

## On the ethology and ecology of a small and isolated population of the Dusky Large Blue Butterfly *Glauropsyche (Maculinea) nausithous* (Lycaenidae)

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**Summary.** During a study of a small, relatively isolated population of *Glauropsyche (Maculinea) nausithous* (Bergsträsser, 1779), nearly every new adult entering the population was individually marked in summer 1990. Marked individuals were regularly recaptured. The population assessment was nearly complete, as shown by a comparison with estimates based on the Jolly-Seber-model. The average adult residence time was estimated at 2.3 days. Individual observations were made of the diurnal distribution of the following activities: resting, flight, nectaring, oviposition, copulation, and [other] movements. Our results show sex and age specific differences. On the day of marking, which was normally the day of eclosion, all activities were comparatively low. Older individuals of both sexes were generally active for the same amount of time per day, but differed with regard to activity profiles. Males undertook longer flights to search for females within the habitat, while the females flew more often but over much shorter distances, resulting in a shorter total flight time. Instead, females stayed on the flower buds of *Sanguisorba officinalis* — the only larval host plant and main adult nectar source — for much longer, and laid eggs. Females copulate directly after hatching and then immediately start to oviposit.

**Zusammenfassung.** Eine kleine, isolierte Population von *Glauropsyche (Maculinea) nausithous* (Bergsträsser, 1779) wurde im Sommer 1990 nahezu vollständig erfaßt. Aufgrund der intensiv angewendeten Fang-Wiederfang-Methode wurden im Habitat Tiere mit hoher Wahrscheinlichkeit am Tag des Schlüpfens markiert. Immigration konnte weitgehend ausgeschlossen werden. Dadurch kennen wir mit großer Sicherheit das Alter der Tiere, an denen ethologische Messungen durchgeführt wurden. Von Individuen dieser Population liegen zeitliche Messungen der Aktivitäten Ruhen, Fliegen, Saugen, Eierlegen, Kopulieren und Bewegen (Sammelgruppe für weitere Aktivitäten) im Tagesgang vor.

Unsere Ergebnisse zeigen, wie sich die Aktivitäten geschlechtsspezifisch unterscheiden und wie sie sich im Verlauf des Falterlebens verändern. Am Tag der Markierung, der in den allermeisten Fällen mit dem Tag des Schlüpfens zusammenfiel, waren die Aktivitäten vergleichsweise gering. Beide Geschlechter verbrachten ungefähr gleich viel Zeit aktiv, allerdings mit deutlich verschiedenen Schwerpunkten. Während die Männchen längere Suchflüge nach Weibchen im Habitat unternahmen, waren die Flüge der Weibchen zwar zahlenmäßig häufiger, insgesamt verbrachten sie aber deutlich weniger Zeit fliegend. Dafür bewegten sich die Weibchen länger auf den Blütenköpfen der Saug- und Eiablagepflanze *Sanguisorba officinalis* und legten Eier. Weibchen kopulierten unmittelbar nach dem Schlüpfen und begannen direkt danach mit der Eiablage.

**Résumé.** À l'occasion de l'étude, l'été 1990, d'une petite population relativement isolée de *Glaucoopsyche (Maculinea) nausithous* (Bergsträsser, 1779), presque chaque individu nouveau entrant dans la population a été marqué individuellement, puis régulièrement recapturé. L'évaluation de la population était presque complète, comme l'a montré la comparaison avec le modèle de Jolly-Seber. La moyenne de la durée de séjour des adultes est de 2.3 jours. L'observation des individus est basée sur la répartition des activités diurnes: repos, vol, alimentation, copulation, oviposition et autres. Nos résultats montrent des différences selon le sexe et l'âge. Le jour du marquage, qui est normalement celui de l'émergence, toutes les activités sont comparativement réduites. Les vieux individus des deux sexes sont généralement actifs pour la même durée chaque jour, mais différent par leurs profils d'activités. Les mâles passent de longues périodes en vol à la recherche des femelles dans le milieu, alors que les femelles volent moins souvent et sur des distances plus réduites, résultant donc en une durée de vol total plus courte pour celles-ci. À la place, les femelles se reposent sur les inflorescences de *Sanguisorba officinalis* — la seule plante-hôte des chenilles et la principale source de nectar — pour des durées plus longues et déposent leurs œufs. Les femelles copulent immédiatement après l'émergence et commencent la ponte des œufs juste après.

Key words: Lepidoptera, Lycaenidae, *Glaucoopsyche (Maculinea) nausithous*, diurnal behaviour, age dependent behaviour, etho-chronogramme, population structure, dispersal, residence time, MRR-study, Rhineland-Palatinate, S. Germany.

## 1. Introduction

The ecology of the Dusky Large Blue *Glaucoopsyche (Maculinea) nausithous* (Bergsträsser, 1779) has been quite well studied. This is due mainly to its high level of vulnerability as expressed in Red Lists (for Germany e.g. Pretschner, 1998) and the annexes of the Habitat Directive of the EU and in the Bern Convention (Gruttke, 1996; van Helsdingen *et al.*, 1997), and also to its fascinating *Maculinea*-type ecology.

The present study aims to improve knowledge on the adult ethology and population ecology of the species with special respect

to small and isolated populations. An example of such a population was studied in 1990 throughout the flight period. As the individuals of *G. nausithous* fly slowly compared to other butterfly species, they are easily followed. The species may reach high densities in its habitats, and is closely associated with its principal nectar source and larval host plant *Sanguisorba officinalis*. For a mark-release-recapture study, it is therefore sufficient to search for patches with flowering plants.

## 2. Materials and methods

2.1. **The species *Glaucopsyche nausithous*.** *G. nausithous* is univoltine. Eggs are exclusively deposited on *Sanguisorba officinalis*, where the first three larval instars develop. Hereafter the caterpillar reaches the ground to be adopted by ants of *Myrmica rubra* L., the only known host ant of the butterfly. Within the ant nest the larvae live predaciously and later pupate. On average, 2.5 pupae are found in one nest. This and further recent information on the ecology of the species are to be found e.g. in SBN (1991), Elfferich (1998), Thomas *et al.* (1998), Thomas & Elmes (1998) and Wynhoff (1998).

2.2. **Study sites.** The study was conducted on a ca. 2000 m<sup>2</sup> fallow grassland within the Mooswieser Tal (Mooswieser Valley, site M hereafter) south of the city of Kaiserslautern, between the settlements Aschbacherhof and Weiherfelderhof at an elevation of 300 m above sea level. The site was characterised by a high density stand of *Sanguisorba officinalis*, unlike the meadows located both to the East and to the West of the site. The northern and southern limits of the site are dense pine forests of the Pfälzerwald (Palatine Forest). Thus, the area of suitable habitat was relatively isolated. The only possible immigration of *G. nausithous* from its immediate surroundings was from the margins of meadows lying west of the study site, where some *S. officinalis* plants flowered during the flight period and where some individuals of *G. nausithous* were found. No host plant was found to the East of the site. This relatively isolated site was chosen for the study because it seemed possible to mark a high percentage of all individuals at the day of emergence with the manpower available and to identify their age for the behavioural analysis.

The site was divided into two parts. The northern sub-area of the Aschbach (a little creek) was drier with *Sanguisorba officinalis* dominating the vegetation, while the wetter sub-area south of the Aschbach held high densities of *Lythrum salicaria* L. and sedges, but only occasional exposed *S. officinalis* plants.

An additional site Hagelgrund (in the Eselsbachtal, site H hereafter), north of the city of Kaiserslautern, was also studied. This was used mainly to test our method of using small portable computers (see 2.5). In some cases we later used data obtained from Hagelgrund to enlarge the basis of our study (see Tab. 1 below).

There the first *G. nausithous* could be observed on 13 July, one day before the first male on site M. As the next observations at site M have only been made from 17 July onwards, we made some more studies at site H until that day.

**2.3. Marking.** Adult butterflies were caught at rest with our fingers. A waterproof pen was then used to write numbers on the underside of both hindwings so that the individual could be easily recognised while following it. The site in the Mooswieser Tal was visited almost daily during the flight period (see Fig. 1), and all unmarked individuals encountered were marked and previously marked specimens were recorded.

The *S. officinalis* stands of the more western meadow margins were visited less often. All newly encountered individuals were also marked and we searched for marked adults which might have emigrated from our main study site.

**2.4. Estimation of population size.** One way to quantify the size of a population is to sum the minimum number alive (MNA). As the name implies, this gives the minimum number of animals that are present in the population at one particular time. To reach that number, the number of marked individuals registered (or marked) in the particular time step (e.g. day) and the number of individuals marked before that time step and recaptured again after the time step, but not registered at the time step itself, are added. Individuals that have left the population in the meantime, as well as those which were overlooked at the time step and were not re-sighted later (because they have died, emigrated or been overlooked repeatedly) do not contribute to the MNA of a particular time step. The total number of individuals present (for a particular time step,



like one day or the whole time of a species activity, e.g. 5 weeks) must therefore be at least as high as this minimal number alive, but normally is much higher. As the number directly depends upon the mark recapture efforts invested and the size of the population, its application is more appropriate in small populations of animals with a comparatively high recapture rate, but it cannot be reliably used to compare different populations (Settele *et al.*, 2000).

In order to compare population sizes, the Jolly-Seber method might be suitable to get a first rough idea on daily as well as total population sizes (see e.g. Seber, 1982, and Pollock *et al.*, 1990, for details). For the latter one may e.g. sum up the *B*-values (i.e. the individuals added to the population between two population estimates) resulting from the Jolly-Seber model (see Settele *et al.*, 2000 for an example and further details with respect to butterflies). However, one has to keep in mind, that Jolly-Seber estimates are not very robust with respect to population size.

Table 1. Origin of additional data for the diurnal etho-chronogrammes (Figs 3, 4), which served as a basis for the computing of the age dependent etho-chronogramme (Fig. 5) (M – Mooswieser Tal (Aschbachtal), H – Hagelgrund (Eselsbachtal)).

Completed classes		Origin of data	
Age class	Period	♂ ♂	♀ ♀
0	before 10:50	♂ ♂ 1–2, before 10:50, M	♀ ♀ 1–2, before 10:50, M
	10:50–11:40	♂ ♂ 0, 10:50–11:40, M+H	♀ ♀ 0, 10:50–11:40, M+H
	11:40–12:30	♂ ♂ 0, 11:40–12:30, M+H	
	15:50–16:40	♂ ♂ 0, 15:50–16:40, M+H	
3–10	15:50–16:40		♀ ♀ 1–2, 15:50–16:40, M
	16:40–17:30		♀ ♀ 1–2, 16:40–17:30, M
	after 17:30		♀ ♀ 1–2, after 17:30, M

Strictly spoken, only for the age class 1–2 days a complete diurnal etho-chronogramme could be constructed. Thus, in some cases additional data have been used from the site Hagelgrund to construct an age dependent etho-chronogramme out of the diurnal etho-chronogramme. Data of the class 1–2 day old butterflies have been used, if still the pooled data from both sites (M and H) have not been sufficient. There have been no data of both sexes of age class 0 for the daily time before 10:50 h. Therefore data of 1–2 day old butterflies have been used. For the period 10:50 h – 11:40 h of the 0 day old butterflies of both sexes the data of M and H had to be combined to achieve enough observation time. For the males it also has been necessary to use data from H for the other age classes. For the 3–10 day old females data of 1–2 day old females have completely been taken for the last 3 time classes in order not to miss the age dependent etho-chronogramme.

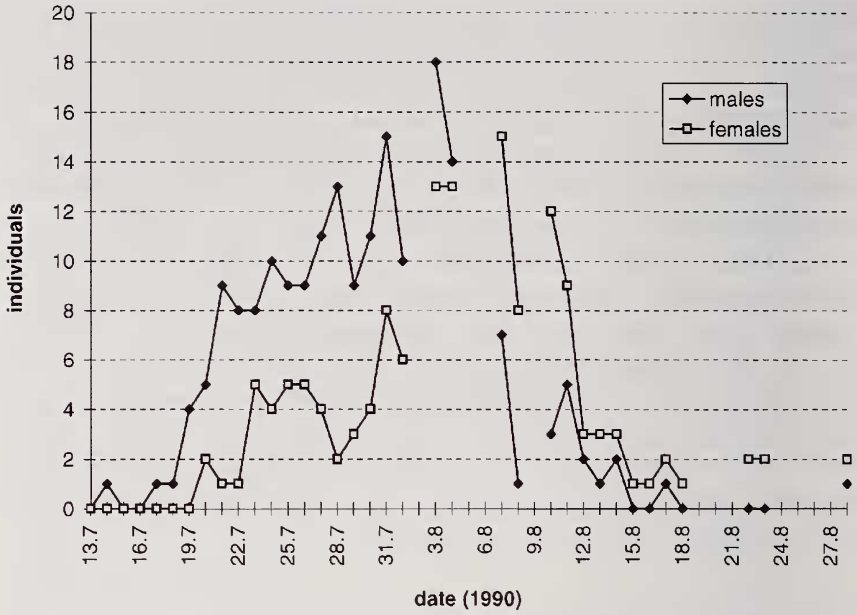
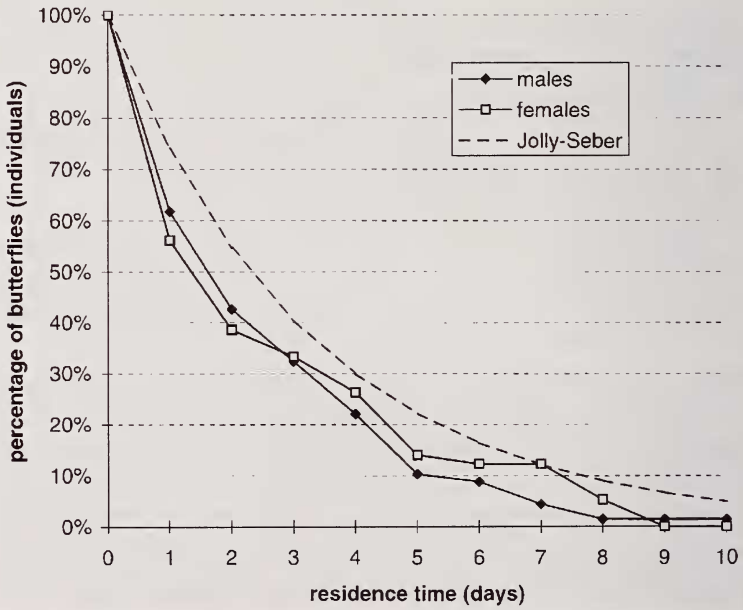


Fig. 1. Minimum daily population sizes (minimal number alive; for days without observations no entries have been made).



## 2.5. Ethological observations.

2.5.1. **Definitions.** The activities flight, moving, nectaring, oviposition, copulation, and resting were recorded separately for each individual. Registration was performed with small portable computers, using a programme especially written for our study. The observer randomly chose a butterfly and entered its number into the computer. For each activity an abbreviation, consisting of one letter, was used. At the beginning of each activity the observer pressed the relevant letter, which was saved together with the time. The duration of one activity was obtained from the difference between the start of the present activity and the start of the next one.

The activity moving consisted of diverse activities, which were registered separately in the field, but have been lumped here. These activities were: walking, turning (e.g. females turning on the flower heads to look for suitable egg laying niches), cleaning, fluttering while sitting, and the characteristic lycaenid behaviour of parallel up and down movement of the closed wings. Thus, turning when looking for a suitable egg laying niche was not counted as egg laying behaviour, as it could not be clearly separated from nectaring. A female looking for an egg laying locality and turning therefore on the flower, every once in a while is nectaring. Oviposition was defined as the time while the butterfly has put its abdominal tip between individual flowers of a flower head. Sometimes females rapidly changed between different single flowers, performing abdominal bends and touching the surface of the flower head with the abdominal tip. Each of these events was regarded as one oviposition behaviour (*sensu* Figurny & Woyciechowski, 1998).

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Fig. 2. Relative observed residence time and residence time according to the Jolly-Seber-method. There are hardly any differences between males and females. The residence probability within the population is 74% for each age, according to Jolly-Seber. This means that 74% of all individuals reside for 1 day, 55% for 2 days, ... 5% for 10 days. This exponential dependence only is valid if residence probability is age independent. As the observed number of residing individuals decreases exponentially as well, age independence can be assumed. The figure proves the intensive assessment of the population, because otherwise the Jolly-Seber-curve would be clearly above the observed values.

Nectaring was scored as the time when the butterfly put its proboscis into the flowers or when it rapidly moved from one flower to the next looking for the best nectar source.

About 150 hours of observations were registered on our portable computers, consisting of about 11,000 events.

## 2.5.2. Analysis of behavioural observations

2.5.2.1. **Procedure and classification.** The data have been analysed so that on the one hand the diurnal distribution of the single activities can be described (diurnal etho-chronogramme), and, on the other to quantify how the sexes differ in their behaviour and how behaviour changes with age (age dependent etho-chronogramme).

The data were therefore classified as follows:

- sex: male, female
- age: 0 days, 1–2 days, 3–10 days
- time intervals: 10:00–10:50, 10:50–11:40 ... 17:30–18:20
- activities: flight, moving, nectaring, egg laying, copulation, resting

The classes were kept as small as possible. Even so, the activity copulation caused problems in analysis, as there have been relatively few events lasting for relatively long time.

This procedure resulted in every day consisting of 10 classes of 50 minutes each. The total observation time within each class (i.e. the total of all single events) had a length of at least 3,000 seconds (= 50 min.). However, because few activities occurred early and late in the day, the first class summarised all results before 10:50 Central European Summer Time (= GMT or 9:20 local time), starting with the first observations at around 9:30; the last class summarised results after 17:30 (GMT), with last observations around 19:30. Most data of the first class are indeed from 10:00 – 10:50 and of the last class from 17:30 – 18:20.

Sexes were treated separately and three age classes formed (see also results) with an approximately even distribution of total observation time. This resulted in the age classes 0, 1–2, and 3–10 days.

2.5.2.2. **Diurnal Etho-Chronogrammes** (Figs 3, 4). Observation time (t) of one activity was summarised within one class (e.g.: males, age: 1–2 days; time: 10:50–11:40):



$$\sum t_{\text{flight, 1-2days, 10:50-11:40, all males}} = t_{\text{flight, 1-2days, 10:50-11:40, male 1}} + t_{\text{flight, 1-2days, 10:50-11:40, male 2}} + \dots + t_{\text{flight, 1-2days, 10:50-11:40, male n}} \quad (1)$$

Then the relative proportion ( $\tau$ ) of one activity compared to the total duration of all activities was calculated. This was done as in the following example for flight of the 1–2 day old males for the period 10:50–11:40:

$$\tau_{\text{flight, 1-2 days, 10:50-11:40, all males}} = \sum t_{\text{flight, 1-2 days, 10:50-11:40, all males}} / (\sum t_{\text{flight, 1-2 days, 10:50-11:40, all males}} + \sum t_{\text{moving, 1-2 days, 10:50-11:40, all males}} + \sum t_{\text{nectaring, 1-2 days, 10:50-11:40, all males}} + \sum t_{\text{copulation, 1-2 days, 10:50-11:40, all males}} + \sum t_{\text{resting, 1-2 days, 10:50-11:40, all males}}) \quad (2)$$

Figs 3 and 4 show the diurnal etho-chronogrammes of 1–2 day old males and females. Within the other age classes, data were insufficient to provide a complete diurnal distribution. Nevertheless, diurnal etho-chronogrammes were computed as these were needed in the age dependent etho-chronogrammes.

**2.5.2.3. Age dependent Etho-Chronogrammes** (Fig. 5). The age dependent etho-chronogrammes show how the distribution of activities changes with increasing age and how the sexes differ. Absolute values (in minutes) were calculated from the relative proportions of the time classes of the diurnal etho-chronogrammes. In other words, we calculated how long a virtual butterfly of a certain age class performed each activity during a whole day. The computation is shown for the total flight time of 1–2 day old male butterflies:

$$\sum t_{\text{flight, 1-2days, all males}} = (\tau_{\text{flight, 1-2 days, before 10:50, all males}} + \tau_{\text{flight, 1-2 days, 10:50-11:40, all males}} + \dots + \tau_{\text{flight, 1-2 days, after 17:30, all males}}) * 50 \text{ min} \quad (3)$$

In some classes the data were insufficient (observation time in the 50 minute class was less than 3,000 seconds) to reach a balanced distribution of activity. In these cases, additional data were included from a nearby locality (H – Hagelgrund, see chapter 2.2). Even so, data for the last three time classes of 3–10 day old females were still too few (see Tab. 1). Since the values for the first six time classes (10:50–15:50) of 3–10 day-old animals were very similar to those for the diurnal etho-chronogrammes of 1–2 day old insects, we assumed that the values of the three remaining classes were only slightly different from the values of 1–2 day old females. Although this is not entirely correct, for the sake of obtaining a

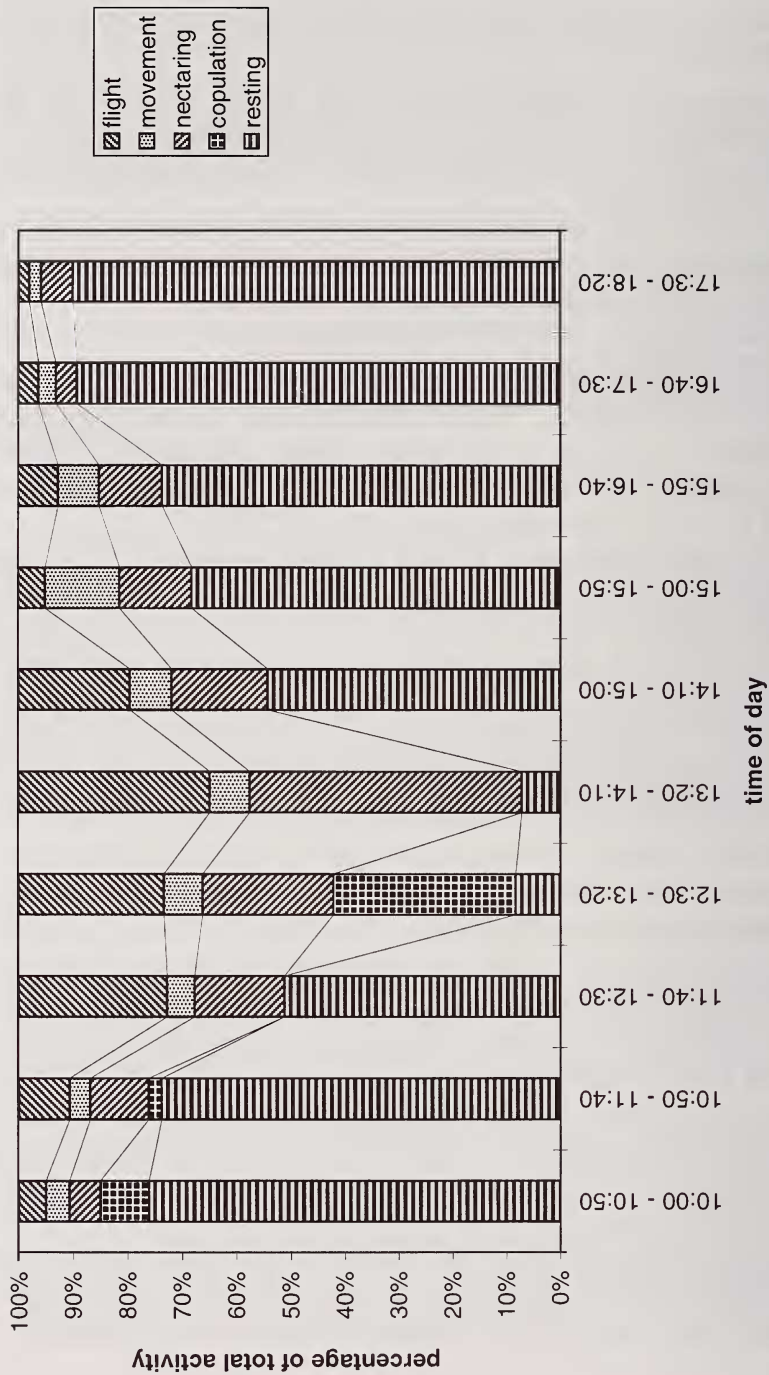


Fig. 3. Diurnal distribution of activities (diurnal etho-chronogramme) of 1-2 days old males (for computation compare chapter 2.5.1).

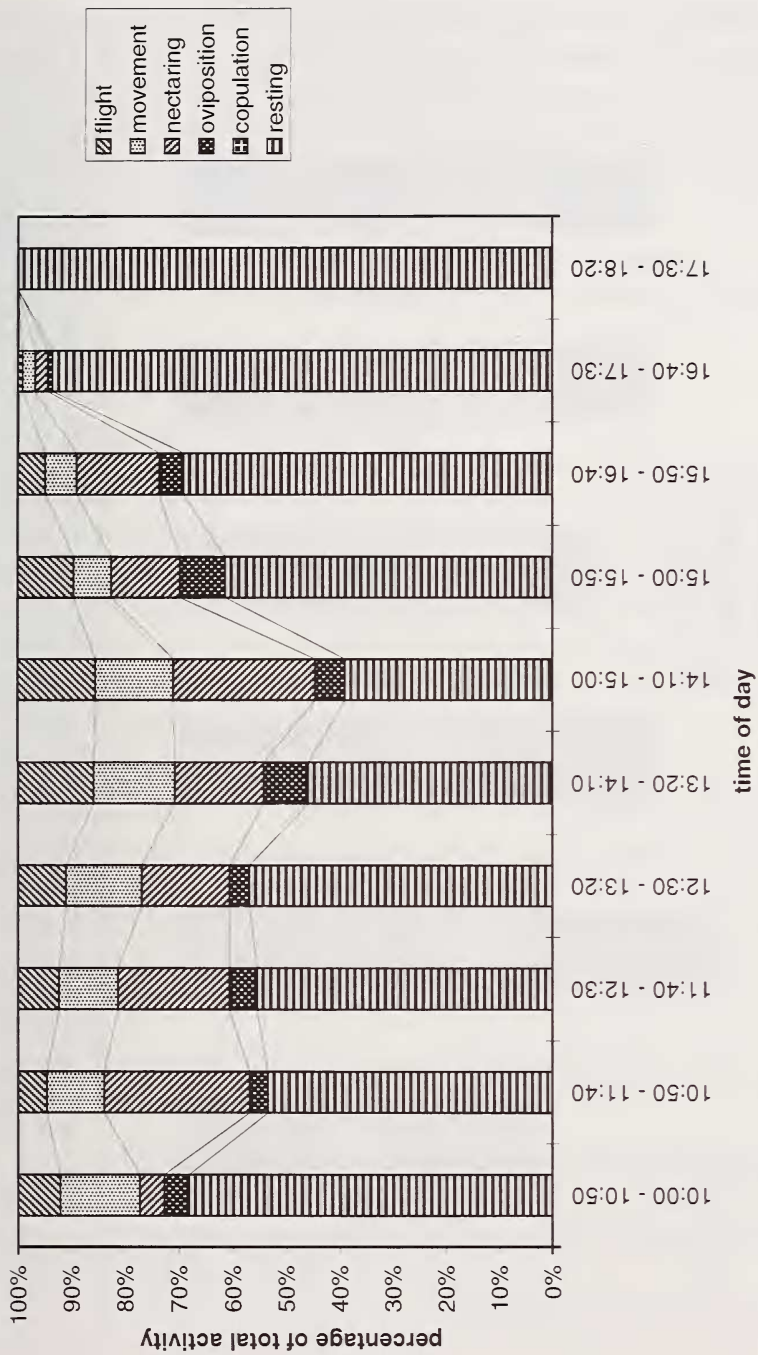


Fig. 4. Diurnal distribution of activities (diurnal etho-chronogramme) of 1-2 days old females (for computation compare chapter 2.5.1). In both sexes (Figs 3, 4), the maximum of activity of 1-2 days old individuals is around noon time.

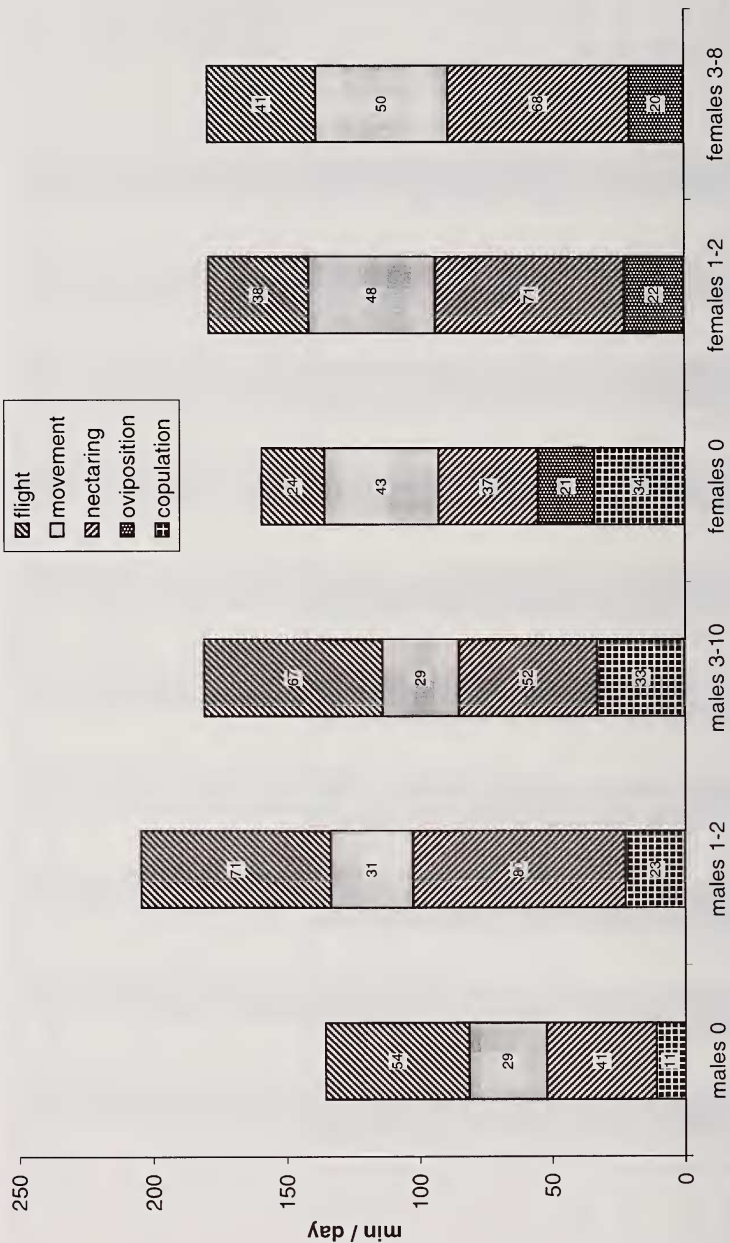


Fig. 5. Age dependent distribution of different types of activities (age dependent etho-chronogramme). 0 day old individuals are less active than older ones. Whether this is a handling effect or natural indolence is unclear. The figure shows, that both sexes are active for approx. the same time, however in different ways. Uncertainty referring to time consumed for copulation is large. Copulation events observed are only a few, which however last rather long compared to other activities. Thus, an over- or underestimation can not be excluded.



complete picture of the age dependent etho-chronogrammes we decided to include values of 1–2 day old females for computing values of 3–10 day old females. In the first class (before 10:50) of the 0 day old insects, no data were available, as the insects had just been marked. To achieve a complete picture, the values of the 1–2 day old butterflies were also used in the first time class of the 0 day old ones.

For an overview of the manipulations performed for the computation of the age dependent etho-chronogrammes see Table 1.

## 2.6. Discussion of methodology

**2.6.1. Handling and behaviour.** Morton (1984) states that handling in some butterfly species can affect recapture probability. He also mentions that different species react quite differently in this respect. However, for *G. nausithous* there is no indication for a handling effect. For example, neither Geißler-Strobel (2000) nor Binzenhöfer & Settele (2000) detected any behavioural change after handling this species; some individuals even copulated immediately after the handling and females continued to lay eggs (Binzenhöfer & Settele, 2000).

**2.6.2. Observation and behaviour.** The presence of (generally) three observers on a relatively small site might have influenced adult behaviour, especially flight activity and emigration. However, our observations suggest that the insects were not affected. We observed the butterflies from an average distance of about 2 meters, where they did not show any reaction, although one can approach as close as few decimetres without noticeably affecting behaviour. Although the *S. officinalis* plants were occasionally shaken, this was greatly outnumbered by the number of natural disturbance events e.g. by males performing courtship behaviour or by other insects.

**2.6.3. Limits of observation time due to methodological constraints.** The insects were observed for as long as possible. However, we sometimes lost track of flying adults, especially males, leading to an underestimate of this activity.

Table 2: Residence times of *G. nausithous* on the main research site (n – total number of butterflies marked)

Number of days	0	1	2	3	4	5	6	7	8	9	10
Males (n = 68)	26	13	7	7	8	1	3	2	0	0	1
Females (n = 57)	25	10	3	4	7	1	0	4	3	0	0

Table 3. Average residence time of the *Maculinea* species.

Species	Sex	Average residence time [days]	Reference
<i>Glaucopsyche (Maculinea) nausithous</i>		1.9	present paper <sup>a</sup>
<i>G. (M.) nausithous</i>	♂ <sub>1</sub> ♀ <sub>1</sub>	2.0	present paper <sup>a</sup>
<i>G. (M.) nausithous</i>		2.3	present paper <sup>b</sup>
<i>G. (M.) nausithous</i>		5.4	Geißler-Strobel (2000) <sup>c</sup>
<i>G. (M.) nausithous</i>		3.3	Geißler-Strobel (2000) <sup>c</sup>
<i>G. (M.) nausithous</i>		1.3	Laux (1995) <sup>b</sup>
<i>G. (M.) nausithous</i>		0.8	Laux (1995) <sup>b</sup>
<i>G. (M.) nausithous</i>		ca. 4	Seiler (1991) <sup>a,c</sup>
<i>G. (M.) nausithous</i>		ca. 3	Seiler (1991) <sup>a,c</sup>
<i>G. (M.) nausithous</i>		ca. 0.7–2.3	Wynhoff (1998) <sup>c,d</sup>
<i>G. (M.) teleius</i> (Bergsträsser)		♂ <sub>1</sub> ♀ <sub>1</sub>	0.7
<i>G. (M.) teleius</i>	♂ <sub>1</sub> ♀ <sub>1</sub>	ca. 0.3–2.8	Wynhoff (1998) <sup>c,d</sup>
<i>G. (M.) arion</i> (L.)	♂ <sub>1</sub> ♀ <sub>1</sub>	1.8	Pauler <i>et al.</i> (1995) <sup>a,c</sup>
<i>G. (M.) rebeli</i> (Hirschke)	♂ <sub>1</sub> ♀ <sub>1</sub>	1.8	Kockelke <i>et al.</i> (1994) <sup>a,c</sup>
<i>G. (M.) rebeli</i> (Hirschke)	♂ <sub>1</sub> ♀ <sub>1</sub>	2.5	Kockelke <i>et al.</i> (1994) <sup>a,c</sup>

<sup>a</sup> Average residence time; difference between first and last sighting.

<sup>b</sup> Average residence time based on Jolly-Seber estimates.

<sup>c</sup> The authors mention one day more, as they regard an individual at the day of first sight as one day old already. Thus the data have been corrected by –1 for this contribution, to make comparison of data possible.

<sup>d</sup> data from 1991 until 1996.

Table 4. Number of eggs laid per female per day, based on mean daily behavioural profiles.

Age class	Number of eggs laid (estimated*)
0 day	80
1–2 days	94
3–8 days	81

\* according to our estimate; we assume that in about 95% of all oviposition behaviour events eggs have really been laid (compare text).

Table 5. Average number of flights and average flight duration of 1–2 days old males and females of *Glaucopsyche nausithous* during one day of observation (10:00 to 18:20 h Central European Summer Time).

Sex	events/day/individual	duration/day/individual	duration/event
♂	161	71 min	26 sec
♀	223	38 min	10 sec

### 3. Population ecological results and their discussion

**3.1. Population dynamics.** The flight period of the population lasted from 13 July until 28 August 1990 (at the site Mooswieser Tal). Weather conditions were favourable for nearly the whole period, with the exception of two rainy days and one further day with maximum temperatures below 20°C. Thus, periods of reduced abundance were neither expected nor observed during the course of the population curve (based on the minimal number alive; see Fig. 1).

The proterandric phenology of *G. nausithous* is clearly visible in Fig. 1. For example, the date when half the males in the whole population had been observed (29 July) is clearly (5 days) earlier than the date for half the females (3 August). In *G. nausithous*, proterandry has been observed in many instances (Geißler-Strobel, 2000; Garbe, 1991; Laux, 1995) and is a common phenomenon in other butterfly species (see e.g. Wiklund & Fagerström, 1977).

Our population reached its maximum on 3 August 1990, with a minimum number (see chapter 2.4) of 18 males and 13 females (see Fig. 1). This was also the day of maximum male numbers, while that of females (with 15 individuals) occurred on 7 August. As the population curve is asymmetric (left sided), the date at which half of the total annual population appeared is earlier (29 July for males and 3 August for females, see above).

**3.2. Population size.** In total, 68 males and 57 females were marked on the main site. A further 18 males and 20 females were marked elsewhere, of which 28 butterflies were encountered near the settlement Alte Schmelz, >1.5 km away. None of these marked specimens were found entering the main site, nor was any specimen found outside after being marked on the main site.

Due to the intensive effort, nearly every adult entering the population was marked on the day it emerged. Thus, an estimate based on the daily estimates and a summation of the  $B$ -values (i.e. the individuals added to the population between two population estimates) of the Jolly-Seber model (see e.g. Seber, 1982, and Settele *et al.*, 2000) resulted in 122 specimens, three specimens less than the 125 marked individuals.

The use of this method was not ideal for this study because the small population size and short residence time of individuals resulted in few recaptures on some days. Thus, for a more thorough statistical analysis, only the central 18 days of field assessment could be used (omitting the first 5 and the last 7 days). For this period the total population size is 119, with a 90% confidence interval of  $\pm 16$  (and a MNA of 112; resulting in a population size between 112 and 135; calculation according to Settele *et al.*, 2000:181, Tab. 5.14a; but see "<http://www.ufz.de/spb/nat/settele/tagfalter.html>" for corrections).

Estimates of total population size support our notion that the population was almost completely assessed on the main site. In contrast, the number of individuals outside the main site was undoubtedly larger than the marked 38 specimens (due to low intensity of field work and thus low numbers of marked and recaptured specimens Jolly-Seber estimates can not be performed). But, as no individual among those marked outside the main site was recaptured within the site and vice versa, we assume that the number of individuals immigrating into the site must have been very low. Additionally, none of the specimens freshly marked on the site showed obvious signs of extensive previous flight activity (like loss of scales or fringed wing margins), which would have suggested it was an immigrant.

**3.3. Dispersal and isolation of the population.** Our assumption of low emigration and immigration is consistent with the statements of low mobility of the species by Bink (1992) or Weidemann (1995). New studies however reveal that it is much less sedentary (Settele *et al.*, 1996). The longest dispersal distance observed so far is 5100 m (Binzenhöfer & Settele, 2000). Detailed studies on the species' mobility (e.g. Geißler & Settele, 1990; Binzenhöfer & Settele, 2000) have mainly been performed in landscapes with numerous local populations and rather large habitat patches. There-



fore these distances might be due to mobility within habitats or between habitats, using stepping stones (e.g. singular *Sanguisorba* stands) in the latter case. The low density of habitats in the study region and the isolated situation of the study site (due to a large portion of surrounding forests) makes it less probable, that butterflies immigrate from other populations in large numbers. As in the study of Laux (1995), high recapture rates indicate comparatively sedentary behaviour in these types of environments. Some emigration as well as immigration can of course never be excluded.

**3.4. Residence time.** It follows from 3.3 that the vast majority of butterflies must have hatched from the site itself. We can also be confident that the majority of animals has been marked on the day of hatching, so their date of eclosion is known. Consequently, it was generally possible to identify the exact age of a butterfly at each activity or recapture.

The average residence time was estimated based on Jolly-Seber (Seber, 1982; Pollock *et al.*, 1990) estimates of the population size and residence rate ( $\varphi$ ). The average residence rate equals  $-(\ln\varphi)^{-1}$  and resulted in a value of 0.74, which is a weighted average (with respect to the daily populations size), covering the whole flight period. Because of the small population size, both sexes were combined, which does not introduce bias so long as both sexes have similar recapture rates, as here (61.8% for males, 56.1% for females; compare Tab. 2, which also gives an indication for the frequency of capture as assessment was made nearly every day and the z-values for the Jolly-Seber-estimate are mostly 0).

The residence time of the different age classes (in days) can thus be expressed as function  $f(\text{age}) = 0.74^{\text{age}}$  (Fig. 2). The average residence time is the average time one individual spends in the population or the time when the population is reduced by 50%, i.e.  $f(\text{age}) = 0.5$ . In our case, the average residence time was 2.3 days, which is only slightly higher than the average value resulting from the difference between the day of marking and the day of last observation of all butterflies (2.0; compare Fig. 2 and Tabs 2, 3). This is a function of the comprehensiveness of our observations.

As our population has both been studied intensively and experienced low losses due to emigration, we can regard the average residence time as a good approximation of the average life time. If we

additionally regard the average residence times of other authors (see Tab. 3), we can state that the longevity of adult *G. nausithous* is rather short compared to other butterfly species (compare e.g. Scott, 1973). Looking at other *Maculinea* species (Tab. 3), this seems to be typical for the whole taxon (but not exclusive, as shown for many other temperate-zone Lycaenidae: Väisänen *et al.*, 1994; Arnold, 1983; Warren 1992).

The observed age independent survival probability of the species also indicates that the butterflies reach their potential physiological age only in few exceptional cases, as in all free living organisms. On our study site we had 6 cases of spider casualties (web or crab spiders). 2 butterflies were killed by cars on a nearby road. One specimen just died and dropped off a *Sanguisorba* stem for no obvious reason. Despite our intensive study, we thus know the reasons for the death of only 8 out of 125 marked specimens. We only can assume the high activity of potential predators (high densities of damselflies, dragonflies and birds along the nearby creek; further spiders with undiscovered prey, or nocturnal predators).

**3.5. Availability of *Sanguisorba* flower heads as nectar sources.** The number of flower heads was partly counted. Stands with counted flower heads were used to estimate further *Sanguisorba* stands by eye. The number of heads increased from ca. 400 in the early flight days to ca. 1600 towards the end of the emergence. The number of flower heads must have been sufficient throughout the flight period, as it probably has only to provide the carbohydrates needed for flight, as is the case with most short lived butterflies, which normally acquire the resources needed to develop eggs during the earlier larval stage (capital reserves, compare Sibly & Calow, 1984, 1986).

**3.6. Availability of oviposition sites and emigration.** Eggs are exclusively laid on *Sanguisorba officinalis*. As shown by Thomas (1984) and intensively studied by Figurny & Woyciechowski (1998), closed or only slightly opened flower heads are preferred. Nearly all flower heads on the study site were in the preferred stage. The total number of flower heads then steadily increased, reaching a maximum of about 1600 towards the end of the flight period, although the number of closed or only slightly opened ones was lower than in the beginning.

Based on our behaviour data (see below) we tried to estimate the average number of eggs laid per female per day. Laux (1995) stated, that in *G. nausithous* only an egg laying behaviour that lasts at least 3 seconds results in an egg being laid. In most cases she registered one egg per egg laying event. In our study, in 95% of all cases, egg laying behaviour lasted at least 3 seconds. In fact, only in 22 of 53 egg laying events (42%) observed by Laux (1995) were eggs actually laid. However, we were unaware of this observation when we collected our data, nor did we interrupt the time registration when a female quickly inserted her abdomen between single flowers, which led to the high value of 95%. On the other hand, this presumed overestimate will be compensated for, as several egg laying behaviours sensu Laux (1995) have been regarded as only one. This has to be kept in mind when interpreting the following rough estimates of eggs laid.

(Precise empirical data on egg production and its dynamics are lacking for all *Maculinea* species. Such data are urgently needed in order to evaluate the usefulness of published estimates, like in Bink (1992), as well as for parameterizing models.)

According to our estimates, just under 10,000 eggs were laid on our study site (assuming 60 females with an average life expectancy of 2 days and an egg production of 85 per day; see Tab. 4). The number of *Sanguisorba* flower heads was around 1600 at the end of the flight period, many of which were not available during the peak of population density at the main flight period. Other flower heads never reached the size necessary for *G. nausithous* females to lay eggs on (according to Figurny & Woyciechowski, 1998, the flower head has to have a length of at least about 6.5 mm). If we assume that about three quarters of all heads were used for oviposition, we would have 1200 flower heads used. This would give an average of 8 eggs per flower head. This is of the same order of density reported by Fiedler (1990), who found an average of 7.65 eggs per head in habitats with high density of butterflies but relatively few *Sanguisorba* plants (with a maximum of more than 20 per head).

Fiedler (1990) found that more than 3 larvae seldom survived in one flower head. Larger numbers of eggs per flower head thus have low survival probability, which means that the number of egg-lay-

ing possibilities may limit population size. *G. nausithous*, according to Figurny & Woyciechowski (1998), does not seem to be able to recognise whether a flower head already contains eggs. Hence, the increased tendency for dispersal within the second half of the flight period, which was observed by Garbe (1991), may be stimulated by decreasing number of flower heads available in a suitable stage. As in our study, the number of preferred non-flowering flower heads (compare Figurny & Woyciechowski, 1998) was (even absolutely, not only relatively) decreasing towards the end of the phenology, in spite of an increasing total number of flower heads, we could also imagine such effects to be of relevance for our population. However, due to the small number of marked butterflies, we have no proof for differences in residence times during the phenology of the species. This merits further study.

#### 4. Results and discussion of behavioural observations

4.1. **Preconditions for the interpretation of behavioural observations.** As the population results show, most adults were marked on the day of hatching. Thus we could identify the age of the butterfly at a later recapture. We considered that there was no lack of food, resting sites or similar resources. We assume that the flower heads often receive more eggs than they can support, as the females cannot identify whether a head is already occupied. Thus the behaviour of the adults would not have been affected.

4.2. **Handling.** Our results show that <1 day-old individuals are less active than older ones (Fig. 5). For the age class 3–10 days (diagrams not shown) the diurnal etho-chronogrammes for both sexes are very similar to those of the 1–2 days old adults (Figs 3, 4). In contrast, the results for age class 0 (diagrams not shown) are very variable and show no clear maximum of activity around noon. As stated, Binzenhöfer & Settele (2000) found no handling effect for this species (see 2.6.1). Our data show that insects are less active on the day of marking than on other days. This might be explained as natural for the species or as a handling artefact. However, as males and females have been affected in a very similar way, we regard the comparisons between both sexes as justified.

4.3. **Copulation and oviposition.** For the 1–2 day-old males, the diurnal distribution of activities is strongly influenced by the



occurrence of copulations (see Fig. 3). Although we observed only 2 copulations, these have a strong influence because of their long duration. The females of this age class normally had no copulations (Fig. 4). In total, three copulations were observed for their entire length, which lasted between 24 and 34 minutes.

If observations from Eselsbachtal are included, we know the age of 12 females and 10 males of a total of 13 copulating couples. Females probably copulate only once, in all but one observed case on the day of emergence. Of the 13 copulations, 11 were in the morning or early afternoon (until ca. 14:30 h). Only twice was copulation observed after 17:00 h. These results indicate that females copulate as early as possible. Only in one female at Eselsbachtal was copulation observed on the next morning after the day of marking (but then earlier than all other copulations with newly hatched females; at 10:27 h, when the couple was sighted, copulation was already going on).

The 10 males of known age at copulation were up to 7 days old. The sexual activity of males seems to last for their whole lifetime. Two of the males were observed copulating twice. According to SBN (1991), older *Maculinea* males are more often involved in copulations than younger ones, which also fits to the observed lower activity of 0 day adults in our study. And if males mate less often when they are young, it would not be surprising as they first have to reach sexual maturity (sclerotization of genitalia, maturation of testes), which may take longer in males of protandrous species (own unpubl. data; Fiedler, pers. comm.).

In one case, egg laying behaviour was observed as soon as 17 seconds after the end of copulation, although we did not see whether an egg was actually laid. In a second case, a female did not lay for 35 minutes, and was then lost from sight; however, after 1 hour and 44 minutes, the same female was resighted laying eggs. The copulation of females immediately after eclosion and mating may be seen as consequence of their short residence time. Before leaving the population (due to death or emigration) they leave as many eggs as possible in their habitat of origin. According to Fiedler (pers. comm.) this has to be regarded as a remarkable exception from all other Polyommatae lycaenids, where noticeable egg production starts about 1–2 days after mating and reaches its peak another 1–2 days later.

4.4. **Flight.** Flight in both sexes peaked shortly after 12:00 h local time (i.e. 13:30 h central European summer time) when the sun was already in its highest position, but temperature had not yet reached its maximum (compare Figs 3 and 4). Diurnal changes in activities were more pronounced in males (Fig. 3) than in females (Fig. 4). In the males they are clearly paralleled with the time spent for nectaring, while in females the times are similar but less clear. During a whole day, males fly twice as long as females (Fig. 5), although there has been an underestimation in the latter (compare 2.6.3). The number of flights per day however is greater in females (Tab. 5), resulting in a much lower duration per flight. Thus, within the habitat females mainly undertake very short flights (i.e. from one flower head or plant to the next in search for oviposition sites). In both sexes, some flights serve to reach nectar sources. Females also fly to reach egg laying sites. Potential nectar and egg laying plants can normally be reached in very short distances. Males repeatedly undertake longer flights searching for females. The more a male flies, the higher his probability of finding an unmated female. On each male there is selection to be more active in flying and thus more successful in finding unmated females than other competing males. Thus, we can expect a higher reproductive success in more actively flying males, which explains the observed differences in sexes in terms of flight.

In some butterfly species there are temperature-dependent differences in male searching behaviour for females, which might indirectly lead to a diurnal switch. In *Coenonympha pamphilus* (L.), for example, Wickman (1985) observed that males tend to perch within their territories at lower temperatures, while at higher temperatures they patrol. Also in *G. nausithous* males, the greatest flight activity is around noon, but temperature dependent change in behaviour (e.g. from patrolling to perching) was neither observed nor expected. As females copulate directly after eclosion and are not active flyers, it would represent a poor strategy for males to perch rather than patrol and actively seek newly eclosed females (see Rutowski, 1991, for a review on male mate-locating behaviour).

Because they patrol and mate with freshly emerged females, males have to stay within their habitat to reproduce successfully

rather than undertake long distance flights. The latter risk does not exist for females, which makes them more suitable agents for the (genetic) exchange between populations and the colonisation of new habitats (independent of the numbers of males which also leave the habitat). This fits to the observed higher flight distance of females and the observations that females have, perhaps temporarily, left the site more often than males.

Dispersal of males from one habitat to another, as observed by Binzenhöfer & Settele (2000) and Geißler-Strobel (2000) cannot be disregarded. Its relevance depends much on the distance between habitats or the degree of isolation of the original habitat. Nearby habitats might be reached so easily that individuals might be regarded as belonging to the same population (compare discussions of gradual changes from subpopulations to proper populations and finally metapopulations; e.g. Hanski 1999, Settele 1998). In such cases, male dispersal is expected.

**4.5. Movement and nectaring.** Nectaring is strongly associated with flight, especially in males (Fig. 3). Females of all age classes show more pronounced movement on flower heads than males (Figs 3, 4, 5), as females have to move for nectaring as well as between each egg laying event. In females, nectaring and egg laying may be combined as both activities often happen within a short time on the same flower head. Males and females both spend less time nectaring on the day of eclosion than when older (Fig. 5). The strong decline in nectaring of 3–10 days old males is probably due to the strong influence of the few but long lasting copulation events. Most probably in males and females, nectaring has the same duration, as e.g. also observed for *Anthocharis cardamines* (L.) by Wiklund & Åhrberg (1978).

As shown in Fig. 5, both sexes are active for the same period of time, although the type of activity is very different: males spend more time on long patrolling flights while females invest more time visiting flower heads and egg laying. It can be assumed that time of activity is temperature limited. However, the butterflies often rest around noon (Figs 3, 4), presumably to recover or to avoid overheating.

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