

The last population of the Woodland Brown butterfly (*Lopinga achine*) in the Czech Republic: habitat use, demography and site management

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Abstract The distribution of *Lopinga achine* (Lepidoptera Nymphalidae, Satyrinae) in the Czech Republic has declined from thirty grid squares before 1950 to just one extant population, restricted to a single area of deciduous woodland. A review of historical sites shows that this species used to occur in various types of deciduous woodland with a relatively sparse canopy maintained by coppicing and/or grazing. The extant population inhabits mature woodland with a mean canopy cover of 60% (quartiles 50% and 65%), sparse shrubs and a species-rich herb layer containing plant species requiring dry, warm and nutrient-poor conditions. The larval host plants are the fine-leaved sedges, *Carex fritschii* and *C. michelii*. In 2006, the total population contained about 10,000 adults but this may be an over-estimate, biased by male behaviour. Measurements of adult mobility, well approximated by an

inverse-power function, suggested that all existing colonies are interconnected by dispersal. Continuing existence of the population depends on two conditions; nutrient-poor conditions for a diverse ground flora and a sparse tree canopy. While canopy closure is gradually increasing, the herb layer is threatened by soil enrichment due to the demise of traditional grazing, litter raking and grass mowing in woodlands. Any future management to favour *Lopinga achine* should include both measures to maintain a sparse canopy and measures to export biomass, such as raking or mowing of ground flora or, preferably, re-establishment of grazing.

Keywords Butterfly conservation · Canopy · Forest ground flora · Lepidoptera · Mark-recapture · Pasture woodland · Population size

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Introduction

Several European butterflies depend on sparse or open forest structures, preserved for centuries by such techniques such as coppicing or forest pasture, yet largely abandoned by modern forestry (Warren 1985; 1987; Warren and Key 1991; Konvicka and Kuras 1999; Benes et al. 2006). To preserve these species, it is necessary either to maintain traditional management methods (Warren 1991; Bergman 2001; Freese et al. 2006), or to apply alternatives mimicking their effects (Greatorex-Davies et al. 1993).

Individual woodland species may exhibit highly exacting habitat requirements, requiring specific management approaches (e.g., Konvicka et al. 2005, Benes et al. 2006). Alternatively, different forestry operations may create conditions that are similarly favourable from a butterfly

perspective (Cizek and Konvicka 2005; Freese et al. 2006). Species also vary geographically in such life history traits as host plant use (cf. Wahlberg 1998). With critically endangered species, transposing generic management prescriptions across regions must be done with care as it can sometimes cause irreparable losses.

The Woodland Brown, *Lopinga achine* (Scopoli, 1763) (Lepidoptera: Satyridae) is a continentally threatened (Van Swaay and Warren 1999) butterfly of European temperate woodlands (Kudrna 2002). Detailed ecological information exists from southern Sweden, while practically none is available from other regions. The Swedish populations inhabit sparse (60–90% canopy) woodlands maintained by cattle grazing (Bergman 2001; Bergman and Landin 2001, 2002; Bergman and Kindvall 2004). Shadier conditions are too cold, while too much sun causes the desiccation of locally used larval host plant, *Carex sylvatica* (Bergman 1996[2001]; 1999). Outside Sweden, some authors (e.g., Weideman 1995; Höttinger and Pennerstorfer 1999) mentioned an association with coppice forests but other biotopes can also be inhabited, such as wooded savannahs in the Carpathians (Kralicek and Gottwald 1984) or sparse evergreen forests in the Alps (Lepidopterologen Arbeitsgruppe 1987).

This lack of information on biotope structure, life history and demography is also true for the Czech Republic, where the species has declined from thirty occupied 12×11.1 km grid squares prior to 1950 to just one after 1995 (Benes et al. 2002). The absence of information hinders any effective conservation actions. This paper, based on two years of intensive surveys, seeks to supplement this knowledge. It presents (i) an overview of the current status of most of the sites in which *Lopinga achine* was historically present, used to interpret the species' decline; (ii) a quantitative description of habitats used at the last occupied site, with particular respect to vegetation conditions; (iii) information on adult behaviour, including such elements as host plant use; and (iv) information on patterns of population structure and dispersal, including population size estimates.

Material and methods

Evaluating reasons of decline

We collated information on post-1960s distribution, using a Czech butterfly database (cf. Benes et al. 2002). In 2000–2006, we visited the sites of former colonies that could be precisely identified in the database and which once contained large populations. We also contacted lepidopterists who had been familiar with the sites when the populations still existed.

Study site: location of the last population

The last population inhabits the Hodoninsky Wood, a 40 km² lowland woodland surrounded by arable farmland (Fig. 1, Table 1). It is renowned for vegetation diversity due to a diverse geology. Base-rich alluvial sediments are buried under nutrient-poor sand layers. The sands are deep in the east, where psammophilous vegetation prevails, and shallow in the west, with wetland carr. A central part is intermediate, covered by a mosaic of forested dry dunes and swampy depressions. It is believed that capillary action draws base ions up through nutrient-poor sands, promoting vegetation that requires base-rich but nitrogen-poor conditions (V. Grulich, pers. comm).

For centuries, the wood had been coppiced and used for livestock grazing, fodder mowing and litter raking (Kralicek and Gottwald 1987). These practices have gradually declined over the last century, ceasing between the 1950s (grazing) and 1970s (mowing). Today, about half of the wood retains a semi-natural, deciduous tree cover, dominated by oak and lime. Within this semi-natural woodland, some areas have retained a sparse structure typical of traditional pasture woodlands. The rest has been gradually replaced with conifer plantations over the last 60 or 70 years. A central part of the wood (3,029 ha) is a proposed Site of Community Importance under the EU Habitats Directive (Pannonian oak-hornbeam forests and Euro-Siberian steppe oak forests: Chytrý et al. 2001).

Habitat use

We carried out two surveys during the adult flight period—a *Pilot survey* in 2005 and a *Detailed survey* in 2006.

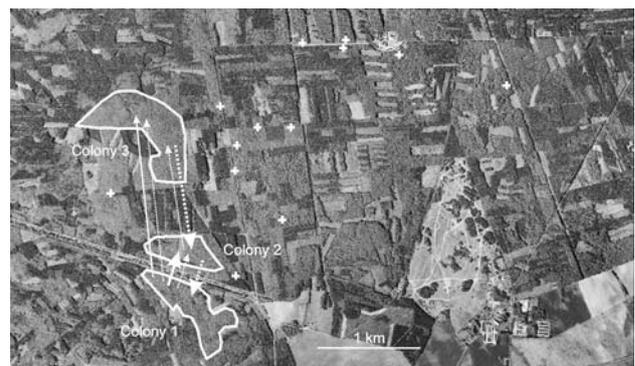


Fig. 1 Aerial view of Hodoninsky Wood (central part) showing the three large colonies of *Lopinga achine* and locations of single records in eastern part of the wood. Dashed darts stand for male and solid darts for female movements between colonies (thin line: less than three individuals, thick lines: more than three individuals). Note that all the colonies are restricted to sparse deciduous stands, and that large areas are covered by pine (dark colour) and clearings, and are hence completely unsuitable for the butterfly

Table 1 Overview of selected historical sites of *L. achine* in the Czech Republic

Local name	Position—N; E; alt.	Extinct in	(i) Character of biotope; (ii) historical management; (iii) likely reason of decline	Principal reference
Bílé Karpaty	48°51'; 17°25'; 350 m	Mid-1980s	(i) Sparse oak groves within savannah-like grasslands; (ii) early summer hand mowing, followed by light grazing; (iii) demise of grazing, machine-mowing causing disappearance of smooth edges	Kralicek and Gottwald (1984)
Borův Wood	48°44'; 16°50'; 200 m	1996	(i) Sparse oak-dominated woodlands on base rich soils, the largest population in the country in the 1980s; (ii) grazing, coppice with standards; (iii) felling of oldest stands followed by coniferisation, canopy closure elsewhere	Lastuvka (1994)
Borova (Hlucin)	49°58'; 18°06'; 300 m	Late 1970s	(i) Sparse oak-birch woodlands on acidic soils; (ii) coppice with standards; (iii) massive coniferisation, canopy closure, reportedly also spraying with insecticides	Benes and Kuras (1997), Stiova (1973)
Domanovický Wood	50°06'; 15°20'; 230 m	Early 1980s	(i) Alluvial base-rich oak-ash woodland; (ii) coppice with standards; (iii) coniferisation of drier parts, closure of canopy layer	Lekes (2000)
Hodonínský Wood	48°54'; 17°06'; 180 m	Extant	This paper	This paper
Lednice	48°44'; 16°50'; 170 m	Late 1990s	(i) Oak-hornbeam tracks growing on elevated mounds within floodplain forests; (ii) grazing, since 19th century part of large landscape park; (iii) demise of grazing, canopy closure	Lastuvka (1994)
Libický luh	50°06'; 15°10'; 180 m	Early 1980s	(i) Alluvial oak-ash woodland; (ii) coppice with standards; (iii) total canopy closure, accelerated by establishing a reserve	Benes and Konvicka (2006)
Litovelské Pomoraví	49°43'; 17°03'; 250 m	Late 1980s	(i) Sparse oak woodlands on sandy bedrock; (ii) coppice with standards combined with grazing; (iii) coniferisation of about half of the area by pine and spruce, subsequent invasion of ground flora by <i>Calamagrostis epigetos</i>	Stiova (1973), Konvicka (1999)
Milovický Wood	48°50'; 16°42'; 250 m	2001	(i) Abandoned low coppices on base rich soils; (ii) low coppice until 1950s, deer park containing dense network of rides and tracks afterwards; (iii) overstocking by deer combined with closure of canopy layer	Benes et al. (2006)
Moravský Kras	49°13'; 16°42'; 370 m	Late 1960s	(i) Low coppices on carstic bedrock; (ii) coppicing, possibly combined with grazing; (iii) total closure of canopy layer	Lastuvka and Marek (2002)
Starý Poddvorov	48°52'; 17°00'; 240 m	1980s	(i) Mature oak-hornbeam wood, historically a pasture woodland; (ii) former coppices with standard, possibly grazed; (iii) total closure of canopy layer	Benes et al. (2002)

Included are only sites which still contained the species after 1950, for which there are > 5 independent records in Czech butterfly database, and which we visited after 2001. Note that “historical management” typically refers to the first half of 20th century

The *Pilot survey* intended to map *L. achine* distribution in detail and to obtain basic information on habitat use. From the 12–18 June, 2005, we spent 26 person-days surveying all *openings* (clearings, tracks and sparse stands without full canopy closure) within the wood (Fig. 2). A clearing (minimum: 400 m², median: 4000 m²) was a section with all trees removed by harvest, replanted either by broadleaf trees or by pine. As there were no clearings with standard trees retained, clearings did not form a continuum with sparse stands, which all contained at least 50% of canopy cover. At each perceived opening, a transect was walked to ascertain the absence or presence (and numbers) of *L. achine*. The following parameters of each opening were recorded: (i) area; (ii) type (clearing, track, sparse stand); (iii) perimeter biotopes (i.e., percentage of perimeter comprising of young pine/oak thicket, mature oak, mature pine); (iv) percentage cover of tree canopy, shrub and ground layers (estimated by eye as a projection of open open sky visible from ground for canopy, and as a percentage of open ground for shrub and ground layers); (v) covers of individual tree and shrub species; and



Fig. 2 Biotopes in the Hodoninsky Wood, Czech Republic. (a) A clearing created by felling of mature deciduous forest, completely unsuitable for *Lopingsa achine*. (b) A sparse stand inhabited by *L. achine*. Note the high representation of forbs in ground layer

(vi) broad character of ground layer, expressed as percentage cover of short forbs, short grasses, tall grasses, the expansive grass *Calamagrostis epigeios*, bramble (*Rubus* spp.), and tall ruderal herbs (e.g., *Urtica dioica*, *Solidago canadensis*, *Rumex* spp.).

Many sparse stands were not occupied despite an appropriate suitable coarse structure. To investigate the requirements in more detail, we conducted a *Detailed survey* in June 2006. It consisted of collecting standard phytosociological *relèves* (each 400 m²) from 68 sparse stands, 21 occupied and 48 unoccupied in previous year. We recorded cover of all vascular plants in tree, shrub and herb layer, using the nine-point Braun-Blanquet ranked scale (Braun-Blanquet 1964). The dataset contained 235 plant species in total.

To detect how would occupied sites differ from unoccupied ones, we used, separately for each survey, the redundancy analysis in CANOCO v. 4.5 (Leps and Smilauer 2003). Presence (or semi-quantitative abundance) of the butterfly was a predictor, while parameters of the openings, or plant species composition of *relèves*, were species data. We also controlled for spatial autocorrelation among the samples by constructing models with sample coordinates as spatial terms.

For the *Detailed survey* we used ordinal plant indicator values (Ellenberg et al. 1992) of temperature, light, humidity, soil reaction and soil nutrients to compare used and unused *relèves*. We used values given by Borhidi (1995) for the Hungarian flora, summarised by Horvath et al. (1995), since Ellenberg's original list does not encompass all the species we identified.

Demography

We carried out a mark-recapture program between June 9 and 26, 2006. The marking proceeded on a daily basis at three *colonies* (Fig. 1), clusters of openings with high adult densities; we divided the area of each colony *a priori* into several *subsites*, distinguished by terrain landmarks, whose centroids were used as dispersal coordinates. Captured individuals were marked using numeric codes. For each we recorded sex, time of capture, behaviour prior to disturbance, and height above the ground when first spotted.

We used the *POPAN* formulation of the Jolly–Seber approach within the framework of constrained linear models (Lebreton et al. 1992; Shtickzelle et al. 2003), as incorporated in MARK, v. 4.3., to estimate demographic parameters for the three colonies. *POPAN* estimates three primary parameters, residence (a probability of staying in population, ϕ), catchability (p), and probability of entering the population (combining births and immigration, $pent$). Derived parameters are; daily number of births (B_i), daily population size (N_i) and total population (N_{tot}).

We followed the heuristic approach suggested by Schtickzelle et al. (2002). A computation-faster Cormack–Jolly–Seber approach (MARK: *recapture only*) was used to find responses of ϕ and p to sex (g) and time (t), the latter as either a factorial (t), linear (t_{lin}) or polynomial ($t_{\text{lin}+\text{lin}}^2$) response. We then used the *recapture only* results as starting points in POPAN. After finding a provisional best-fitting POPAN model (a model with the lowest AIC-value relative to all competing models), we iteratively checked for potentially better-fitting models derived from the provisional best model. Average catchability (p') and residence (ϕ') are simple arithmetic means from POPAN daily values; longevity is obtained as $-\ln(\phi')^{-1}$. We used MARK model averaging procedure to obtain estimates of total population sizes from sets of competing models.

Capture coordinates of all individuals captured more than once were used to fit the inverse-power function (IPF), a scale-invariant function that fits the cumulative probability of movements (I) against movement distances (D) (Fric and Konvicka 2007). It takes the form

$$I = c \cdot D^{-m} \quad \text{or} \quad \ln I = \ln c - m \ln D$$

and is fitted by regressing the natural logarithms of the cumulative proportions of individuals moving to certain or greater distances, against the natural logarithms of the distances.

Results

Revisiting historical sites

An overview of historically occupied sites (Table 1) reveals a remarkable diversity of past management, varying from low coppice through coppice with standards to grazing. Canopy closure seems a prevailing reason of decline, but other mechanisms, such as destruction of ground layer by overstocked deer (Milovicky Wood), or a change of ground layer following felling of a mature woodland (Bori Wood, Litovelske Pomoravi), probably played a role.

Last population: habitat association

In the *Pilot Survey*, the butterfly occurred in 45 out of 357 openings, forming three rather distinct clusters in mature, oak-dominated stands in a central part of the wood. It was absent from wet and sandy eastern areas of the wood (Fig. 1).

The positive records originated from sparse stands (38 occupied vs. 181 unoccupied) or tracks (7 vs. 87), but not clearings (0 vs. 44) ($\chi^2 = 13.10$, $df = 2$, $P < 0.01$). The occupied openings had a sparse canopy (mean cover: 60.0,

median: 60, range: 20–90, 2nd and 3rd quartiles: 50 and 65), some shrubs (17.0, 10, 1–50, 6 and 25), a well-developed herb layer (75, 80, 10–100, 70 and 90) a third of it formed by forbs (26, 25, 0–50, 20 and 35) (Fig. 2). Unoccupied openings differed in having a more closed canopy ($t = -1.97$, $P < 0.05$) and denser ground cover ($t = -2.00$, $P < 0.05$); whereas shrub cover had no effect ($t = 0.61$, $P = 0.54$) (all tests with 355 df). These patterns were partly due to the large effect of unoccupied clearings in the analyses. When these were excluded, the effects of canopy ($t = -0.23$, $P = 0.82$) and shrubs ($t = -0.07$, $P = 0.94$) disappeared, while the herb layer effect remained significant ($t = -2.28$, $P < 0.05$) (all $df = 311$). Exclusion of data from clearings also suggested that occupied openings contained greater forb cover ($t = -6.61$, $P < 0.0001$) and lower ruderal herbs cover ($t = 2.14$, $P < 0.05$).

Ordinations supported the above patterns (Fig. 3). The butterfly was associated with (i) oak, lime and such shrubs as hawthorn (*Crataegus*), rather than with pine (i.e., plantations) or trees and shrubs of wetter soils (e.g., buckthorn, *Frangula alnus*); (ii) openings surrounded by mature oak rather than pine or oak thickets; and (iii) low ruderal plants cover.

In the *Detailed Survey*, occupied and unoccupied openings differed significantly in vegetation composition, even after considering spatial effects (Table 2). *L. achine* was positively associated with plant species characteristic of open woodlands, and negatively associated with tall, coarse grasses (e.g., *Arrhenatherum elatior*, *Dactylis glomerata*) and forbs of nutrient-rich soils (e.g., *Galium aparine*, *Urtica dioica*) (Fig. 4). Ellenberg-Borhidi values revealed that occupied sites were warmer (Mann–Whitney $U = 375.0$, $z = 2.23$, $P < 0.05$), drier ($U = 332.0$, $z = -2.77$, $P < 0.01$) and contained fewer soil nutrients ($U = 367.0$, $z = -2.23$, $P < 0.05$). Soil reaction and light had no effects ($P = 0.18$ and 0.20 , respectively).

Last population: adult behaviour

We observed 234 instances of oviposition (or behaviour directly linked to oviposition, such as parachuting to herbaceous vegetation). They all occurred in short (20–40 cm) ground vegetation where sedges were common. Of the seven eggs that we actually saw being laid, three were deposited on *Carex fritschi*, two on *C. michelii*, one on sedge litter and one on a *Potentilla* leaf interwoven with *Carex* foliage.

Both sexes were active near the ground (up to ca. 1 m) during the morning, males patrolling above sunny spots and females basking, resting or laying eggs (Fig. 5). Towards midday, both sexes progressed to shrubs and tree branches. Males apparently established perches there, and

Fig. 3 RDA ordinations of presence vs. absence of *Lopinga achine* versus simple parameters describing 357 forest openings visited during *Pilot survey* in 2005. Only variables having the best fit to the respective ordination models are shown, F and P values are based on Monte-Carlo tests with 999 permutations. **(a)** Perimeter biotopes: *eigenvalue* (first ordination axis) = 0.010, $F = 3.45$, $P < 0.05$. **(b)** Covers of trees and shrubs, M stands for canopy, U for understorey: *eigenvalue* = 0.036, $F = 12.79$, $P < 0.001$; **(c)** Coarse ground vegetation data: *eigenvalue* = 0.035, $F = 12.80$, $P < 0.001$

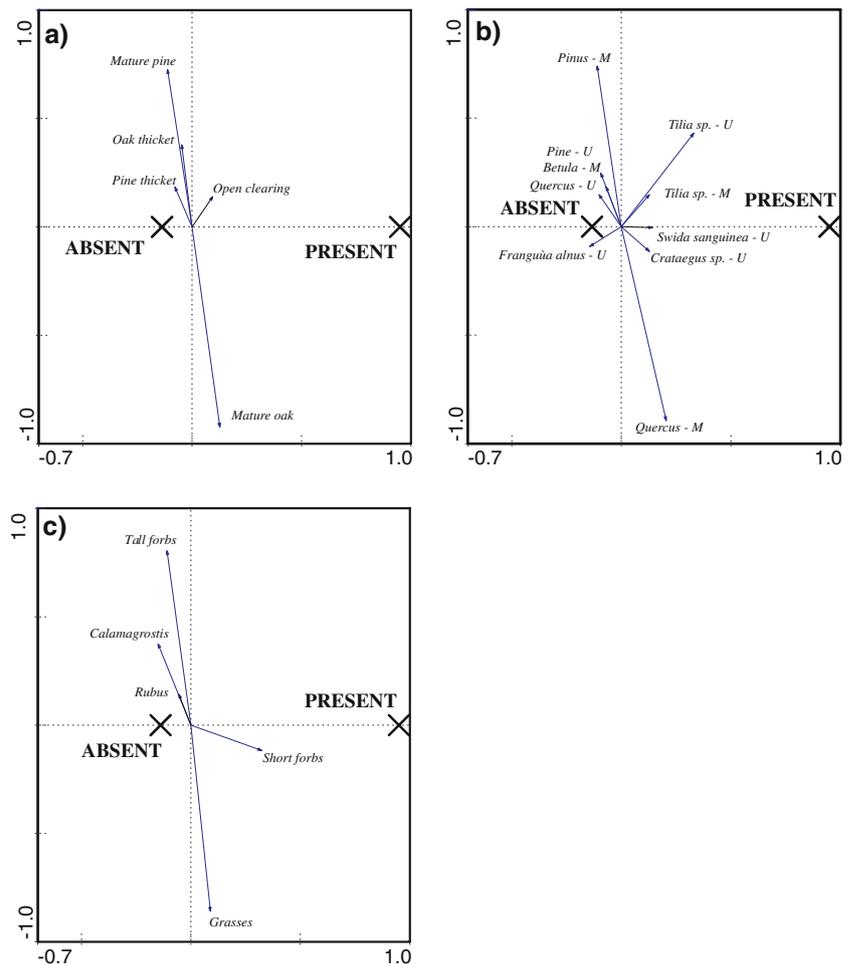


Table 2 Results of redundancy analysis, comparing plant species composition of vegetation relieves from woodland openings occupied ($n = 21$) and not occupied ($n = 48$) by *Lopinga achine*

	Eigenv. 1	Eigenv. 2	Eigenv. 3	Eigenv. 4	Explained variation	F , P —first axis	F , P —all axes
Spatial model*	0.096	0.022	0.103	0.071	0.108	6.15***	0.108***
<i>L. achine</i> presence							
General model**	0.056	0.132	0.072	0.067	0.056	3.95***	
Partial model***	0.037	0.086	0.066	0.060	0.037	2.83***	
<i>L. achine</i> relative abundance							
General model	0.088	0.112	0.070	0.063	0.088	6.39***	
Partial model	0.056	0.080	0.067	0.052	0.056	4.36***	

Eigenv.—eigenvalues of ordination axes; F , P refer to Monte-Carlo tests (999 permutations)

* Containing latitudinal position of samples (LA) plus its second-order polynomial (i.e., species composition $\sim LA + LA^2$). Selected via a forward procedure from longitude (LO), latitude (LA), their second-order polynomials, and all possible interactions ($LA \times LO$, $LA \times LO^2$...)

** Testing for significant effect of predictors without considering spatial terms

*** Significant effect of predictors after considering the terms of spatial model as covariates

quite frequently ($n = 62$) engaged in chases with either conspecifics ($n = 51$) or other butterflies. Still later in the day (after 2 p.m., CE summer time) the butterflies ascended to greater heights, resting in the canopy in late afternoons.

For the shrub-dwelling butterflies, it was difficult to tell apart activities such as perching, resting or honeydew-feeding. We hence pooled all stationary activities (herein referred to as sitting), and compared them with pooled flight data. Using this pooled data showed that sitting in-

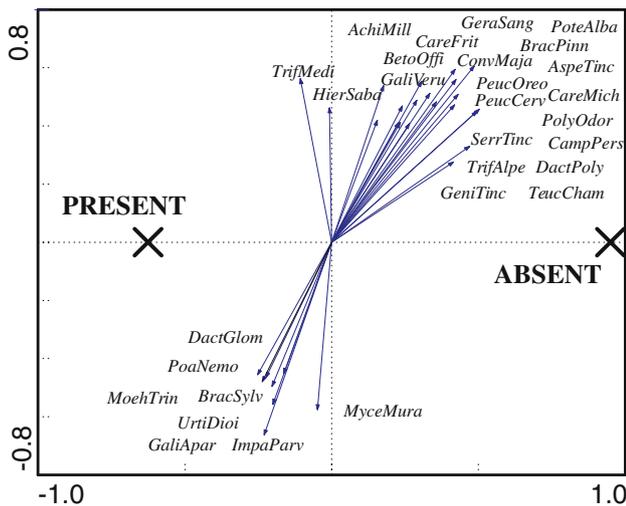


Fig. 4 Results of RDA ordination of plant composition of 69 reléves taken during *Detailed survey* from sparse deciduous stands ($n = 21$) and unoccupied ($n = 48$) by *Lopinga achine*, with *L. achine* presence used as predictor. Only plant species best fitting to the model are shown. Plant names: *AchiMill*—*Achillea millefolium*, *AspeTinc*—*Asperula tinctoria*, *BetoOffi*—*Betonica officianlis*, *BraSylv*—*Brachypodium sylvaticum*, *CampPers*—*Campanula persicifolia*, *CareFrit*—*Carex fritschii*, *CareMich*—*C. michelii*, *ConvMaja*—*Convallaria majalis*, *DactGlom*—*Dactylis glommerata*, *DactPoly*—*D. polygamma*, *GaliApar*—*Galium aparine*, *GaliVeru*—*G. verum*, *GeniTinc*—*Genista tinctoria*, *GeraSang*—*Geranium sanguineum*, *HierSaba*—*Hieracium sabaudum*, *ImpaParv*—*Impatiens parviflora*, *MoehTrin*—*Moehringia trinerva*, *MyceMura*—*Mycelis muralis*, *PeucCerv*—*Peucedanum cervaria*, *PeucOreo*—*P. oreoselinum*, *PoaNemo*—*Poa nemorosa*, *PolyOdor*—*Polygonatum odoratum*, *PoteAlb*—*Potentilla alba*, *SerrTinc*—*Serratula tinctoria*, *TeucCham*—*Teucrium chamaedrys*, *TrifAlpe*—*Trifolium alpestris*, *TrifMedi*—*T. medium*, *UrtiDioi*—*Urtica dioica*

creased with day time in males (logit regression [LR] of sitting vs. flight records: $n = 1353$, $\chi^2 = 46.7$, $df = 1$, $P < 0.0001$), apparently due to a shift towards perching, but not in females (LR, $n = 702$, $\chi^2 = 1.1$, $df = 1$, $P = 0.29$) (Fig. 5). Both sexes moved from the ground towards shrubs and trees (LR, males, $n = 1575$, $\chi^2 = 11.6$, $df = 1$, $P < 0.001$, females $n = 955$, $\chi^2 = 6.7$, $df = 1$, $P = 0.01$) and towards greater heights (linear regression, males: $b = 0.19$, $F = 7.92$, $df = 1,1545$, $P < 0.01$, $R^2 = 0.01$; females: $b = 0.04$, $F = 12.56$, $df = 1, 954$, $P < 0.001$, $R^2 = 0.01$). A seasonal shift in male activity seemed to reflect the diurnal pattern. Males settled more often and flew less frequently with progressing flight period (LR, $\chi^2 = 16.0$, $P < 0.0001$), the opposite pattern occurred in females (LR, $\chi^2 = 6.1$, $P < 0.05$) (Fig. 6).

Last population: adult numbers and dispersal

Proportionally, males dominated, both in ratios of capture (1.3) and recapture (1.9) (Table 3). Capture probability depended on time in a factorial manner (Table 4).

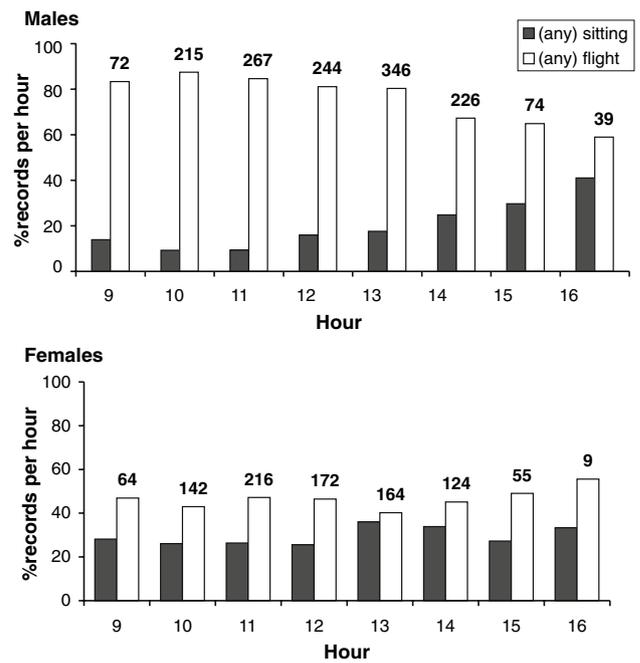


Fig. 5 Diurnal behavioural pattern of adults of *L. achine* butterfly, based on activities of individuals prior to capture. Summed observations of (pooled) flying and sitting activities across entire duration of mark-recapture study, expressed as percentages of all activities in a given hour and plotted against that hour. The numbers above hourly bars show total numbers of observations

Recruitment was either polynomial in time or linearly decreasing. Daily population estimates (Fig. 7) indicated that the survey period missed the very beginning of the male flight in colonies 2 and 3, and the end of female flight in colonies 1 and 3. Estimated total population sizes suggests a surplus of females in colonies 1 and 2, and slight surplus of males in colony 3. Combined, the three colonies hosted about 10,000 individuals.

Mean total movements were 170 m (± 339 SD) for males and 100 m (± 228 SD) for females, a non-significant difference (Mann-Whitney U : $z = 1.40$, $P = 0.09$). Eight males and one female moved over 1 km, the longest male and female movements were 2,750 m and 1,930 m. Ten males and four females moved between colonies (Fig. 1).

Fitting IPF to movement data returned the following equations:

$$\text{Males: } \ln I = -3.58(\pm 0.091 \text{ SE}) - 1.48(\pm 0.089 \text{ SE}) \ln D; R^2 = 0.93$$

$$\text{Females: } \ln I = -4.28(\pm 0.169 \text{ SE}) - 1.58(\pm 0.125 \text{ SE}) \ln D; R^2 = 0.94$$

Slopes of the equations did not differ ($t = 0.60$, $df = 33$, $P > 0.10$). The predicted movement probabilities were, for

Fig. 6 Seasonal behavioural pattern of adults of *L. achine* butterfly, based on activities of individuals prior to capture. Summed observations of (pooled) flying and sitting activities across entire duration of mark-recapture study, expressed as percentages of all activities in a given day and plotted against that day. The numbers above daily bars show total numbers of observations

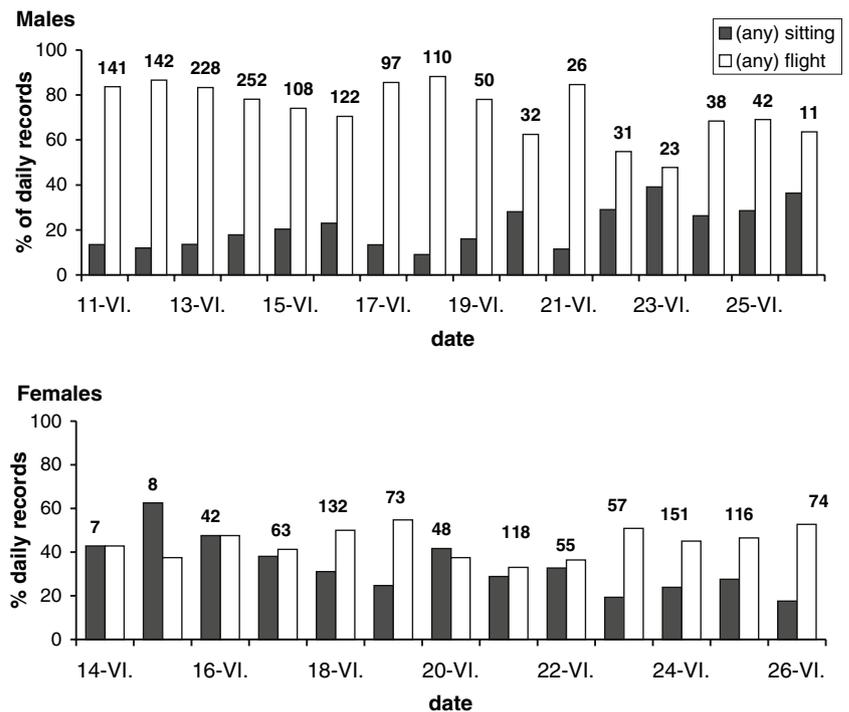


Table 3 Overview of mark-recapture data for population of *Lopinga achine* in the Hodoninsky Wood

Colony	Sex	Duration	Marking days	Marked	Recaptured	Handlings
1	♂♂	July 9–26	18	568	155	781
	♀♀	July 14–26	13	448	67	527
2	♂♂	July 11–26	15	216	73	317
	♀♀	July 14–26	12	197	29	234
3	♂♂	July 11–26	16	295	95	457
	♀♀	July 11–26	16	170	25	199
Total	♂♂	July 11–26	49	1,081	323	1,556
	♀♀	July 11–26	41	815	121	958

males, 0.028 to 1 km (observed: 0.022), 0.003–5 km and 0.001–10 km; and for females, 0.011–1 km (observed: 0.009), 0.002–5 km and 0.0006–10 km.

Discussion

The last Czech population of *L. achine* consists of fairly large interconnected colonies within a large wood. Its habitat is a mature deciduous woodland containing patchworks of sun-penetrated gaps due to wide (15–20 m) spacing among grown trees. Further necessary components are shrubs or low-hanging branches and ground layer containing fine-leaved *Carex* sedges used as larval host-plants. This structure has developed as a result of historical land-use, mainly forest pasture and litter collection that slowed down tree regeneration. More recently, some gaps are formed by removal of single grown trees (i.e., selective harvest). The habitat is similar to that occupied in southern Sweden, where Bergman

(2001) demonstrated that glades formed by past grazing are subject to successional change that would eventually render them unsuitable. The larval host plants used in the Czech Republic require relatively dry, warm, and nutrient-poor conditions. They are poor competitors (Horváth et al. 1995), suppressed by coarse, tall grasses as nutrients accumulate. The competitive grasses also suppress more sensitive forbs: this relationship creates the apparent association of *L. achine* with short forbs. Apart from the complete destruction of sites via planting conifers, the threats to the last Czech population include: (i) canopy closure; (ii) nutrient enrichment of soils; and ultimately, (iii) ensuing decline of current population size.

Demography, behaviour, and reliability of population size estimates

Basic demographic patterns of the studied population are also similar to those in Sweden (Bergman and Landin

Table 4 Results of the Jolly–Seber analysis (POPAN module in MARK): selected models, numbers of model parameters, and estimates of average longevity (*Long.*), catchability (*p'*), and population size (*N*_{tot.})

Model*	AIC	ΔAIC	Parameters	<i>Long.</i> _{♂♂}	<i>Long.</i> _{♀♀}	<i>p'</i> _{♂♂}	<i>p'</i> _{♀♀}	<i>N</i> _{tot.} ♂♂ ± SE	<i>N</i> _{tot.} ♀♀ ± SE
<i>Colony 1</i>									
$\phi(t)p(g*t)pent(g + t_{lin+lin}^2)N(g)$	1902.4	0.00	53	7.0	7.0	0.13	0.02	1,700 ± 150	5,700 ± 1000
$\phi(.)p(g + t)pent(g + t_{lin+lin}^2)N(g)$	1902.8	0.50	24	n.a.	n.a.	0.04	0.03	1,800 ± 260	4,300 ± 800
$\phi(t)p(g + t)pent(g + t_{lin+lin}^2)N(g)$	1904.4	1.99	38	7.6	7.6	0.05	0.06	2,000 ± 220	3,800 ± 620
Model averaging								1,800 ± 380	4,800 ± 1190
<i>Colony 2</i>									
$\phi(t_{lin+lin}^2)p(t)pent(g + t_{lin+lin}^2)N(g)$	970.4	0.00	22	6.4	6.5	0.04	0.04	600 ± 120	1,500 ± 250
$\phi(t_{lin})p(t)pent(g + t_{lin+lin}^2)N(g)$	970.9	0.48	21	6.4	6.4	0.07	0.07	620 ± 100	1,580 ± 200
$\phi(g)p(t)pent(g + t_{lin+lin}^2)N(g)$	971.0	0.57	21	15.1	15.1	0.06	0.06	550 ± 90	1,550 ± 250
$\phi(t_{lin+lin}^2)p(g + t)pent(g + t_{lin+lin}^2)N(g)$	971.8	1.39	23	n.a.	n.a.	0.05	0.04	590 ± 120	1,700 ± 380
$\phi(.)p(t)pent(g + t_{lin})N(g)$	972.1	1.67	19	6.2	6.2	0.07	0.05	430 ± 40	1,380 ± 160
Model averaging								560 ± 380	1,520 ± 280
<i>Colony 3</i>									
$\phi(g * t_{lin})p(t)pent(g * t_{lin+lin}^2)N(g)$	1288.1	0.00	25	5.8	24.5	0.09	0.09	840 ± 100	660 ± 120
$\phi(g * t_{lin+lin}^2)p(g + t)pent(g * t_{lin+lin}^2)N(g)$	1288.9	0.80	28	4.6	15.6	0.09	0.09	950 ± 220	690 ± 140
Model averaging								870 ± 150	690 ± 130

* Models were selected according to AIC-criteria. For each colony, models with the lowest AIC value, plus all models with ΔAIC < 2.00 are shown

2001; 2002). In both countries, the butterfly forms dense colonies, exhibits strong protandry and males are more catchable than females. Bergman and Landin (2002) found shorter total flight distances differing between sexes (50–100 m for males, 100–150 m for females) and shorter maximum movements (around 700 m). These patterns were most probably due to differences in how dispersal reference points were allocated. The Swedish authors used finer delimitation of ‘glades’, based on perceived male territories. In our study, each of the woodland tracks considered contained several such glades. Our estimates are hence less precise for short-range movements, but should be adequate for detecting longer movements, which require the covering of a relatively large total area (Schneider 2003). Sex did not significantly influence longer-range movements in our study and both males and females migrated among colonies.

Total population size, summed across the three colonies, reached about 10,000 individuals. This estimate is subject to two sources of bias. First is the effect of terminating the marking before the end of the female flight period, which could have diminished estimates of female catchability, thus inflating estimates of female numbers. It could also underestimate total female movements if individuals showed a propensity to move longer distances later in their adult life. Such a pattern was found in Sweden (Bergman and Landin 2002) and in our data, it was suggested by increasing frequency of females encountered in flight towards end of flight season.

The second bias concerns changes in activity over time. Jolly–Seber models assume homogeneous capture probability for all individuals. This was likely violated because the butterflies flew more frequently in the mornings and at the beginning of the flight season, hiding in shrubs with progressing daytime and season. They were less apparent while in shrubs, and if detected, they more easily avoided capture. If, in addition, fresh butterflies emerge early in the mornings, which seemed to be the case, older butterflies could have been less catchable than younger ones.

Diurnal and seasonal changes in activity are common in butterflies with discrete generations, in which fitness value of mating declines with average age of females (Ide and Kondoh 2000; Konvicka et al. 2002). In woodlands with complex structure, such diurnal patterns may reduce the reliability of mark-recapture results. Notably, a change from morning/early season patrolling to afternoon/late season perching also occurs in the Asian butterfly *Lethe diana*, closely related to *L. achine* and also inhabiting sparse woodlands (Ide 2004). Detecting a magnitude of the possible biases would require a more carefully designed study, possibly with recording numbers of observed individuals that evaded capture.

In any case, the population consisted of thousands of individuals. This high number, however, does not rule out the potential threats associated with low population numbers. Bergman (2001) reported a threefold drop in peak numbers populations over just 3 years.

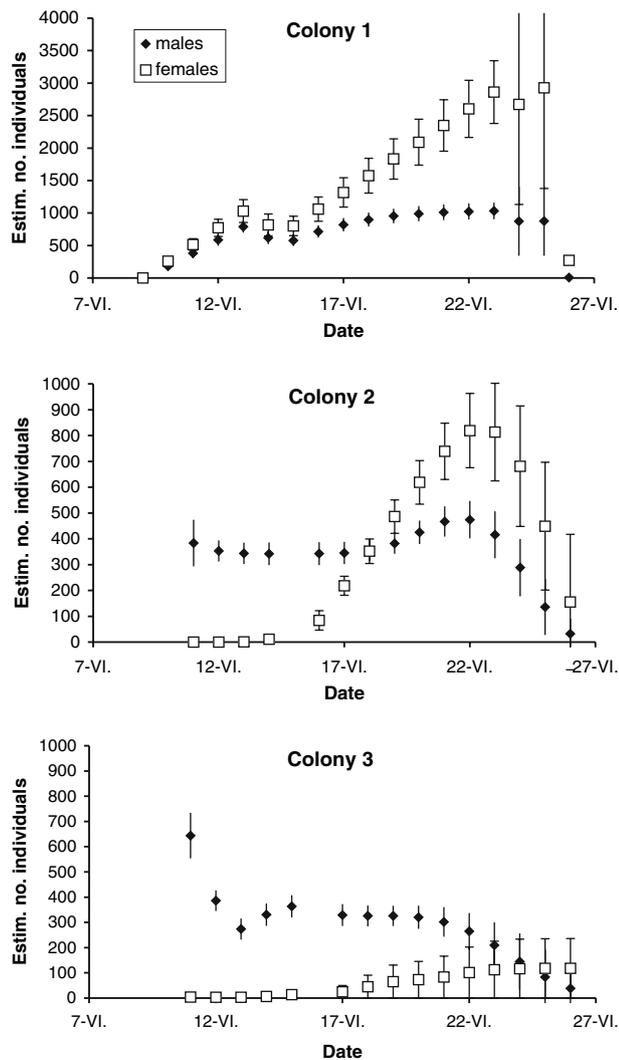


Fig. 7 Daily numbers of *L. achine* adults, and respective standard errors, in the three large colonies within the Hodoninsky Wood, as estimated by the POPAN module in MARK

To mitigate this risk, any loss of the currently occupied habitat should be prevented and efforts should be developed for restoring further patches within flight range of the butterfly.

Management implications of habitat use

There are two components of suitable *L. achine* habitat: sparse canopy and nutrient-poor ground conditions. Providing the former is technically simple via methods such as occasional selective harvest of individual trees that would maintain a spacing of 15–20 m, not followed by replanting. Eutrophication of the forest floor, however, is an increasingly recognised problem in European deciduous forests with less simple solutions (Tybirk and Strandberg 1999; Hofmeister et al. 2002; Rolecek 2005). Although

sometimes blamed on such large-scale effects as atmospheric nitrogen deposition, the cessation of forest use methods that have included exports of biomass lead to an accumulation of litter, an increase in nutrients and humidity, and gradual cooling of forest floors (Jakubowska-Gabara 1996; Rolecek 2005). Pollard et al. (1998) showed that the spread of coarse grasses in a nature reserve suppressed sensitive Lepidoptera, despite favourable management of the canopy layer. The dependency of *L. achine* on competitively poor sedges (and, possibly, on the microclimate of nutrient-poor sites: cf. Bergman 1999) indicates that soil eutrophication represents a grave risk.

As in southern Sweden (Bergman 2001; Bergman and Kindvall 2004), the past management of Czech woodlands combined coppicing, grazing, mowing and litter raking. Grazing and litter raking were prohibited in what is now the Czech Republic in the late 18th century, but the policy was hard to enforce in arable regions, where farmers had no other source of feed for their animals. Such land-use was effectively halted following centralisation of property rights in the 1950s, but small-scale, illicit mowing of the forest floor continued into the 1970s, when the last farmers of the pre-war generation gradually gave up. It is remarkable that although these developments occurred at about the same time in all woodlands formerly inhabited by *L. achine*, the butterfly has only survived in this one wood because the sandy soils have allowed nutrient leaching that likely buffered the eutrophication process.

The peculiar conditions of the last site also explain why the distribution is so restricted despite fairly good dispersal propensity. Based on the population size and parameters of the inverse power function, approximately 30 males and 20 females should move 5 km per annum. The last population is situated within an extensive forest track, but the alluvial parts to the West and sandy parts to the East are unsuitable due to completely different ground vegetation. The closest historical site, Stary Poddvorov (cf. Table 1), is situated 6 km to the north-east, but is unsuitable due to dense, closed canopy. Two further sites situated ca 20 km apart, Bile Karpaty and Bori les, still contain open stands, superficially suitable for the butterfly. However, the ground flora is now dominated by tall grasses and other nitrogen-demanding species, suggesting eutrophication has played a role in historical extinctions. Although no quantitative past/present comparisons exist, local botanists agree that the ground flora has changed substantially over last 2–3 decades, concurrently with the decline of *L. achine*. Therefore, although dispersal might allow communication among individual woodlands, the absence of appropriate management prevents a recolonisation of the historical sites.

To make matters worse, opening up the canopy (e.g., via selective harvest) may speed up eutrophication by changing light conditions and increased mineralisation of harvest

remnants (Whigham 2004). Therefore, any measures to open up the woodland should be followed by active forest floor management, be it grazing or a harvest of herbaceous vegetation and litter. Managing *L. achine* habitats is hence more challenging than managing habitats of open forest butterflies such as *Euphydryas maturna* (requiring *Fraxinus* saplings in sunny but humid conditions: Freese et al. 2006), or *Parnassius mnemosyne* (any open clearings will do: Konvicka and Kuras 1999). Still worse, the technically easiest management, occasional light grazing following removal of selected trees, remains illegal according to national legislation and is abhorred by foresters.

The establishment of the Site of Community Interest ensures that remnants of mature deciduous woodlands in the area are safe from a clearance and coniferisation. It is now the responsibility of conservation authorities to promote a management regime that would maintain the now-sparse deciduous stands in sparse conditions, open-up further stands that are now too dense, and ensure exports of nutrients from forest floor vegetation. Management of canopy might be achieved via periodic selective harvest, retaining ca 60% of canopy cover. Management of forest floor will require hand-mowing of small panels, removing of litter, and, preferentially, reintroducing of grazing. Research onto effects of these actions on ground vegetation is urgently needed, as there are few studies manipulating ground conditions in Central European woodlands. Last but not least, these actions must be accompanied by compensation payments to woodland owners, if they incur any economic losses.

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