Spatio-temporal dynamics in a population of the copper butterfly *Lycaena hippothoe* (Lycaenidae)

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Summary. A mark-recapture analysis showed a strong decline in *Lycaena hippothoe* numbers (and changes in the spatial distribution) between 1995 and 1999 within a western German population. Neither land-use practices nor adult mortality could be accounted for this development. Based on a close correlation between *L. hippothoe* numbers and the mean daily cloud cover during previous flight period, the hypothesis is advanced that the observed decline basically reflects a series of flight periods with adverse weather conditions. These should constrain the time available for feeding and oviposition. Given a strong reliance of the reproductive output in *L. hippothoe* on adult-derived nectar resources, reduced fecundity is regarded as the proximate reason for the population decline. These findings may have implications for conservation, as reduced availability of nectar sources, be it caused by adverse weather conditions or by modern agricultural techniques, may contribute to regional declines.

Zusammenfassung. Eine Fang-Wiederfang-Studie zeigte einen kontinuierlichen Rückgang von *Lycaena hippothoe* sowie Änderungen des räumlichen Verteilungsmusters zwischen 1995 und 1999 in einer westdeutschen Population. Weder Habitatveränderungen noch eine erhöhte Imaginalmortalität können für diese Entwicklung verantwortlich gemacht werden. Basierend auf einem engen Zusammenhang zwischen Falterzahl und Tagesmittel der Bewölkung während der vorhergehenden Flugsaison wird die Hypothese entwickelt, daß der beobachtete Rückgang Ausdruck einer Folge von Flugperioden mit ungünstigen Witterungsbedingungen ist, wodurch die für Nahrungsaufnahme und Oviposition verfügbare Zeit reduziert wird. Da die Eiproduktion von *L. hippothoe* in hohem Maße vom Zugang zu Kohlenhydraten abhängt, wird eine reduzierte Fekundität als proximater Mechanismus angesehen. Die Befunde könnten für den Schutz nektarsaugender Falter in Zusammenhang mit einer großflächigen Reduzierung des Nektarangebotes infolge moderner landwirtschaftlicher Bewirtschaftungsmethoden (oder aber ungünstiger Witterungsbedingungen) Bedeutung erlangen.

Resumé. Une analyse de marquage-recapture a révélé un importante déclin numérique au sein d'une population ouest-allemande de *Lycaena hippothoe* (Linné, 1761) (ainsi qu'une modification de la distribution spatiale) pour la période de 1995 à 1999. Cette tendance ne peut être imputée ni à des changements au niveau de l'habitat, ni à une augmentation de la mortalité adulte. Sur base d'une étroite corrélation entre les nombres de *L. hippothoe* et la durée moyenne journalière de couverture nuageuse pendant la période de vol précédente, l'hypothèse est avancée que le déclin observé reflète une série de périodes de vol successives à conditions météorologiques adverses. Celles-ci devraient limiter le temps disponible à la nutrition et à l'oviposition. Vu la forte dépendance de la capacité de reproduction de *L. hippothoe* d'hydrates de carbone dérivés du nectar obtenu au stade adulte, la fécondité réduite est considérée comme étant la raison proximale du déclin de la population. Ces résultats pourraient avoir des implications pour la conservation, étant donné que la disponibilité limitée de sources nectarifères, qu'elle soit due à des conditions météorologiques adverses ou à des techniques modernes d'agriculture, peut contribuer à des déclins régionaux.

Key words. *Lycaena hippothoe*, population dynamics, weather, imaginal resources, realised fecundity.

Introduction

Many animal populations, in particular those of insects, undergo pronounced dynamics in space and time (e.g. Ehrlich 1984; Thomas & Harrison 1992; Dempster *et al.* 1995; Zwölfer 1999). Although this has been known for a long time, dynamic processes were largely neglected in conservation biology, being dominated by static approaches

(Reich & Grimm 1996). Only recently, the rebirth of metapopulation concepts (e.g. Hanski & Gilpin 1997; Hanski 1999; Mousson *et al.* 1999; Gutiérrez *et al.* 2000; Thomas 2000) brought dynamic aspects into the focus of conservation research. In spite of a concomitant increase in publications on metapopulation topics, most of which basically deal with the incidence of species on a landscape level (e.g. Thomas *et al.* 1992; Hanski 1994; Hanski *et al.* 1996; Settele 1998), there is a lack of studies concerned with spatio-temporal dynamics on a local scale (but e.g. Murphy *et al.* 1986; Pollard & Yates 1993), providing quantitative data on the size of specific populations over a range of years.

Against this background we report here on the dynamics within a population of the butterfly *Lycaena hippothoe* between 1995 and 1999, using mark-recapture techniques. Such data are crucial to gain a better understanding of the underlying proximate factors and thus the exact mechanisms causing changes in population size, which are still largely unknown (Dempster & Pollard 1981; Kingsolver 1989; Zwölfer 1999; but see Roy *et al.* 2001). Based on our results we suggest a causal relationship between adverse weather conditions and *L. hippothoe* numbers in subsequent generations.

Material and Methods

Study organism. – *L. hippothoe* (Linnaeus, 1761) 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; Tuzov 2000). In central Europe, adults fly in one generation from about early June through late July (Ebert & Rennwald 1991; Fischer 1998). The species inhabits different kinds of wetland as well as unimproved grassland. The principal larval host-plant is *Rumex acetosa* L. (Polygonaceae), a common and widespread perennial herb.

Field methods. – Field work was carried out at two adjacent sites (study sites A and B, situated only a few kilometres apart from each other) in the Westerwald area (Rhineland-Palatinate, western Germany; cf. Fischer 1998). Both sites were formerly used as rough cattle pastures, which have been abandoned decades ago (last turning out to pasture 1962 and about 1965) and are now sporadically grazed by sheep or wild game only. During the complete flight seasons 1995 (site A only), 1997, 1998, and 1999 both *L. hippothoe* populations were sampled on every favourable day. All individuals encountered for the first time were captured using an insect net, individually marked (by writing a number with a permanent ink, felt-tip pen on the hindwing undersides), and afterwards immediately released at the point of capture. As evidenced by the observation of single individuals over extended periods of time in the same territories, the capture and marking procedure did not evoke adverse handling effects (Fischer & Fiedler 2001b).

Data analysis. – For this paper we analysed recapture rate (percentage of butterflies recaptured at least once), distance moved between capture and subsequent recapture event, minimum number alive, and total number of brood. For the latter three different methods were used (all based on Jolly-Seber estimates; see Southwood & Henderson

2000) as described by Watt *et al.* (1977), Matsumoto (1984) and Kockelke *et al.* (1994). The minimum number alive comprises the sum of individuals seen on a specific day plus those which were previously marked and recaptured at a later date, but not seen that specific day (see Blower *et al.* 1981). To investigate a possible relationship between butterfly numbers and weather conditions during the previous flight period (site A only), we used the mean daily cloud cover during June and July in 1994, 1996, 1997, and 1998. Data on cloud cover were obtained from Deutscher Wetterdienst (1997-2000), measured at a nearby (ca. 8 km) meteorological station (Bad Marienberg).

Results

Across the emergence periods, the number of individually marked butterflies (Tab. 1) decreased in site A between 1995 and 1999 from 262 to 72. For the period 1997-1999, a comparable decline in butterflies was found for both sites (Tab. 1). The same pattern emerged if statistical estimates of total brood sizes, rather than the numbers of marked individuals, were considered (Tab. 1). A close correlation occurred between butterfly number observed in a given year and the mean daily cloud cover during the previous flight period, i.e. population size decreases as cloud cover increases (Fig. 1). Nevertheless, the minimum number alive showed no indication of direct effects of weather conditions within an emergence period on adult longevity (see examples in Fig. 2). Even after spells of unfavourable (rainy) weather that precluded flight activity for up to four days, no reduction in population abundance could be noticed. In addition to the decline in numbers over the years, changes in the spatial distribution were observed in site A (Fig. 3). Prominent examples with large deviations between subsequent years include grid cells C5, C6, D5, E4, E5, F4, and G4. For instance, cell E4 contained only 6.2 % of all observations in 1997, but 25.7 % in the following year. Regarding sexual differences, males exhibited higher recapture rates than females throughout (Tab. 1). Moreover, males were generally more stationary than females, confirmed by lower distances between capture and subsequent recapture event (Tab. 2).

Tab. 1. Number of *L. hippothoe* individuals marked, population size (total number of brood, given as mean of three methods; see above), and recapture rates [%] for two study sites in different years. Sex-specific differences in recapture rates were analysed using pairwise Bonferroni-corrected χ^2-tests (significance threshold: $p<0.007$; null hypothesis: equal recapture probability in both sexes; ♂: males, ♀: females). Significant p-values are printed in bold.

Site	Year	Marked individuals			Population size	Recapture rates			
		♂	♀	♂ + ♀	♂ + ♀	♂	♀	χ^2_{1df}	p
A	1995	158	104	262	570	58.3	30.6	28.0	**<0.0001**
A	1997	95	95	190	259	49.5	29.5	7.8	**0.0048**
A	1998	73	61	134	173	64.4	36.1	10.7	**0.0011**
A	1999	27	45	72	95	63.0	28.9	8.1	**0.0045**
B	1997	110	76	186	204	79.1	51.3	15.9	**0.0001**
B	1998	68	67	135	164	77.9	46.3	14.4	**0.0001**
B	1999	44	50	94	103	81.8	74.0	0.8	0.36

Tab. 2. Distances [m] between capture and subsequent recapture event for male and female *L. hippothoe* for two study sites in different years. Sex-specific differences were analysed using Mann-Whitney's U-test (Bonferroni-corrected threshold for significance: p<0.007). Significant p-values are printed in bold.

Site	Year	Males		Females		Z	p
		Mean ± s.d.	n	Mean ± s.d.	n		
A	1995	46.9 ± 54.4	325	80.9 ± 69.0	66	4.07	**<0.0001**
A	1997	43.4 ± 54.1	136	84.7 ± 65.1	47	4.11	**<0.0001**
A	1998	46.2 ± 49.2	134	68.0 ± 61.5	36	2.03	0.04
A	1999	33.7 ± 63.0	82	39.2 ± 49.1	25	1.26	0.21
B	1997	30.1 ± 41.6	271	52.1 ± 49.0	88	4.29	**<0.0001**
B	1998	33.3 ± 40.7	152	65.2 ± 58.8	59	4.33	**<0.0001**
B	1999	18.3 ± 37.9	158	43.5 ± 40.9	91	6.18	**<0.0001**

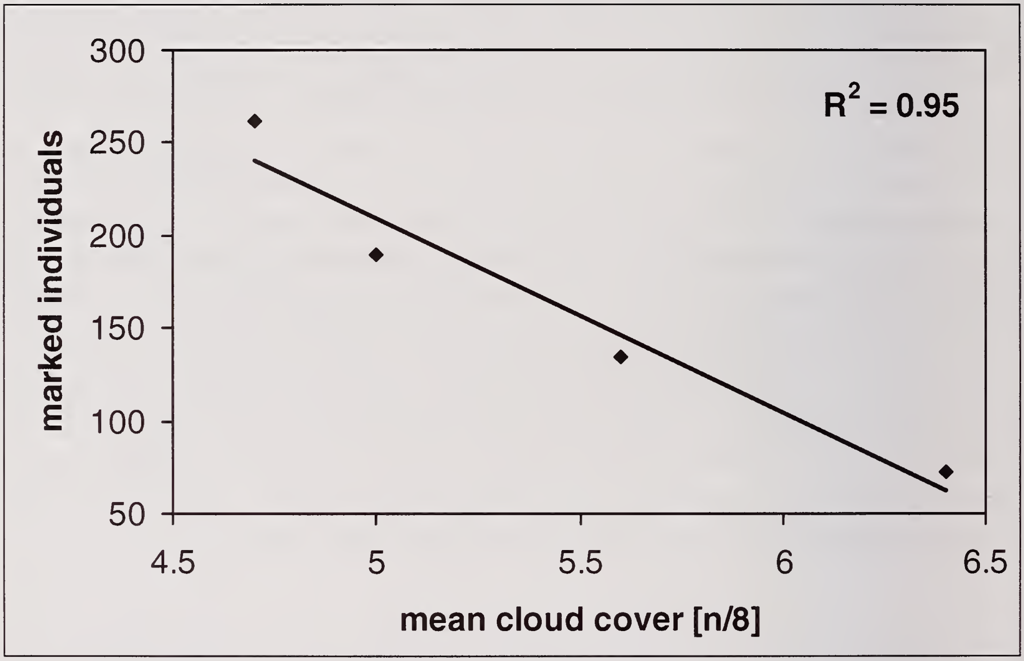

Fig. 1. Total number of marked *L. hippothoe* butterflies in site A during flight seasons 1995, 1997, 1998, 1999 in relation to mean daily cloud cover [n/8 of sky] during previous flight period.

Discussion

For study site A, our data show a steady decline in butterfly numbers between 1995 and 1999 as well as changes in the spatial distribution within this site. The decline in numbers was apparent from both, the number of individuals marked as well as the estimated total number of brood. This is not surprising since the relatively high recapture rates indicate that a large proportion of the population has actually been marked during each flight period. Interestingly, the decline in site A was paralleled by a very similar one in site B (Tab. 1), which is only a few kilometres away. Habitat changes due to

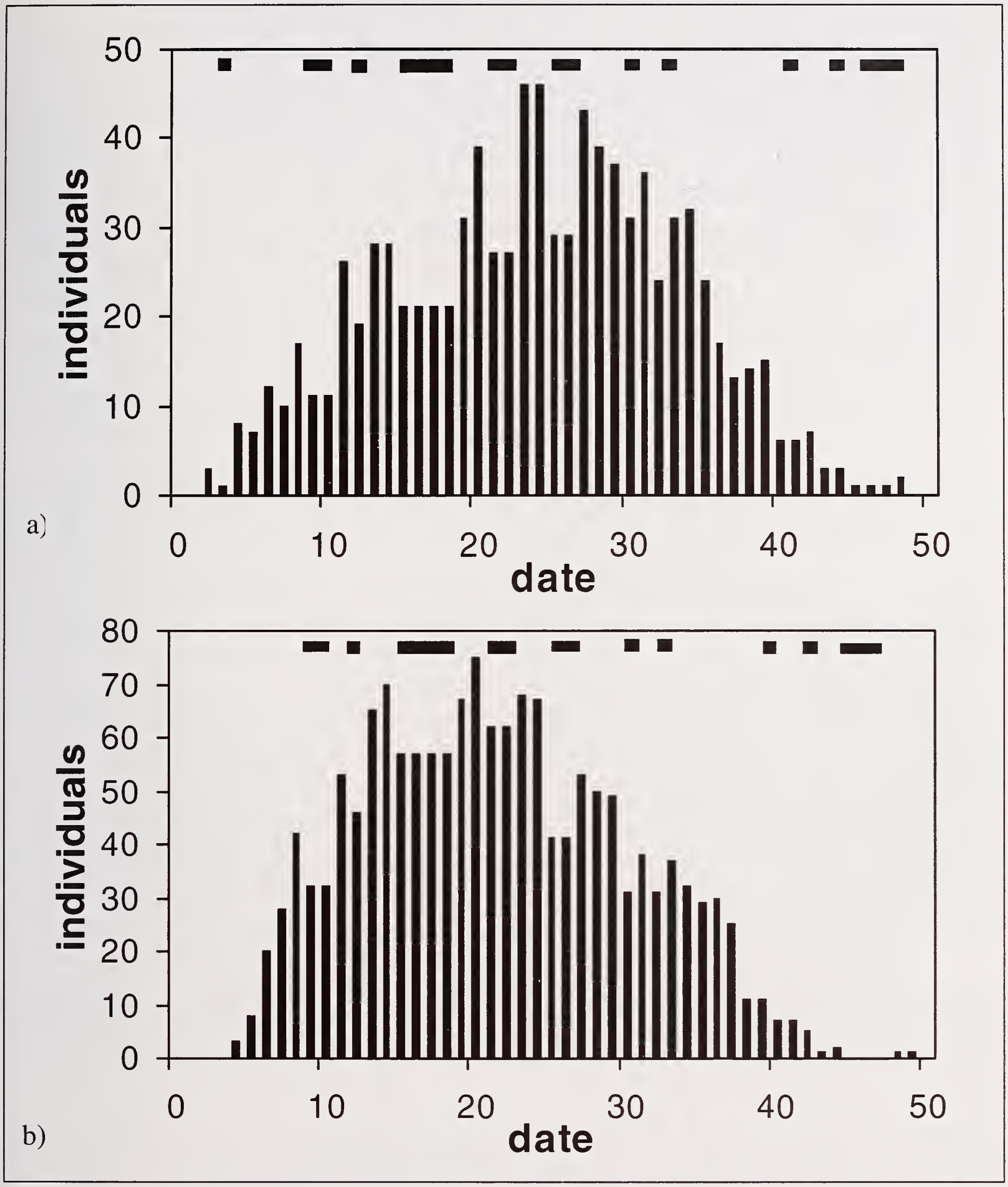

Fig. 2. Daily minimum number alive for *L. hippothoe* in study sites A (a) and B (b) 1997 (date 1: 07.06). Dates with adverse weather conditions are indicated by bars at the top of the graphs.

altered land-use practices can be ruled out in causing these declines, as both sites are lying fallow for decades. Likewise, no changes attributable to secondary succession and concomitant changes in vegetation could be observed during the study period, although this was not examined in detail. The comparable decline of *L. hippothoe* in both study sites, however, may favour a common explanation rather than site-specific reasons. Perhaps the most important and wide-spread factor affecting local butterfly

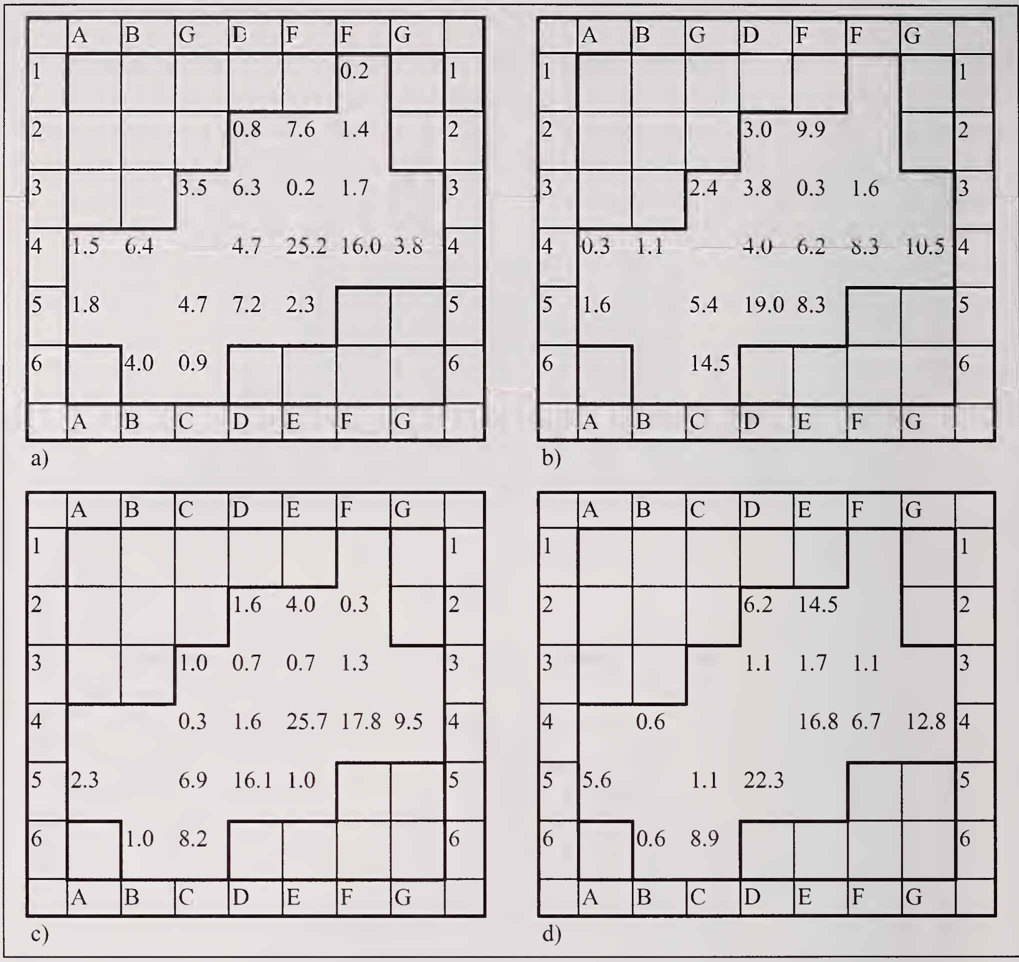

Fig. 3. Schematic map of study site A. Figures within grid cells give the proportion of *L. hippothoe* observations per grid, expressed as percentage of all observations made during the whole flight period in different years (a: 1995, n (total number of observations) = 656; b: 1997, n = 373; c: 1998, n = 304; d: 1999, n = 179). Internal lines indicate the boundaries of the study site. One grid cell = 2500 m².

populations equally, and thus causing synchrony of population fluctuations on regional scales, is weather (e.g. Pollard & Lakhani 1985; Pollard 1988, 1991; Roy *et al.* 2001). The close relationship between *L. hippothoe* numbers and cloud cover (and other indicators of favourableness of weather conditions for butterflies such as amount of precipitation or mean maximum temperature; results not shown) during the previous flight period suggests that weather conditions may have been important during this study as well, although the finding rests on a small sample size of four years and two study sites only. In a number of univoltine butterfly species which hibernate as small larvae, Roy *et al.* (2001) likewise observed that weather conditions during the preceding flight period explain abundance data better than do temperature and rainfall in the year of emergence. Thus, we assume that the observed decline in *L. hippothoe* was probably caused by adverse weather conditions during a sequence of flight periods.

As our results show no reduction in adult numbers within one flight season following cold and rainy weather (cf. Fig. 2), the decline is unlikely to be due to increased adult mortality. However, we do not have any data on larval mortality. A few studies confirmed a higher mortality of butterfly larvae during droughts due to desiccation of larval food plants (e.g. Ehrlich *et al.* 1980; Endo *et al.* 1986; Pollard *et al.* 1997). Adverse effects of particularly cold or wet conditions are apparently largely unknown, except for mortality under rather extreme conditions (i.e. flooding; see Webb & Pullin 1996, 1998). However, correlational evidence does suggest that low temperatures or high levels of rainfall during early stages of a life cycle may play a role in abundance fluctuations of various butterflies (Roy *et al.* 2001). Overall, predation and parasitoid attacks appear to be the main mortality factors during larval development in insects (Moore 1989; Cornell & Hawkins 1995; Rosenheim 1998), which may, however, in itself be related to weather conditions (Warren 1992).

Regarding the adult life stage, carbohydrate ingestion (i.e. nectar) can profoundly affect longevity and fecundity in many temperate-zone nectar-feeding butterflies (e.g. Murphy *et al.* 1983; Karlsson & Wickman 1990; Boggs & Ross 1993; Rusterholz & Ehrhardt 2000). Fecundity in *L. hippothoe* butterflies, showing a seven-fold increase when fed concentrated sucrose solution as compared to water only, depends far more on adult-derived resources than in any other nectar-feeding butterflies for which comparable data exist (Fischer & Fiedler 2001a). The crucial role of nectar sources for the reproductive output in *L. hippothoe* is highlighted by field data on its behavioural ecology (Fischer & Fiedler 2001b). Males exhibit aggressive territorial behaviour by defending areas rich in flowering nectar plants (resource-based territoriality). The concomitant site tenacity is indicated by the higher recapture rates and shorter distances moved between capture events in males than in females, resulting in sex-related differences in these traits in the present study (Tables 1 and 2). Given the strong dependence of the reproductive output on adult resources, the monopolisation of nectar sources is a straightforward strategy in spite of the males' high investments.

From these findings we draw the conclusion that the most likely mechanism through which weather influences *L. hippothoe* abundance may be a reduction in realised fecundity (cf. Courtney & Duggan 1983; Dempster 1983; Kingsolver 1989; Warren 1992). In nature, female *L. hippothoe* were found to exhibit residence times of about 8 days (Fischer & Fiedler 2001c). Under semi-natural conditions, within such a period of time about 160 eggs per female were laid, comprising 32% of the species' mean potential fecundity (Fischer & Fiedler 2001a). However, under optimal (laboratory) conditions females may have reached a value close to their maximal fecundity after 8 days only (Fischer & Fiedler 2001a). Thus, given a rather short life span similar to the residence times found, a series of rainy days may strongly reduce realised fecundity.

Moreover, a high incidence of rainy or overcast days would constrain not only the time available for egg-laying, but also for feeding. The resulting lack of nourishment, causing a reduced egg production (Porter 1992), should impede compensation of time limitations through an increase in oviposition rate. In particularly bad seasons, females may be able to lay those about 60 eggs only which are already well developed at emergence (Fischer & Fiedler 2001a). In contrast to species in which reproduction relies less strongly on adult feeding, population dynamics of *L. hippothoe* should be far more affected if access to adult nutrient resources is limited. These findings may also be important for the conservation of this and other species, as a reduced availability of nectar sources caused by modern agricultural techniques (e.g. due to high mowing frequencies and recurrent applications of fertilizer; e.g. Barabasz 1994; Ellenberg 1996; Erhardt 1995) may well play an important role for regional declines.

Acknowledgements

We would like to thank J. Settele and an unknown reviewer for valuable comments on this manuscript, and the Koblenz district government for granting permission to pursue this study. The work was partially supported by grants from the Friedrich-Ebert-Foundation to K. Fischer.

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