

Habitat utilization and behaviour of adult *Parnassius mnemosyne* (Lepidoptera: Papilionidae) in the Litovelské Pomoraví, Czech Republic

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Summary. Within-habitat distribution and diurnal behaviour of adults of the Clouded Apollo (*Parnassius mnemosyne*) were studied in the Litovelské Pomoraví, Moravia, Czech Republic. Data were collected by censuses along a regular transect route, which crossed three clearings in a mature deciduous forest. A loglinear model was constructed in order to explain variability in collected behavioural data. Hour of observation, Transect section, Behaviour, Sex and the interactions among factors Transect section-Behaviour and Sex-Behaviour significantly influenced the number of butterflies seen. More males compared to females were seen, both sexes markedly prevailed at the clearings, they hardly ever entered the high forest. Mating, oviposition and late afternoon basking-resting were all also restricted to the clearings. These findings further highlight the importance of sunny forest gaps for conservation of the species in Central Europe. There was no distinct diurnal pattern in behaviour, except for the fact that males patrolled for most of day-time, but predominantly basked in early mornings and late afternoons. Females behaved much more cryptically, they spent their time by nectaring (more so than males) and laying eggs. The lack of distinct diurnal patterns in behaviour is tentatively explained by high-altitude origin of the species.

Zusammenfassung. Das Vorkommen adulter Tiere des Schwarzen Apollos (*Parnassius mnemosyne*) innerhalb ihres Lebensraumes sowie deren tageszeitliche Verhaltensmuster wurde im mährischen Gebiet Litovelské Pomoraví in der Tschechische Republik untersucht. Die Datenerfassung erfolgte entlang eines Transekts, welcher drei Lichtungen in einem alten Laubwald kreuzte. Ein logarithmisch-lineares Modell wurde entwickelt, um die Variation der gesammelten Verhaltensdaten zu veranschaulichen. Die Stunde der Beobachtung, Transektbereich, Verhalten, Geschlecht sowie die Interaktionen zwischen Transektbereich-Verhalten und Geschlecht-Verhalten beeinflussten die Anzahl der gesichteten Falter signifikant. Es wurden mehr Männchen als Weibchen beobachtet; beide Geschlechter waren vorherrschend auf den Lichtungen und flogen kaum in den Hochwald. Kopulation, Eiablage und die spät-nachmittägliche Sonnenbad-Ruhe waren ebenfalls auf die Lichtungen beschränkt. Diese Ergebnisse machen die Bedeutung sonniger Waldlichtungen für die Erhaltung der Art in Mitteleuropa deutlich. Es gab keine unterschiedlichen Verhaltensmuster am Tage, mit Ausnahme der Tatsache, daß die Männchen die meiste Zeit des Tages mit dem Patrouillieren verbrachten und sich vorwiegend am frühen Morgen sowie am späten Nachmittag sonnten. Die Weibchen verhalten sich deutlich kryptischer, verbringen mehr Zeit beim Nektarsaugen und natürlich mit der Eiablage. Das Fehlen eines ausgeprägten Verhaltensmusters im Tagesverlauf wird mit einem stammesgeschichtlichen Ursprung der Art in hohen Berglagen erklärt.

Resumé. La répartition dans l'habitat et le comportement diurne des adultes du Semi-apollo (*Parnassius mnemosyne* (Linnaeus, 1758)) ont été étudiés dans le Litovelské Pomoraví, République tchèque. Les données ont été collectées lors de parcours réguliers sur une voie qui croise trois éclaircies dans une forêt déciduée mature. Un modèle loglinéaire a été établi pour expliquer la variabilité des données sur le comportement. L'heure d'observation, la section du transect le comportement, le sexe et les interactions de facteurs telles que transect-comportement et sexe-comportement, influen-

cent significativement le nombre de papillons observés. Il y avait plus de mâles observés que de femelles, les deux sexes se rencontrant principalement dans les clairières et pénétrant difficilement dans les sous-bois forestiers denses. Les phases d'accouplement, de ponte et de repos de fin d'après-midi étaient limitées exclusivement aux clairières. Ces résultats confortent l'importance primordiale d'espaces ensoleillés en forêt pour la conservation de l'espèce en Europe centrale. Il n'y a pas de partition journalière distincte du comportement, hormis le fait que les mâles patrouillent presque toute la journée et se reposent principalement tôt le matin ou en fin d'après-midi. Les femelles ont un comportement encore plus cryptique, passent l'essentiel de leur temps à s'alimenter (plus que les mâles) et à pondre. L'absence de partition journalière comportementale pourrait s'expliquer par l'origine de haute altitude de cette espèce.

Key words. *Parnassius mnemosyne*, butterfly conservation, diurnal behaviour, mate locating, copulation, sphragis, forest Lepidoptera.

Introduction

The endangered Clouded Apollo, *Parnassius mnemosyne* (Linnaeus, 1758) is a forest-dwelling butterfly in western part of its range (i.e. north-western and central Europe). Its larvae feed on *Corydalis* plants in early spring. At its localities, it forms relatively sedentary populations with limited adult dispersal (Väisänen & Somerhaugen 1985; Napolitano *et al.* 1988; Aagaard & Hanssen 1992; Kudrna & Seufert 1991; Konvička & Kuras 1999; Megléc *et al.* 1999). Genetic separation was documented for populations separated by about 10 km of non-hospitable habitats (Descimon & Napolitano 1993; Napolitano & Descimon 1994; Megléc *et al.* 1997b; Megléc *et al.* 1998). It was also suggested that the species persists at its localities via metapopulation dynamics (Konvička & Kuras 1999; Megléc *et al.* 1999). From the studies cited, conclusions regarding causes of vulnerability and implications for conservation of *P. mnemosyne* in North-western and Central Europe emerged. In the area of interest, the butterfly inhabits structured habitats that consist of deciduous forests interspersed with clearings, glades and forest meadows. The cited authors agree that (1) smaller clearings are preferable to large-sized clear-cuts and (2) with regard to conservation management, it is recommended to generate new clearings concurrently with the succession on old habitat patches. Despite indisputable importance of such information for conservation management, only a few of the studies cited above (e.g. Kudrna & Seufert 1991) provide evidence for the dependency of *P. mnemosyne* on sunny patches and gaps. Particularly, there are contradictory information, even from geographically close areas, regarding location of oviposition sites of females (i.e. larval habitats) and microhabitat distribution of adults. Megléc *et al.* (1999), who studied *P. mnemosyne* in NE Hungary, stated, that „females lay their eggs in the forests near clearings“, while Kudrna & Seufert (1991) and Konvička & Kuras (1999) (working, respectively, in the Rhön Mts., Bavaria and in the Litovelské Pomoraví, Czech Republic) observed that majority of egg-laying occurred at forest clearings. However, no study to date aimed specifically on deducing patterns of *P. mnemosyne* adult habitat utilisation. Here, we investigate within-habitat distribution of *P. mnemosyne* adults, as well as changes of adult distribution and behaviour during day time. We basically asked, which sections of their habitats do adult butterflies frequent and what do they do there.

Material and methods

This study was performed in the Litovelské Pomoraví Protected Landscape Area, Moravia, Czech Republic (49°40'N and 16°55'E). The area is a Moravian stronghold of *P. mnemosyne* (Kuras *et al.* in press). There are several distinct colonies of the butterfly, which are interconnected by imaginal dispersal. Prior to this study in 1996, the total adult population size was estimated, using mark-release-recapture methods, to exceed 1000 individuals (Konvička & Kuras 1999) and did not change abruptly ever since (unpublished). The colonies are largely confined to commercial clearings within mesophilous deciduous forests, which grow on mild hills of the Třesínský Práh Ridge (left bank of the Morava River). The fieldwork was carried out at southern slopes the Mlýnský Vrch Hill (370 m); the study site is inhabited by the largest of the local colonies.

In May 1999, we delimited a regular transect route across the colony site. The route, which was 800 m long, was divided into 5 sections, which were clearly differentiated by vegetation. The sections were as follows: A – Clearing 7 years old, reforested by oak and ash saplings, dense shrub layer consisting mainly of *Rubus* spp. and *Sambucus* spp. B – Sparse and light deciduous forest (oak, hornbeam and basswood) about 100 years old. C – Clearing 3 years old, previously oak and spruce forest, now reforested with oak. D – Mature (80 years) forest consisting of oak, beech and hornbeam, relatively dense and shady. E – Glade, about 10 meters wide which separated a clearing about 12 years old from dense oak-hornbeam forest. The adjoining clearing was reforested by oak and ash (with dense *Rubus* and *Sambucus* shrub layer), the forest was as in subsite D.

We walked the transect on May 17, 19, 20, 23, 24 and 25, 1999, attempting – if weather permitted – to cover entire days, i.e. from 9 AM till 18 PM (Central European summer time). We restricted our observations to one week only, since *P. mnemosyne* is a protandrous species (cf. Ebert & Rennwald 1991), and temporal changes in sex ratio might seriously affect a behavioural pattern observed. For each encountered butterfly, we recorded respective transect section, sex and behaviour. For recording of behaviour, we recognised the following categories: “Flight-Patrolling” (if males, the mate-locating activity as defined in Scott (1974); if females, any rather straight searching flight); “Nectaring”; “Basking/Resting”; “Copulation”; “Oviposition” (any of the specific sequence of behaviours described in Konvička and Kuras 1999); and “Chasing”.

To study the relationships among discrete variables we used log-linear models (LLM) for multidimensional contingency tables (Zar 1996). LLM may be used to analyse surveys, which have complex (multi-way) interrelationships among the variables. We used the program NCSS 6.0.22 (© Jerry Hintze 1997) with default options. The first step in LLM is to find an appropriate model of the data. Hierarchical models are a particular class of models in which no interaction term is specified unless all subset combinations of that term are also in the model. We employed the step-down selection procedure, which begins with the full, saturated model and searches for a model with fewer terms that still fits well. The program uses a backward elimination selection technique. This procedure works as follows. First, a significance level (here: $\alpha = 0.05$) is chosen for the goodness of fit test to signal if a model does not fit the data more severely than just by

random effects. Next, each of the highest-order hierarchical terms is removed, being replaced with appropriate terms so that the resulting expanded model differs only by the term of interest. The G^2 values of the original model and the subset model are then subtracted so that the term may be tested individually. The model with the largest significance probability is chosen for the next step. The procedure terminates when no sub-model can be found with a probability greater than alpha (Hintze 1995). In the model constructed, the number of butterflies seen was the frequency variable, while Behaviour, Hour, Sex and Transect section were factor variables. Since lengths of transect sections were unequal, we standardised all our observations on unified transects lengths before analysis. To avoid empty cells in the data matrix, we did not consider day of observation when constructing the model (not all combinations of date-hour were present in the data). Since zero counts are not permitted in computation of LLM, we added small delta values ($\Delta' = 0.1$) to each cell count. Although the use of LLM requires few basic assumptions, there is the problem of pseudoreplication in our data set. We repeated walks on identical transect multiple times a day and this over six days of observation and thus, in practice, observations are not fully independent from each other which limits the interpretation of the model.

Results

During the 1999 season, we walked 111 transects and obtained 2110 individual observations of *P. mnemosyne* (Table 1). However, the later number does not refer to individual butterflies but to observations, and many of the individuals were most probably seen several times. Males were observed more frequently than females, there were 7.2 times more records of males than females (deviation from 1:1 sex ratio, $\chi^2_{1df}=702$, $p < 0.001$). Also, observations of males markedly prevailed when evaluated on per-transect basis (Wilcoxon's Matched pairs test, $n=111$, $Z=9.10$, $p < 0.001$). There was no significant shift in ratio of observed sexes in consecutive days (logit regression of numbers of observations of males vs females against consecutive days, $\chi^2_{1df}=0.08$, $p=0.78$). This suggests that changes in sex ratio with duration of flight season should not influence the patterns described below.

The individual transect sections differed significantly in numbers of butterflies recorded (Friedman's nonparametric ANOVA, males: $Q^2_{4df}=295.76$, $p < 0.001$; females: $Q^2_{4df}=142.72$, $p < 0.001$) (Fig. 1). Both sexes were mainly encountered on clearings, especially on the clearings C and E, less so on the clearing A. Very few animals were observed to fly under the closed-canopy forest (sections B and D). In fact, the prevalence of butterflies on clearings was even stronger, since the section D was longer than the sections A, B and C (Fig. 2).

Butterflies were on the wing since about 9 AM, the first (basking) individuals were seen at 8:30 AM. Earlier in the morning, the vegetation was covered by dew and most of the clearings were shaded. At about 5 PM, there was a sharp drop in flying-patrolling activity and a corresponding increase in the proportion of basking-resting individuals (Fig. 3). The last butterflies, resting in lower layers of grassy vegetation, were seen shortly after 6 PM. Besides the late-afternoon drop in number of butterflies, there was a

Tab. 1. Descriptive statistics of observations of *Parnassius mnemosyne* individuals along the fixed transect route.

	Total no. of observations	Mean per transect	SE	Range
Both sexes	2110	19.0	0.72	5–54
Males	1852	16.7	0.66	4–50
Females	258	2.3	0.21	0–16

decrease in numbers of observed individuals along noon time contrasting with two “peaks”, which occurred earlier and later (see the numbers above bars in Fig. 3).

For most of days, the males actively patrolled over the clearings. During this mate-locating activity, they frequently chased each other (152 cases of chasing seen). 15 chases with females and 2 chases with other butterfly species (*Pieris napi*) were recorded. Besides of this, males occasionally investigated other light-coloured objects, such as whitish undersides of blackberry leaves (16 cases), or notebooks of observers (7 cases). Attempts to mate with non-receptive (sphragis-bearing) females were frequent (17 cases observed). The male typically approached a basking or resting female, who either ignored his attempt or responded by closing her wings. After a short time (about 10 seconds) the male typically gave up and flew away. No distinct escape reactions of females were seen.

We observed copulation from the beginning in 3 pairs. In addition to this, we observed 4 beginnings of copulations (and 7 mating pairs) in 1996. The three 1999 copulations started at 12:30, 12:30 and 14:40. Males approached virgin females shortly after their emergence: in 1996, two of the recorded 11 copulations started before females’ wings dried. The males “raped” the females in a very short time, ranging from 5 to 15 seconds. While in copula, the pairs slowly crawled over the vegetation, the actively moving sex was always the female. The pairs remained in copula for several hours: the three matings that we observed to the end (one of them in 1996) lasted 110, 170 and 200 minutes. The extended copulation in *Parnassiiinae* is necessary for sphragis formation (Petersen 1928; Scott 1973; Matsumoto 1987); in 2 pairs observed in 1999, the sphragis was well-formed 90–100 minutes after beginning of the copulation. After termination of the mating acts, both sexes basked for a while near the places where they mated.

Besides the females encountered during copulation, we observed only 3 virgin females. Two of them (freshly emerged) were seen in morning hours, the third was basking at 4:45 PM. It was of interest that several males flew nearby the „afternoon“ virgin without paying attention to her.

With regard to utilisation of nectar plants, we recorded 216 nectaring visits on 6 species of flowering plants. Females were seen nectaring more often than males: 19.8% of all observations of females occurred on nectar plants, while in males it was 9.2% ($\chi^2_{1df}=21.42$, $p<0.001$). Numbers of nectaring records of per individual plant species, split according to sexes (males/females), were as follows: *Melandryum rubrum* (92/24), *Rubus* spp. (29/14), *Stellaria holostea* (24/2), *Myosotis nemorosa* (12/6), *Fragaria vesca* (7/1) and *Veronica chamaedrys* (3/2). The sexes did not differ in frequencies of

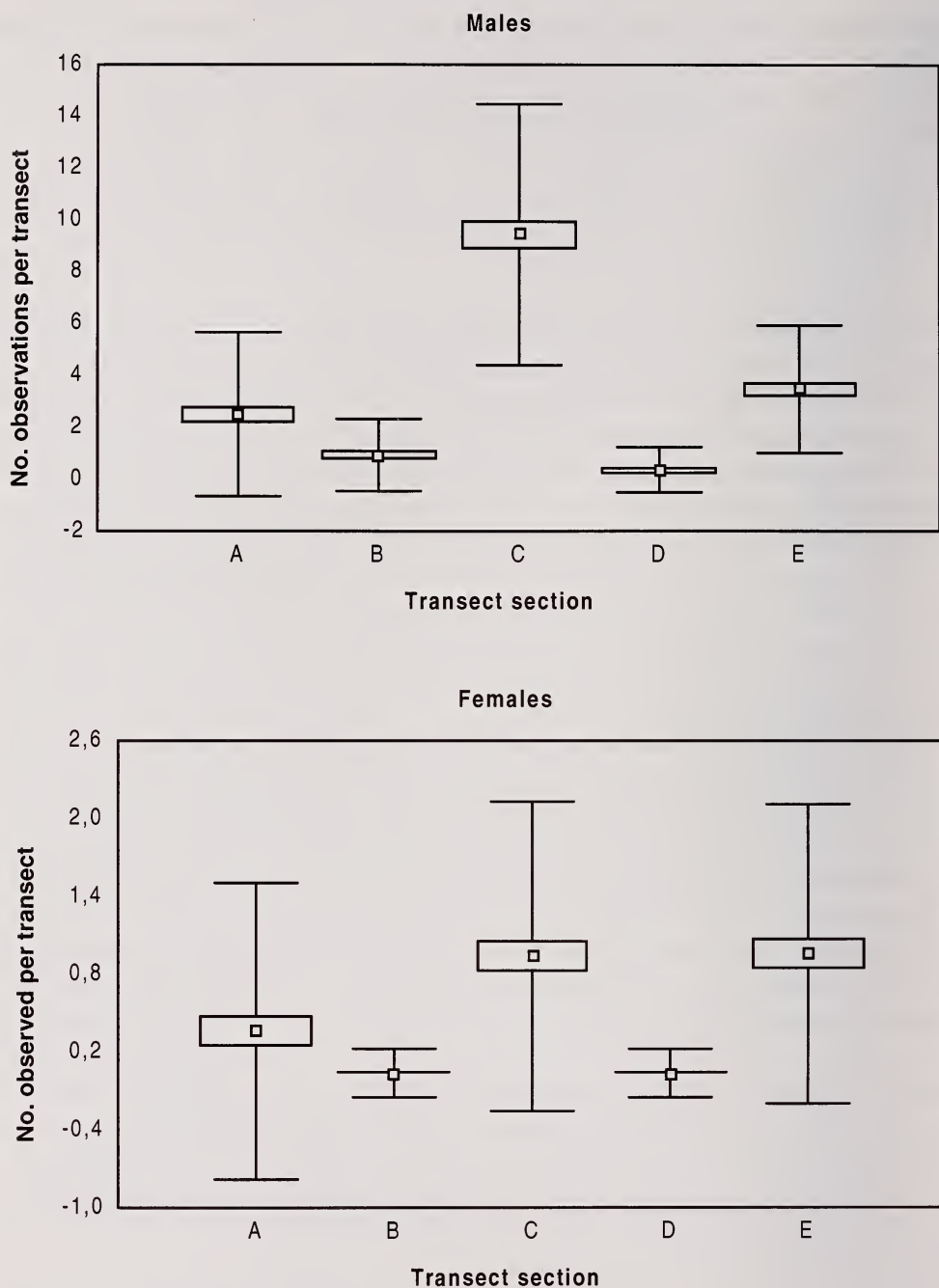


Fig. 1. Plot showing mean, standard deviation and standard error of numbers of *P. mnemosyne* males females seen on individual transect sections. The sections A, C, E were clearings, the sections B and D crossed high forest.

visits on individual plants (maximum likelihood $\chi^2_{1df}=8.99$, $p=0.11$). The nectar plant records in 1999 were necessarily limited to the species which flowered along the transect. In 1996 (cf. Konvička & Kuras 1999), we recorded utilisation of several other nectar plants, namely *Ajuga reptans*, *Alliaria officinalis*, *Ranunculus repens*, *Lychnis flos-cuculi*, *Knautia arvensis*, *Symphytum officinale* and *Taraxacum* spp.

Table 2 summarises all terms (factors and interactions among factors) that were considered in the construction of the loglinear model. The step-down hierarchical model selection procedure selected the 34th model in order of decreasing complexity. Test for goodness of fit revealed good fit with the data (likelihood ratio $G^2_{496df}=470.86$, $p=0.76$; Pearson's $\chi^2_{496df}=543.96$, $p=0.07$). The factors that were included into the model thus sufficiently explained a substantial portion of variability in recorded data. The included factors were Hour, Transect section, Behaviour, and Sex; plus the two combinations of factors "Transect section – Behaviour", and "Behaviour – Sex".

The significant result for the two-factor term "Behaviour – Sex" is rather obvious, given, e.g., the nearly constant patrolling of males, or the fact that a high proportion of observed females were laying eggs (Fig. 2, 3). The significant influence of the interaction Behaviour – Transect section was most likely due to the uniform behaviour of the butterflies that were seen in closed forest (sections B and D), where virtually all the butterflies encountered were just flying as opposed to relatively diverse behaviours observed on clearings (Fig. 2). On the other hand, it was surprising that the interaction Behaviour-Hour was excluded from the final model, although the interaction was nomi-

Tab. 2. Summary of single-term tests of all terms (e.g. factors and combinations of factors) which were considered in construction of loglinear model explaining variability in observational records of *Parnassius mnemosyne* along a fixed transect route. The terms not included in the final model are given in *italics*. Partial G^2 statistic tests whether the term is significant after considering all other terms of the same order. The marginal-association G^2 tests whether the term is significant ignoring all other terms of the same order.

Term	d.f.	Partial G^2	P	Marginal G^2	P
Hour [A]	8	591.82	0.0000	591.82	0.0000
Transect section [B]	4	1752.71	0.0000	1752.71	0.0000
Behaviour [C]	5	2348.81	0.0000	2348.81	0.0000
Sex [D]	1	1327.15	0.0000	1327.15	0.0000
[BC]	20	271.52	0.0000	320.65	0.0000
[CD]	5	381.89	0.0000	425.09	0.0000
[AB]	32	72.33	0.0001	94.41	0.0000
[AC]	40	270.67	0.0000	301.55	0.0000
[AD]	8	12.73	0.1213	28.89	0.0003
[BD]	4	14.04	0.0072	48.45	0.0000
[ABC]	160	143.04	0.8280	158.82	0.5115
[ABD]	32	33.35	0.4013	58.10	0.0032
[ACD]	40	47.33	0.1984	49.99	0.1338
[BCD]	20	13.08	0.8739	11.54	0.9310

nally highly significant when tested separately (see Table 2) and some time-related differences are apparent by visual examination of the data (Fig. 3). However, the interaction Behaviour-Hour was included in the model that directly preceded the final selected model in the step-down selecting procedure, i.e. in the model 33, as well as in all hierarchically higher models. It was thus exclusion of this single factor that rendered the final

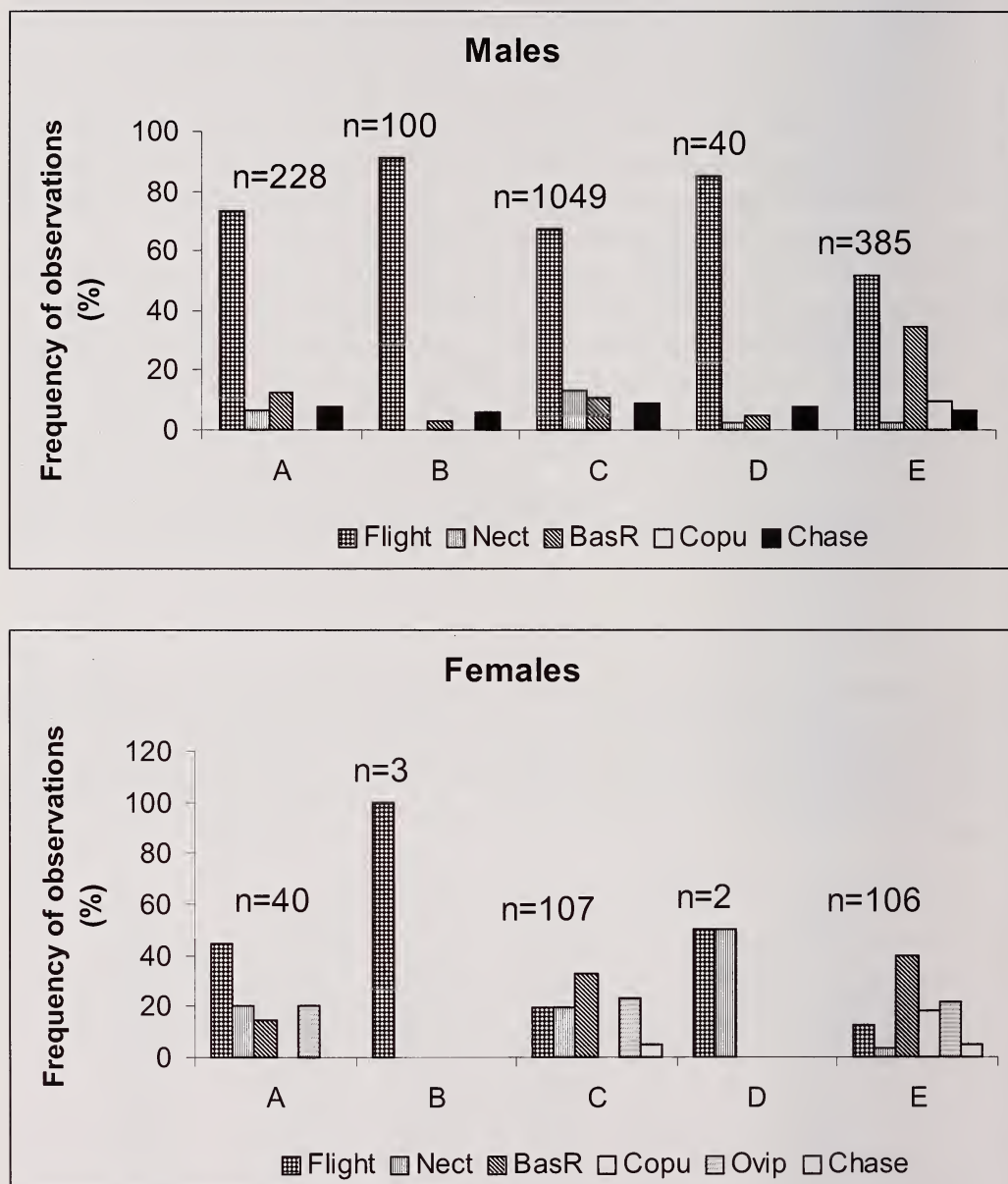


Fig. 2. Types of behaviour of adult *P. mnemosyne* observed at individual transect sections. Legend: Flight – flying and/or patrolling, Nect – Nectaring, BasR – Basking or resting, Copu – Copulation, Ovip – Egg laying, Chase – Chasing. The numbers above bars are total numbers of individuals (100%) seen at individual sections.

model formally significant. We conclude, that there are some diurnal differences in behaviour (e.g. much basking-resting in late afternoon or prevalence of nectaring in afternoon hours, see Fig. 3), but they are not very profound and were masked by other patterns in our data in model construction.

Discussion

P. mnemosyne adults of both sexes spend most of their time at open forest clearings. This further supports the notion of strict gap dependency of European forest dwelling populations of this endangered species and confirms earlier conclusions of many authors (Väisänen & Somerma 1985; Kudrna & Seufert 1991; Konvička & Kuras 1999; Megléc *et al.* 1999). In this respect, *P. mnemosyne* resembles other European forest-dwelling butterflies, many of which are locally endangered by modern changes of forest management (Warren & Key 1991; Robertson *et al.* 1995). Similarly, high forest was identified as a dispersal barrier for a Canadian population of *Parnassius smitheus* (Keyghobadi *et al.* 1999; Ronald *et al.* 2000). At our study locality, the forest clearings did not only serve as mate-locating and ovipositing sites; virtually all crucial events of *P. mnemosyne* adult life, i.e. mating, nectaring and overnight resting, were restricted to them. Although closed forest does not act as impenetrable barrier for *P. mnemosyne* adults (in 1996, as many as 60% of individuals of both sexes moved between “subsites” of the study colony; see Konvička & Kuras 1999), the butterflies seemed to avoid high forest. When crossing it, they did so by either straight flight or flying over treetops. Moreover, the fact that the butterflies stayed on the clearings throughout whole days nearly excludes a possibility of regular within-habitat movements, such as the movements between mate-locating and feeding sites, which have been described for some butterfly species (e.g. Dempster 1997). This information is of practical interest for conservation monitoring (such as transect censuses), because it guarantees that results obtained from any time of day between 10 AM and 4 PM are reliable for at least relative estimation of male population size.

The male-biased sex ratio in observations of individual sexes is in accord with other work done on Parnasiinae butterflies. However, any finding regarding sex ratio, if based solely on observational data, is necessarily biased due to different activity of sexes and resulting higher apparency of males. However, surplus of males in populations of *P. mnemosyne*, and related species, was reported from mark-release-recapture studies as well. Konvička & Kuras (1999) obtained capture sex ratios ranging from 2.0 to 10.6. Megléc *et al.* (1997a, 1999) reported a “deficit of females” in *P. mnemosyne* populations in Hungary, while Scott (1973) and Matsumoto (1985) reported male-biased capture sex ratios in *Parnassius phoebus* F. and *Parnassius glacialis* Butler, respectively. Nothing definite can be said about realised sex ratio in *P. mnemosyne*, until sufficient data from lab rearing, and perhaps from specifically designed experiments (for instance, mark-release-recapture study done by independent workers separately with males and females) are available.

The behaviour observed in this study is in agreement with the patterns previously published for various species of Parnassinae (e.g. Scott 1973; Kudrna & Seufert 1991;

Matsumoto 1984, 1985). The higher relative frequency of nectaring in females is noteworthy, although it probably does not reflect higher energy requirements of that sex, but rather cryptic nature of the main females' activity, i.e. egg-laying. The lack of distinct courtship, frequent male harassment of non-receptive females and prolonged mating are common characteristics of sphragis forming species (cf. Scott 1974; McCorkle & Hammond 1985; Matsumoto 1987; Orr & Rutowski 1991; Matsumoto & Suzuki 1995; Orr 1995). The decrease of male patrolling towards late afternoon seems to concur with reduction of males' readiness to mate, as the only records of males that did not

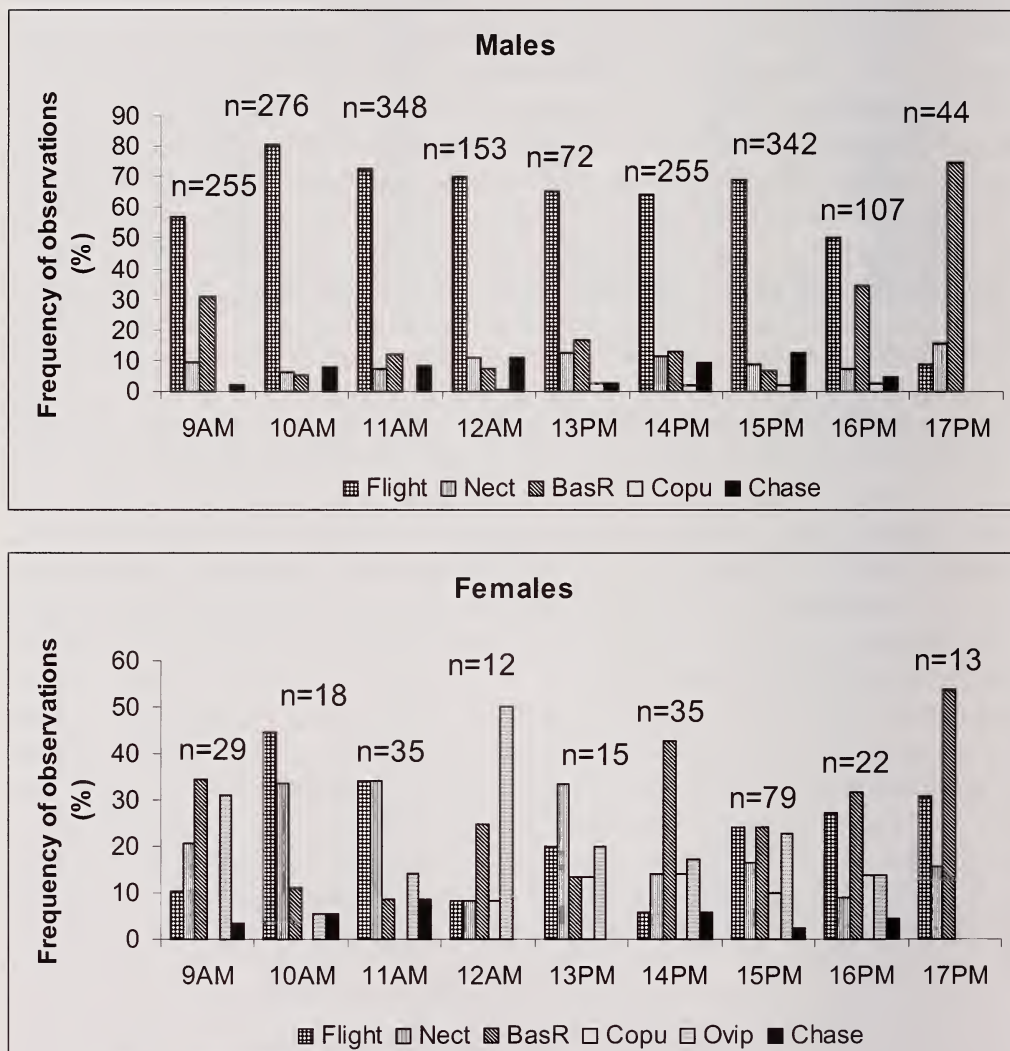


Fig. 3. Types of behaviour of adult *P. mnemosyne* as observed during day time (both sexes and all transect sections combined). Legend: Flight – flying and/or patrolling, Nect – Nectaring, BasR – Basking or resting, Copu – Copulation, Ovip – Egg laying, Chase – Chasing. The numbers above bars are total numbers of individuals (100%) seen in respective hours.

show interest in virgin females came from late afternoon. The same situation was described for *Parnassius phoebus* by Scott (1973) and for *Luehdorfia japonica* by Matsumoto (1987). The late-afternoon disinterest in mating might correspond with the long duration of copulation, since a pair which would initiate copulation in too late an hour could not terminate it before sunset. Staying in copula after sunset would be selected against if there were increased mortality tied to overnight copulation.

The loglinear model did not point to any marked differences in behaviours in different hours of day, although there clearly were some differences, such as prevalence of basking/resting in morning and late afternoon hours. Thus, hour-to-hour behaviour of *P. mnemosyne* butterflies, the early morning and late afternoon hours aside (see Fig. 3), did not show any sharp diurnal changes. This is especially striking when compared to marked diurnal differences in behaviour reported for many nymphalids (e.g. Baker 1972; Bitzer & Shaw 1979; Wickman 1984; Fric & Konvička 2000) or skippers (Dennis & Williams 1987). We suggest that the situation found in *P. mnemosyne* might be explainable by descent of the species. Most of extant *Parnassius* species are found in mountainous regions, the entire genus has its greatest radiation in high-altitude habitats of mountains of Central Asia (Ackery 1975). Mountain origin of the group is supported by its phylogeny (Ackery *et al.* 1999; Holloway & Nielsen 1999). Even today, some populations of *P. mnemosyne* retain the ancestral generic habit to occur at high altitudes. Lack of distinct within-day behavioural patterns coupled with simple patrolling mate-locating behaviour was reported for several alpine and arctic butterflies including *Parnassius phoebus* (Scott 1973), *Erebia* ringlets (Brussard & Ehrlich 1970; Ikejiri *et al.* 1980) and alpine *Colias* species (Watt 1968). Behaviour of such species is strongly constrained by ever-changing, often adverse weather. They must respond immediately, irrespective of time of day, to abrupt changes of conditions in their alpine and/or arctic homelands, since a delayed response to any weather change might have fatal consequences. Lowland populations of *P. mnemosyne* probably retained the trait that allows mountainous populations of the species, as well as of its relatives, to inhabit high altitudes. Closer study of other lowland butterflies of tentative alpine origin (such as some European lowland *Erebia*) could reveal whether there, indeed, is a pattern in behavioural adaptations of mountain butterflies, which persists in their lowland congeners.

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