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Population structure, mobility and habitat selection of the butterfly *Lycaena hippothoe* (Lycaenidae: Lycaenini) in western Germany

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Summary. Mark-release-recapture techniques were used to study a population of the butterfly *Lycaena hippothoe* (Linnaeus, 1761). The flight period lasted 32 days with a peak in early July. The sex-ratio changed with brood aging: males were in the majority early in the flight season, while females predominated at the end of flight. The population size (total number of brood) was estimated at about 600 individuals, equivalent to a density of 68 individuals/hectare. The average adult residence time was 7 days. Both sexes exhibited limited dispersal, with average individual ranges of about 100 metres. Dispersal varied among sexes, probably due to behavioural differences.In the study area moist meadows with flowering nectar source plants are the favoured habitats; the species, however, is not restricted to those biotopes. At least in mountain areas, *L. hippothoe* is able to utilize a fairly wide range of biotopes. Due to a dramatic loss of occupied habitats, conservation measures are seriously needed. Suggestions for habitat management include extensive grazing or mowing, but with retention of some unmanaged areas.

Zusammenfassung. Eine Population von *Lycaena hippothoe* (Linnaeus, 1761) wurde in Form einer Fang-Wiederfang-Analyse untersucht. Die Flugperiode reichte vom 22.06. bis zum 23.07.1995 (32 Tage), das Populationsmaximum wurde Anfang Juli erreicht. Das Geschlechterverhältnis verschob sich von den zunächst dominierenden Männchen zugunsten der Weibchen. Die Größe der Population wird auf ca. 600 Individuen geschätzt, die Abundanz beträgt ca. 68 Ind./ha. Die Mindestlebensspanne liegt bei durchschnittlich 7 Tagen. Beide Geschlechter zeigten ein eingeschränktes Dispersal mit Durchschnittsentfernungen von etwa 100 Metern. Geschlechtsspezifische Unterschiede werden mit abweichenden Verhaltensmustern erklärt. Im Untersuchungsgebiet werden blütenreiche Calthionbestände bevorzugt, woraus keine Beschränkung auf Feuchtgebiete abzuleiten ist. Es wird ausdrücklich auf eine breitere ökologische Amplitude, bezogen auf den Faktor "Feuchte", in montan getönten Gebieten hingewiesen, als dies bisher angenommen wurde. Aufgrund der alarmierenden Bestandsrückgänge sind spezielle Schutzmaßnahmen dringend erforderlich. Als Pflegemaßnahme für die Habitate wird eine extensive Grünlandnutzung (Mahd, Beweidung) unter Belassung von Brachestreifen vorgeschlagen.

Résumé. Les techniques de marquage-recapture furent utilisées pour étudier une population du papillon *Lycaena hippothoe* (Linné, 1761). La période de vol s'étale sur 32 jours avec un pic au début juillet. La sex-ratio évolue avec l'âge de la génération: les mâles volent en majorité en début de saison alors que les femelles prédominent à la fin. L'effectif de la population (nombre total d'éclosions) a été estimé à environ 600 individus, équivalent à une densité de 68 individus/hectare. La moyenne de vie des adultes est de 7 jours. Les deux sexes ont des capacités de dispersion limitées, avec une moyenne par individu d'environ 100 mètres. Ce pouvoir de dispersion varie selon les sexes, certainement dû à des différences de comportement. Dans cette étude les habitats favorables sont des prairies humides avec des plantes nectarifères; l'espèce n'est cependant pas limitée à ces biotopes. Dans les zones montagneuses au moins, *L. hippothoe* est capable d'utiliser un spectre d'habitats plus large. En raison d'une régression dramatique des habitats qu'il occupe, des mesures de conservation sont rapidement nécessaires. Les suggestions pour l'aménagement incluent le pâturage extensif ou la fauche, mais avec la conservation de zones non entretenues.

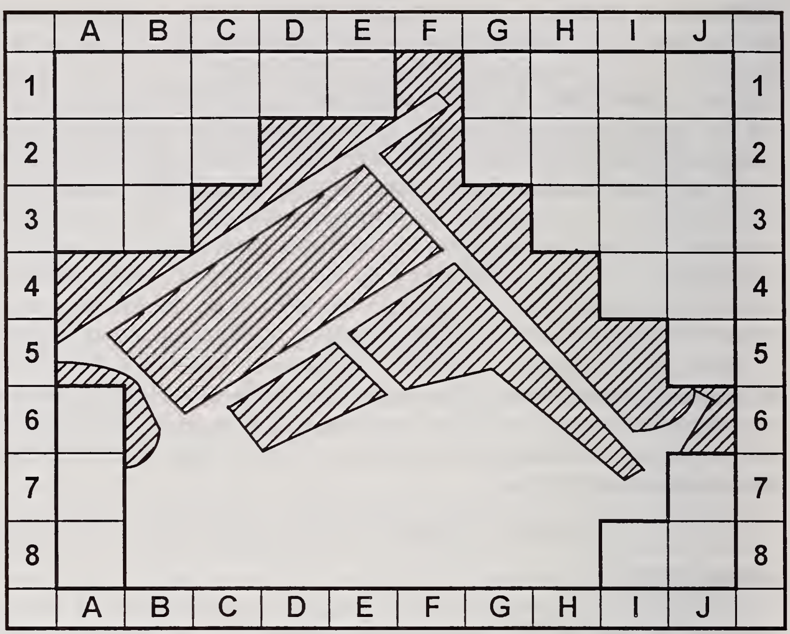
Key words: Lycaenidae, *Lycaena hippothoe*, populations, habitat, Germany.

Introduction

Lycaena hippothoe (Linnaeus, 1761) 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). In southern and central Europe, the species is distributed more locally in wetlands and mountain areas, where it used to be abundant (e.g. Forster & Wohlfahrt, 1984). In the past few decades, however, *L. hippothoe* populations in Central Europe have dramatically declined and local or even regional extinctions have occurred in some areas (e.g. Beuret, 1953; Ebert & Rennwald, 1991; Reinhardt & Thust, 1991, 1993). As with many relatively widespread and previously common butterflies, scientific interest in *L. hippothoe* has been poor. Accordingly, detailed published information about its ecology and habitat requirements is almost non-existent, although such knowledge is crucial for specific and effective conservation measures (e.g. Clark & Seebeck, 1990). This paper aims at filling this gap.

Materials and methods

Study site. The study was carried out in the Westerwald area (western Germany; elevation 580 m) on a former pasture (area = 12.5 ha). After having been abandoned, the pasture had been widely drained and afforestated with spruce trees (fig. 1). Aisles of about 10 metres in width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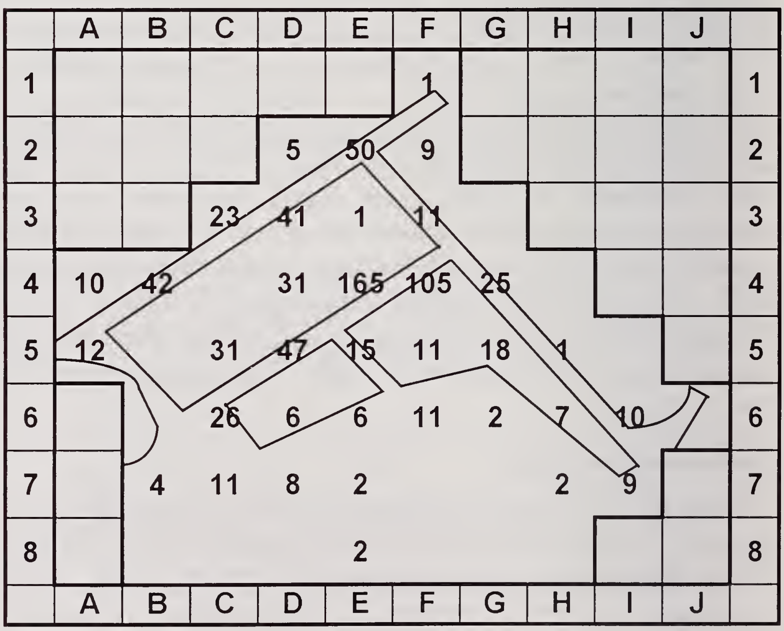
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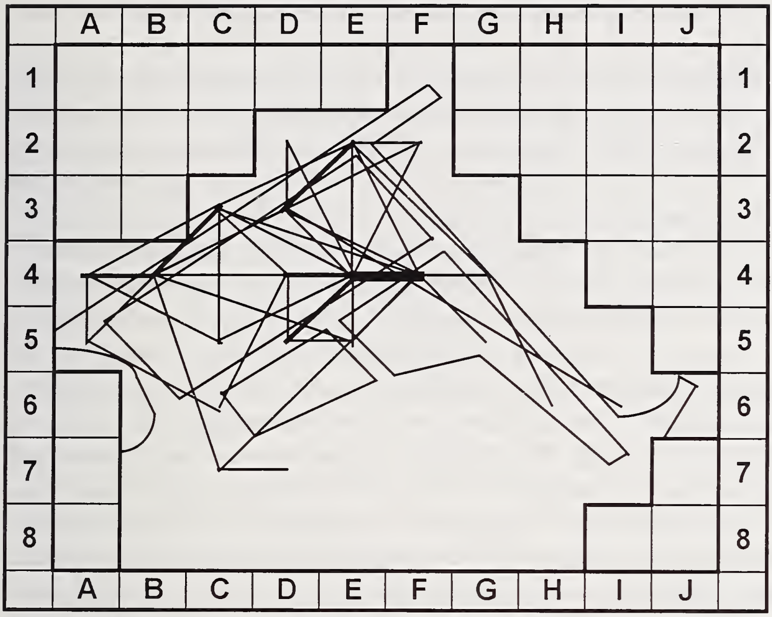


Fig. 1. *Lycaena hippothoe*: study site parameters.
a — schematic map of the study site (hatching: conifer forests; grid size 50 m); b — observation numbers per square; c — movements of *Lycaena hippothoe* between recent and subsequent capture.

separate the different afforestations. Adjacent areas are still used as pastures, smaller ones are lying fallow. The climate can be characterized as oceanic, cold and humid (precipitation > 1000 mm/year, average temperature/year 6 °C, cf. Sabel & Fischer, 1992).

Field methods. To carry out a mark-release-recapture analysis the population was sampled daily between June 22 and July 26, 1995. For practical reasons, the area was divided first in 50 × 50 m quadrats. The adults captured were given unique marks using a permanent ink, felt tip pen and immediately released at the point of capture. To obtain information on population structure, adult mobility and habitat requirements each capture was accompanied by a record including date, number of mark, sex, position of capture (50 × 50 m grid), vegetation height and quantity of flowering plants at the point of capture, behaviour at the moment of encounter, and, if required, nectar source plant. The quantity of flowering plants was subjectively assessed on a relative scale comprising four classes (ranging from *absent* to *very good*).

Data analysis. The daily population sizes were calculated according to Jolly (1965), as this method allows survival rates to vary from day to day (Begon, 1979; Southwood, 1976). The population size (total number of brood) was calculated using three different methods (Watt *et al.*, 1977; Matsumoto, 1984; Kockelke *et al.*, 1994). The estimation of density is based on different methods as well: (1) absolute density (minimum density, using the number of marked individuals during flight period), (2) maximum density observed (using the day with the highest record of observed individuals), (3) density based on the estimated total number of brood. The calculations refer to the number of grid-areas (2500 m^2) with at least one record during flight period (1, 3), or, respectively, during the day with the highest record of observed individuals (2). For calculation of the "minimum number alive" see Blower *et al.* (1981). As a measure of mobility the shortest distance between the places of capture and recapture (centres of 50 m squares) was used. Therefore, this measure does not give information about the butterflies' actual flight pattern. Individual home ranges were determined by the minimum area method (Southwood, 1976), using only data of individuals observed at least four times. For information on the statistical methods used (Mann-Whitney U-test, chi-square procedures) see Zöfel (1992).

Results

Capture results. 371 individuals (211 males, 160 females) of *Lycaena hippothoe* were captured, together with 392 recaptures (326 males, 66 females): this leads to a total number of 763 observations. The sex-ratio of marked males to females (1.3: 1) was not significantly different from an expected sex-ratio of 1: 1 ($x^2_{(2df)} = 3.52$). Among the recaptures a strong male bias can be witnessed (highly significant difference compared to the capture results; $x^2_{(1df)} = 63.19$, $p < 0.0001$). The recapture rate (in per cent of marked individuals) was 46.4%, with a higher rate for males compared to females (58.3% compared to 30.6%; $U = 10699.5$, $p < 0.0001$; $N_1 = 211$, $N_2 = 160$).

Adults of *L. hippothoe* were observed between June 22 and July 23, 1995. Hence, the flight period lasted at least 32 days in 1995 (note the late start of the study). The highest number of observations was recorded on July 4. Along with the state of phenology, weather conditions are important for observation figures (fig. 2). The sex-ratio changed with brood aging: males were in the majority early in the flight season (sex-ratio 4.7: 1 in the first 10 days), while females predominated at the end of flight (sex-ratio 0.6: 1 in the last 10 days; highly significant difference between first and last 10 days, $x^2_{(1df)} = 55.19$, $p < 0.0001$; fig. 3).

Minimum residence time. The highest records of minimum residence time were 19 days (male) and 18 days (female), respectively. The average residence time was 7.6 (± 4.6) days (median 8) for males and 5.3 (± 4.2) days (median 6) for females. This sex-related difference is significant ($U = 2081.0$, $p = 0.0019$; $N_1 = 122$, $N_2 = 49$).

Minimum number alive, population size and density. The minimum number alive again reveals the phenological development of the population, but without weather-related "gaps" (fig. 4a). The population sizes, according to Jolly (1965), give the estimated numbers per day. According to the calculations, the largest daily population size (315 individuals) occurred on July 8 (fig. 4b). The total number of the brood was estimated at about 600 individuals, the concomitant density at 68 individuals/hectare (table 1).

Table 1. Total number of the brood and population density of *Lycaena hippothoe* according to different methods.

Method	**Total number of brood**	**Density ind./ha**
Watt *et al.* (1977)	594	67.9
Matsumoto (1984)	555	63.4
Kockelke *et al.* (1994)	632	72.2
Average 1–3	594	67.9
Absolute density		42.4
Maximum density observed		17.8

Mobility and home range. The majority of individuals remained in the vicinity of the point where they had been captured previously (fig. 5). 77.6% of the recorded distances were less than 100 metres. The average distance covered was 52.7 (± 58.4) metres (median 50). Males were found to be more stationary in comparison to females (46.9 (± 54.4) m compared with 80.9 (± 69.0) m; significant difference: $U = 7315.0$,

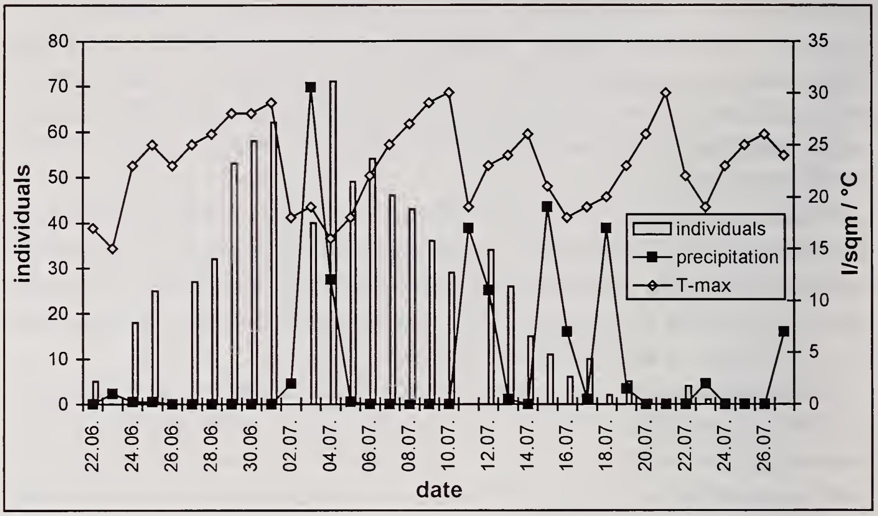


Fig. 2. Adult phenology of a population of *Lycaena hippothoe* in relation to daily maximum temperature and precipitation in the Westerwald area (western Germany) in 1995 (N = 763).

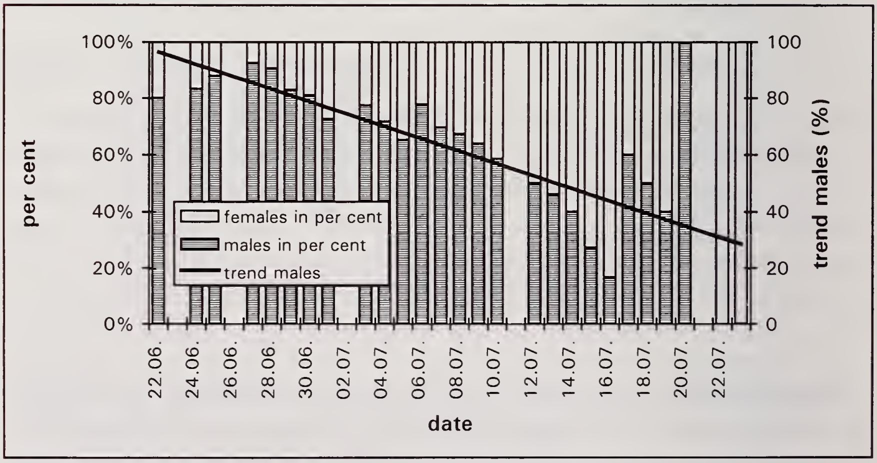
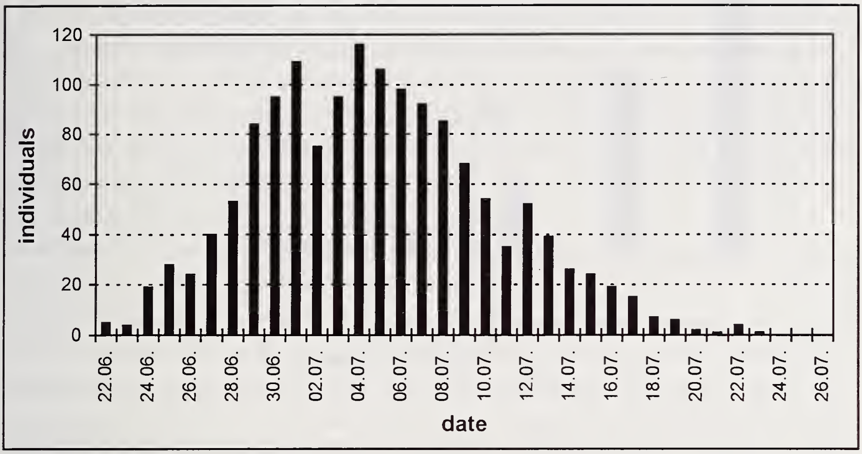


Fig. 3. Change of sex-ratio and trend of males, according to the method of the "smallest quadrats", during flight season. Irregularities towards the end of flight are due to small absolute numbers.



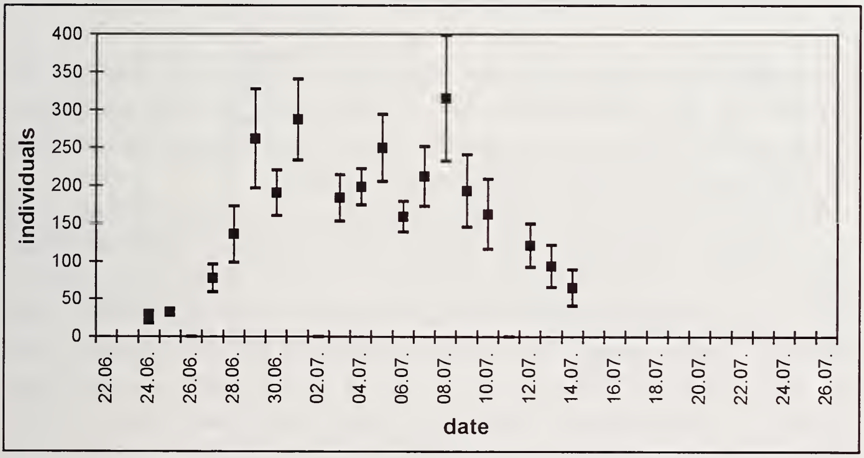


Fig. 4. Population size of *Lycaena hippothoe* in a population studied in the Westerwald area 1995: a — minimum number alive; b — estimates of the daily population sizes, according to Jolly (1965), with standard deviation.

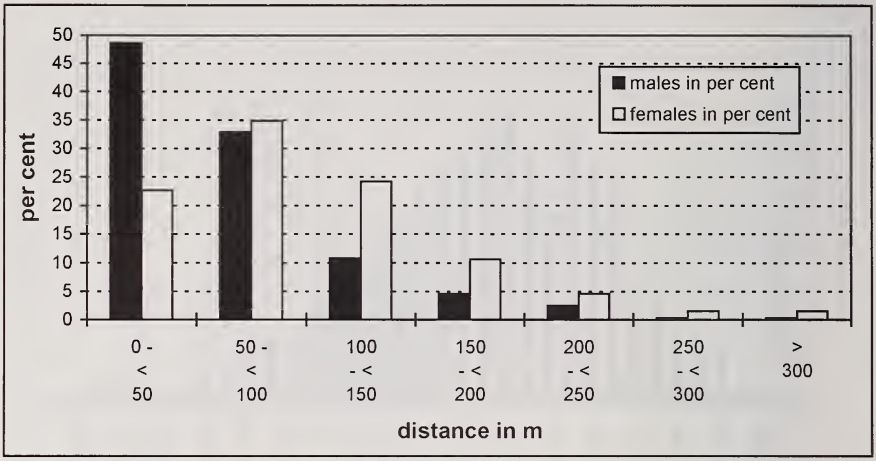


Fig. 5. Relative frequency (%) of registered movements for males and females (N = 391). Sex-specific differences in the average distances covered are highly significant.

$p < 0.0001$; $N_1 = 325$, $N_2 = 66$). The largest distance, 325 metres, was covered by two individuals, one of each sex. A rank correlation (Spearman's) showed no association between the distance covered and the time elapsed between capture and recapture.

When one adds up the respective distances covered by each individual (for multiple recaptures) the results will, of course, shift to higher figures. The average distance increases to 118.2 (± 82.6) m (median 100 m; N = 170), the largest distance amounts to 575 m (female). Most individual home ranges were between 1000 and 4000 m^2 (average 3804 (± 2459), median 2488 m^2; N = 26). Probably due to the higher vagrancy, home ranges of females are larger than those of males, which is indicated by a medium size of 4725 m^2 (females; N = 2) compared to 3728 m^2 (males, N = 24), but due to poor data this could not be proven.

Behavioural aspects. Sex-specific differences in behaviour were highly significant. Observations showed that males were less frequently "flying" (55% compared to 65%) and more frequently "feeding" (32% compared to 16.4%; $x^2_{(1df)} = 16.93$, $p = 0.00004$; N = 651). Oviposition was observed nine times on sorrel (*Rumex acetosa*).

Habitat use. The vegetation of the study area, apart from conifer forests, consisted of unimproved, semi-humid grassland and different kinds of wetland (plant communities: Polygalo-Nardetum, Deschampsia cespitosa-Polygonum bistorta association, Festuco-Cynosuretum, Juncetum acutiflori). In the study area, *Lycaena hippothoe* preferred moist meadows with flowering nectar source plants. Males, however, seemed to have a stronger preference for dense areas of flowering plants than females (average 2.9 (± 0.7) compared with 2.7 (± 0.7); $U = 52821.0$, $p = 0.0018$; $N_1 = 537$, $N_2 = 226$).

Adults fed on 17 different plant species (fig. 6). *Polygonum bistorta* played the most important role as nectar source (59.8% of feeding events). Other important plants were *Ranunculus repens*, *R. acris*, *Cirsium palustre* and *Knautia arvensis*. Significant sex-related differences manifested themselves in the use of certain nectar source plants, e.g. *Polygonum bistorta*, *Cirsium palustre* and *Knautia arvensis* (chi-square-test, $p < 0.05$).

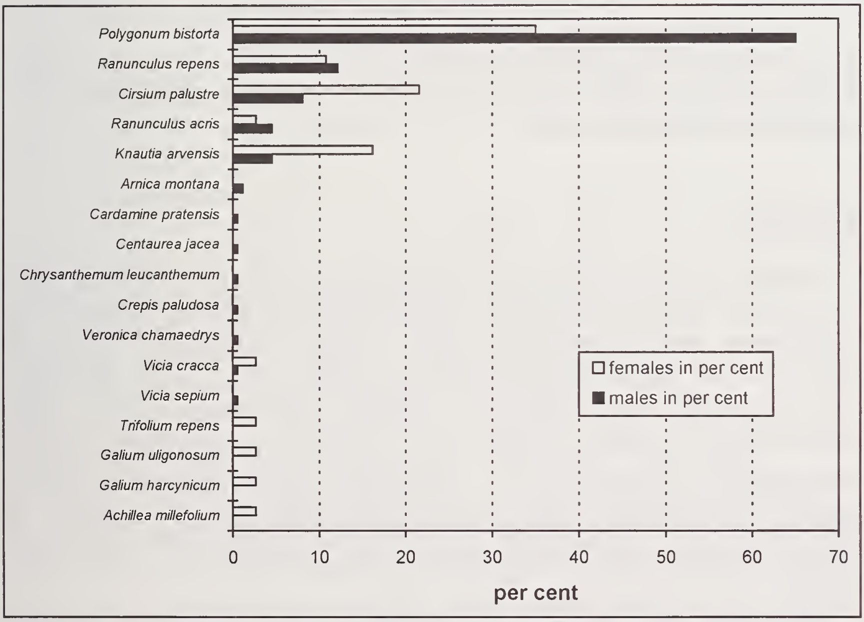


Fig. 6. Relative frequency (%) of feeding events on nectar source plants for males and females (N = 209). Significant sex-specific differences occurred in the use of *Polygonum bistorta*, *Cirsium palustre* and *Knautia arvensis*.

Most observations of adults took place at vegetation heights ranging from 50 to 90 cm (average 68 (± 21) cm, median 60 cm; fig. 7). Females preferred lower vegetation (62 (± 22) cm compared to 70 (± 21) cm; $U = 28630.0$, $p = 0.002$; $N_1 = 537$, $N_2 = 226$).

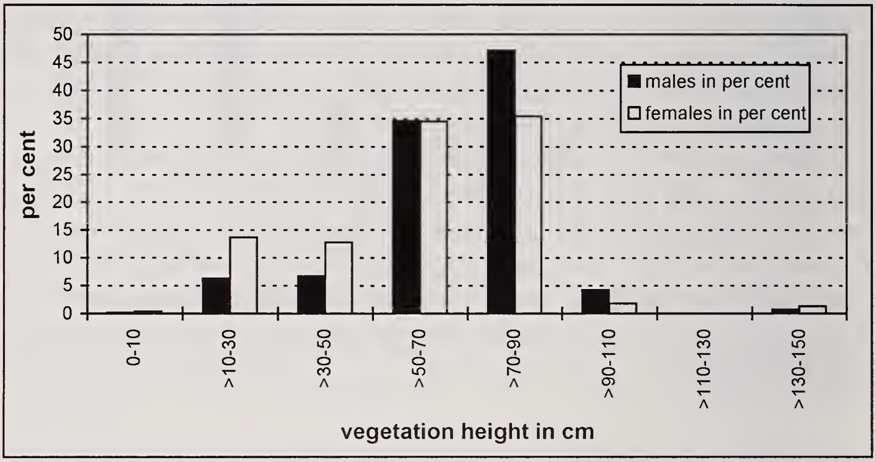


Fig. 7. Relative frequency of observations in relation to vegetation height for males and females (N = 763). Females preferred significantly lower vegetation compared to males.

Discussion

Capture results. The surplus of males agrees with the results of other comparable field studies. Male butterflies are commonly observed to outnumber females (Ehrlich, 1984; see also Lederhouse, 1983 and Warren, 1987). The recapture rate agrees more or less with the results of other studies (e.g. Geissler & Settele, 1990; Pauler *et al.*, 1995; Scott & Opler, 1975) and may, within this scope, be regarded as typical for sedentary species such as *L. hippothoe*. Lower recapture rates for females are probably due to behavioural differences in addition to higher dispersal rates (see below; see also Tabashnik, 1980 and Scott, 1974).

In general, the species is on the wing from mid-June to mid-July (e.g. Bergmann, 1952; Brockmann, 1989). The flight period depends on the elevation. At low altitudes it begins in early June or even late May, in mountain areas it starts and ends later on depending on the altitude (Ebert & Rennwald, 1991). The results presented here (June 22 to July 23) agree with the information given above; the real flight period, however, is supposed to be at least 40 days. In all likelihood, the species was on the wing a week before the study started. This presumption is confirmed by the fact that some females, which usually emerge a week after the males (Bergmann, 1952; Weidemann, 1995), could be observed right at the beginning of field work. Therefore, protandry could not be confirmed, but the resulting shift of sex-ratio during flight period, well known also for many other butterflies (e.g. Fischer, 1996; Watt *et al.*, 1977; Wright, 1983), could be witnessed.

The average residence times ascertained in this study agree with other results on lycaenid butterflies (e.g. Fischer, 1996; Scott, 1973; Scott & Opler, 1975). The shorter residence time of females is probably linked to the lower recapture rate, due to different behavioural patterns and should not, therefore, be interpreted as an actual difference.

Population size and mobility. The total number of the brood (about 600 individuals) is, at this scale, typical for closed butterfly populations; they usually are any number from a few hundred to a few thousand individuals (Ehrlich, 1984; see also Fischer, 1996; Warren *et al.*, 1986; Watt *et al.*, 1977). The density is only intermediate, far higher figures are known for other lycaenids (e.g. Scott, 1975; Fischer, 1996). Nevertheless, the data collected indicate that *L. hippothoe* is spatially fairly restricted.

The short average distances as well as the distribution of distances moved are also indicators of the sedentary nature of *L. hippothoe*. However, the area of the present study is small, and it is likely that distances are underestimated (also due to mark-release-recapture methods). Recent studies show that at least single individuals of so-called sedentary species can migrate considerable distances up to some kilometres (e.g. Dennis & Bardell, 1996; Settele *et al.*, 1996). The sex-specific differences are likely to be related to different behavioural patterns (see Lederhouse, 1982; Scott, 1975; Shreeve, 1992). Males seem to display — at least temporarily — territorial behaviour (perching), while the behaviour of females is determined by the search for oviposition sites. Other lycaenids with male perching behaviour are also known for their poor mobility with corresponding higher figures for females (Douwes, 1975; Fischer, 1996; Scott, 1974; Thomas, 1985).

Behavioural aspects and habitat use. The sex-related differences in behavioural patterns between males and females concerning "feeding" and "flying" could be explained by the choice of perch sites (males; higher feeding frequency, see below) and the search of oviposition sites (females; higher flying frequency).

The observations on oviposition behaviour show that females laid their eggs on sorrel, although knot grass (*Polygonum bistorta*) is far more abundant in the study area. It should be critically examined, whether *L. hippothoe* actually utilizes *Polygonum bistorta* as a host plant, as maintained in several publications (e.g. Forster & Wohlfahrt, 1984; Henriksen & Kreutzer, 1982). This, probably, is not the case in Central Europe.

The favoured habitats in the study area were moist meadows with flowering plants, which was probably due to the richness of flowering nectar plants in this specific biotope during flight period. In contrast to some bibliographical references (e.g. Beuret, 1953; Forster & Wohlfahrt, 1984), however, the species is not restricted to those biotopes, although wetland is likely to be its favoured one. Its ecological amplitude (regarding the humidity of biotopes) certainly is far higher than assumed at present. At least in mountain areas, *L. hippothoe* is able to use a fairly wide range of even drier, extensively managed grassland biotopes such as unimproved, nutrient-poor grassland (Fischer, 1994; see Ebert & Rennwald, 1991). The somewhat inaccurate assessments are probably due to regional differences. Indeed, at low altitudes the species seems to be restricted to wetland, whereas at (preferred) higher altitudes this is not the case. The differences are presumably caused by climatic factors.

The female's preference for lower vegetation can be attributed to a greater availability of plants for oviposition. Eggs were laid exclusively on plants that rose above the surrounding vegetation. The stronger preference for dense areas of flowering nectar plants by males contradicts the results of other studies on lycaenids (Douwes, 1975; Fischer, 1996; Sharp & Parks, 1973), the possible reason being that males tend to take up perch sites near or even in dense zones of flowering plants in order to wait for females to frequent these plants for feeding. However, knowledge on behavioural patterns, sex-specific differences in reproductive strategies, and their variation within and between populations of *L. hippothoe* is still poor.

The choice of nectar source plants is fairly opportunistic. The sex-related differences seem to be caused by phenological reasons rather than intrinsic sex preferences.

Nature Conservation

Due to the dramatic decline of *L. hippothoe* in Central Europe, specific conservation measures are seriously needed. In northern Germany, the species has already become regionally extinct (e.g. Reinhardt & Thust, 1993). The following reasons are responsible for the decline (e.g. Brockmann, 1989; Ebert & Rennwald, 1991; Reinhardt & Thust, 1991; SBN, 1988):

- amelioration, fertilization, drainage, overgrazing, early mowing, and the resulting lack of nectar sources;
- afforestation of grassland;
- succession on fallow land;
- treatment of sorrel as pasture weed.

For these reasons there is an urgent need for conservation measures, aiming specifically at the protection (or restoration) of habitats. Because, in Central Europe, the species lives mainly in agricultural areas, habitat management is necessary (e.g. Ebert & Rennwald, 1991; Fischer, 1994; Meineke, 1982). Therefore, an analysis of reproductive success in relation to different kinds of management is required. From the perspective of nature conservation two measures would be adequate: mowing during flight period (egg laying can then occur in already mown areas, see Ebert & Rennwald, 1991) or in autumn (see Meineke, 1982), following the onset of caterpillar hibernation, or extensive grazing. It is also possible that fallow land is a decisive factor for reproduction (see Ebert & Rennwald, 1991; SBN, 1988), but this requires confirmation. For the time being, extensive mowing in summer or autumn, rotational mowing or extensive grazing, excluding various unmanaged areas, can be recommended for habitat management. However, much more work has to be done to give clear guidelines with confidence.

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