corroborate the relevance of sugar-feeding for egg production in butterflies.

Surprisingly, hatching rate was not affected by adult feeding. We conclude that unfed females are able to lay those eggs only, in which development is already under way at adult emergence (cf. Boggs & Ross 1993). This is supported by the coincidence between the number of well developed oocytes found in females at emergence with the total egg production in the water-fed group (cf. Hill & Pierce 1989, Watanabe 1992). Oogenesis of those eggs must rely exclusively on nourishment gathered during larval stage (probably supplemented by male-derived nutrients received by the female at mating; cf. Boggs 1990, 1997a). The production or maturation of additional eggs is apparently severely constrained in *L.*

hippothoe butterflies without adult carbohydrate intake. In contrast to the sucrose-fed females, most oocytes remaining after death were poorly developed in the water-fed individuals. Obviously, females are supplied with a rather small amount of stored carbohydrates, which are abundantly available from adult nectar resources. On the other hand nitrogenous compounds, which are scarce in the diet of most (temperate-zone) adult butterflies, are commonly capital reserves acquired more or less entirely during the larval stages (but see Beck et al. 1999, Erhardt & Rusterholz 1998). These stored reserves are used throughout adult life (Boggs 1997a), whereas larval-derived carbohydrates decline rapidly and need to be complemented by income.

Our findings could be of importance for the population dynamics of *L. hippothoe* in at least two ways. As the number of eggs laid obviously depends on adult resources in this species, adverse weather conditions can influence population dynamics not only through a higher adult or larval mortality (e.g., Singer & Ehrlich 1979, Pollard et al. 1997), but also through a decrease in fecundity. A high incidence of rainy or overcast days would limit not only the time available for egg-laying, but also for feeding. Unlike factors affecting oviposition rate only, there is no compensation for a reduced egg production caused by lack of nourishment (Gossard & Jones 1977), as nutrient limitations should impede compensation of time limitations through an increase in oviposition rate. In contrast to other species able to produce substantial egg numbers even without any adult feeding (e.g., *Euphydryas editha*; Murphy et al. 1983), population dynamics of *L. hippothoe* should be far more affected if access to adult nutrient resources is limited.

Second, modern agricultural techniques lead to a reduction of nectar sources (i.e., flowers) through a high mowing frequency and recurrent application of fertilizers (Barabasz 1994, Ellenberg 1996, Erhardt 1995, Nigmann 1997). Taking into account the dramatic loss of traditionally managed hay meadows in central European landscapes (e.g., Erhardt 1995, Erhardt & Thomas 1991), the concomitant reduction of flower availability could be an important factor for regional declines in this sedentary species.

Our study revealed that *L. hippothoe* butterflies must be regarded, to an unexpected degree, as income breeders. It remains to be tested whether other temperate-zone lycaenids rely in a similar manner on nectar resources for reproduction. If this were the case, this could explain the decline of other lycaenid species with common and widespread hostplants (e.g., *L. tityrus* Poda, *L. virgaureae* L., sharing the same hostplant, *Rumex acetosa*, with *L. hippothoe*) in modern European landscapes. Hence, the importance of the availability of adult resources for the reproductive biology and persistence of butterfly populations, which is most commonly inferred from field data on spatial distributions (e.g., Hill 1992, Douwes 1975, Loertscher et al. 1996), deserves more experimental studies on a broader range of taxa.

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