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Factors affecting persistence of terrestrial orchids in wet meadows and implications for their conservation in a changing agricultural landscape

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Abstract

We examined the occurrence of *Dactylorhiza majalis*, the most abundant terrestrial orchid species growing in rapidly disappearing wet meadows, at 50 historical sites for 3 years. We aimed to find the most frequent reasons for its recent extinction at many sites. We found that the main reasons for its extinction were absence of mowing, intensive fertilisation and washouts of fertilisers from fields nearby. At extant sites, we studied its biometric characteristics and composition of surrounding vegetation, to determine factors affecting its persistence. Bad performance of persisting populations of this species was associated with prevalence of grasses, low May temperatures and absence of mowing. This confirms, at metapopulation level, what has previously been observed at the level of individual populations. We suggest that the system of agricultural subsidies in the country should change towards more sensitive allocation of funds to those farmers, who will adopt the appropriate management of wet meadows and their surroundings.
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1. Introduction

Extensively cultivated, species-rich wet meadows have until recently been a common part of central European landscape. These – from the viewpoint of a farmer frequently secondary – habitats are still not fully valued, not only from the landscape viewpoint (in particular the retention of water in the countryside with all its consequences for local microclimate), but also because of their high and valuable biodiversity. Decline of wet grasslands, which appeared in the past, particularly in context with intensification of agriculture, was accompanied by extinction of a lot of populations of organisms, including protected and endangered species of plants and animals associated with these habitats, e.g., terrestrial orchids. Among these was a constant companion of wet grasslands, western marsh orchid, *Dactylorhiza majalis* (Reichenb.) Hunt et Summerhayes, which we have chosen as our model species.

D. majalis represents a formerly common species, occurring in most of central Europe. From the 1960s, however, the number of sites of this species started to decline. This was demonstrated by the mapping of Jatiová and Šmiták (1996), who confirmed only 202 out of 1141 known former sites with populations of *D. majalis* in Moravia (eastern part of the Czech Republic). The main reasons for its decline are believed to include agricultural practices and the period of collectivisation (transformation of small-scale private farming into large-scale agricultural cooperatives) accompanied by large inputs of fertilisers, drainage, balk ploughing, conversion of meadows and pastures into arable land and cessation of both cattle and sheep grazing in submontane regions. A similar trend can be observed in many areas throughout the whole of Europe (Reinhard et al., 1991; Hutchings,

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1987a,b; Hutchings, 1998; Willems and Melser, 1998; Kreutz and Dekker, 2000). All these facts are well known and often repeated in literature, but exact quantification of such statements is very rare or missing. In order to fill this gap, we examined occurrence of *D. majalis*, the most abundant terrestrial orchid species in wet meadows in South Bohemia, with the aim to find quantitative answers to the following questions:

- Which plant species and communities are characteristic for occurrence of *D. majalis* and how does species composition of vegetation correlate with abundance of this species?
- How do climatic conditions affect performance of *D. majalis*?
- What were the most frequent reasons for the extinction of populations of *D. majalis* in the past thirty years?
- Can people actively support survival of this species? Specifically – does mowing improve performance of *D. majalis*?
- If the factors for the decline in *D. majalis* can be correctly identified, then this species could be used as a bioindicator for high quality meadows.

2. Methods

2.1. Species studied

Dactylorhiza majalis (Reichenb.), Hunt and Summerhayes has a relatively wide ecological amplitude. It grows from lowlands to mountains, and as one of a few species of this family it tolerates increased soil nutrients because it is less sensitive to presence of nitrogen than other orchid species (Jatiová and Šmiták, 1996). As a slightly mycotrophic heliophyte it does not grow on permanently shaded sites. According to Moravec (1983)

it can be found in stands of the alliances *Caricion fuscae* Koch 1926, Nordhagen 1936 and in *Calthion* Koch 1926, predominantly in the following communities: *Scheuchzerio-Caricetea fuscae*, *Molinio-Arrhenatheretea*, *Nardo-Callunetea*, *Alnetea glutinosa* and *Querco-Fagetea* (Procházka, 1980; Moravec, 1983). It is almost extinct from lowland basins, where it survived only in protected areas (Jatiová and Šmiták, 1996). In a wider context, the IUCN scale classifies it among the most vulnerable species. According to the Decree of the Ministry of Environment of the Czech Republic No. 395/1995 Coll. it is included in the category of nationwide endangered species. The Red Book of Endangered Flora of Czech Republic includes it in the category C3 - endangered taxa, and so does the Commented Red List of Flora of Southern Bohemia (Chán, 1999).

2.2. Study area

We collected our data on the territory of roughly 5000 km^2 in seven bioregions of Southern Bohemia (see Fig. 1): Blatensko, Českobudějovicko, Českokrumlovsko, Třebofňsko, Bechyňsko and Posázaví. Inspected sites were represented mostly by small-sized wet meadows, distributed in an agricultural landscape among forest and arable fields, between 400 and 600 m above sea level. The only exception is the site Věžovatá Pláň with altitude 788 m above sea level. Detailed characteristics of the sites were given in Wotavová (1998) and Balounová and Hrabal (1995). Structure of land cover and other characteristics of the bioregions (according to Culek et al., 1996) are presented in Table 1.

2.3. Experiments

We have used available data on sites of the marsh orchid from the years 1970 to 1989 (Gazda, 1970; Rivola
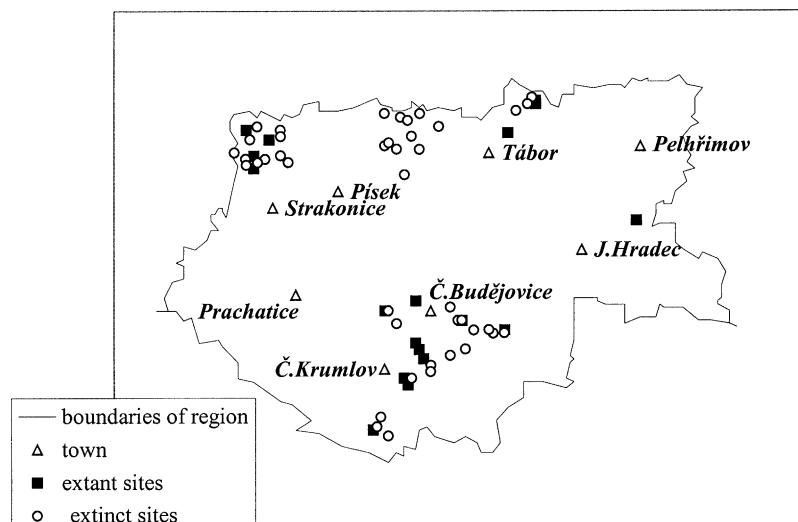

Fig. 1. Map of Southern Bohemia with visited sites.

Table 1
The structure of land cover and number of extant location in bioregions (Culek et al., 1996)

Bioregion	Area (km²)	Arable land (%)	Grassland (%)	Forest (%)	Water (%)	Number of extant sites
Bechyňsko	1613	41	10	36	3.1	1
Posázaví	1908	46	10	30	2.3	3
Českokrumlovsko	1595	29	16	40	1.8	5
Třeboňsko	1720	34	12	38	9.0	1
Českobudějovicko	703	46	13	17	8.7	4
Blatensko	786	47	15	23	4.6	4

and Knížetová, 1970; Rybníček and Rybníčková, 1970; Rivola, 1971; Kaisler and Chán, 1972; Chán et al., 1973; Kovář, 1973; Rivola, 1973; Skalický et al., 1977; Kovář, 1978; Míka, 1981; Staněk, 1982; Deyl and Skočdopolová-Deylová, 1989) for determination of known sites, where *D. majalis* formerly occurred. Fifty of these sites were visited every year during 1995–1997, always at the peak flowering time (May–June).

At each site the presence/absence of *D. majalis* was recorded and whether the site still offered the basic conditions for existence of *D. majalis*: moisture; light conditions. In the case of absence of *D. majalis* during the whole observation period of three years, the site was marked as ''extinct''; in case of finding any plants of this species in any of the years as ''extant''. This is because orchids are known for their so-called irregular flowering regime (Wells et al., 1998; Kindlmann, 1999; Kindlmann and Balounová, 1999, 2001; Carey, 1999), which is an irregular sequence of flowering, dormant and vegetative stages during the life of one individual. Thus, absence of flowering plants at a site in one year may mean that all plants are either dormant or vegetative and therefore inconspicuous and overlooked in the vegetation in that particular year. The claim that a population is extinct should thus be supported by several consecutive years of observations, during which no plant was found at the site. Three years absence does not mean the population is definitely extinct but there is a strong likelihood that it is.

At extinct sites, reasons for extinction of *D. majalis* were estimated and divided into four groups:

- *Fertilisation*: excessive load of nutrients due to artificial fertilizers applied, causing change in trophic conditions and manifested by a change in phytocoenotic conditions in favour of species, which tolerate or require a higher content of nutrients.
- *Drainage*, causing change in water regime.
- *Destruction* of the site (converted into an estate, road, submersion due to building a water dam nearby, etc.)
- *Unknown* – probably increased run-off of nutrients from neighbouring fields and absence of cultivation.

In extant sites, numbers of flowering individuals at each site were counted every year, and the frequency and viability of the population was estimated and expressed using a five-point scale (Table 2). Thus, codes 1 and 2 mean ''bad'' sites, code 3 means ''medium'' site, codes 4 and 5 mean ''good'' sites.

To characterise the phytosociological position of extant sites, one releve on a randomly chosen 2×2 m plot was made using the Braun–Blanquet cover – abundance scale (Moravec, 1994) in the first half of July. Plant nomenclature follows Dostál (1989).

For answering the question, to what extent the species composition of vegetation correlates with abundance of *D. majalis* at extant sites we used CANOCO (ter Braak, 1990) direct redundancy analysis RDA with Monte Carlo permutation test. Direct gradient analysis is a method to find the directions of variability in phytocoenotic data, which correlate with the explanatory environmental variable (Lepš and Šmilauer, 2003), represented in our case by the quality of the site, estimated as the code of population (Table 2).

During the years 1999–2001 detailed biometric measurements were performed at seven extant sites, Hradce (Hr); Vrbenske rybniky (Vr); Milikovice (Mil); Cakov (Cak); Ohrazeni (Ohr); Sumava 1 (Sul) and Sumava 2

Table 2
Key to state of *D. majalis* population

Category	State of population	Number of plants
0	Local extinction of species	0
1	Population close to extinction; declining number of plants	1–10
2	Stable population; low, but not declining number of plants	1–10
3	Stable population	10–100
4	Stable population, large number of plants	100–1000
5	Very large population	1000+

''Stable number of plants'' means that the correlation coefficient between the number of flowering individuals and time was not significantly negative at 5% significance level.

(Su2). These sites contained more than 50 flowering individuals (in order to get statistical significance) and were close enough to the source of our meteorological data to give meaningful climate relationships. Two of them were mown every year (Hr and Vr), one was mown every other year (Mil), and 4 were unmown (Cak, Ohr, Sul and Su2).

At each site 50 flowering individuals were chosen at random in 1999, and marked by a nail with attached number on a metallic stripe close to the plant. Each year, length and width of each leaf of each of these individuals was measured and the total leaf area of the plant was estimated by calculating $\sum_{\text{all leaves}}$(length × width)/2 as in Kindlmann and Balounová (1999). The measurements were always performed in the second half of May, at the peak flowering period of *D. majalis*, when the leaves reached their maximum size.

The influence of site and year on the total leaf area of adult flowering plants was detected by means of a 2-way ANOVA with subsequent post hoc comparisons (Tukey HSD test) on the categorical factor Site and with subsequent correlation analysis on the factor Year characterized by numeric variables: average monthly precipitations and average monthly temperatures. Plants that were vegetative in any of the three years were likely to be juveniles or have been damaged in previous years (Kindlmann and Balounová, 1999, 2001). Because the interest was in the population rather than the individual, these vegetative plants were excluded from analysis. Therefore, we used only 10 randomly selected individuals per site and year, which flowered consecutively for all three years (1999–2001) for the ANOVA analysis (unbalanced ANOVA with all plants would not enable us to calculate interactions).

For the same cohort of 50 plants, type of appearance (flowering, sterility, missing) was monitored also in 2001 and the percentages of flowering, vegetative and missing plants during 1999–2001 were compared between sites. The rate of decline of the number of plants in the cohort that appeared above ground (the parameter r in the equation of exponential decay, $dx/dt = rx$, where x is the number of individuals above ground at year t) was calculated for each site.

The statistical analyses were performed using Statistica software. Meteorological data were obtained from the records of the České Budějovice Meteorological Station located at the centre of the region surveyed.

3. Results

3.1. Correlation between vegetation cover and orchid performance

All extant sites belong to the *Calthion* union in different degrees of degradation. One site belongs to the sub-union *Filipendulenion* with a high degree of coverage of dominant *Filipendula ulmaria* (75%) and the rest belongs to the sub-union *Calthenion*. From the RDA analysis (Monte Carlo Permutation test = 0.01 – Fig. 2) it follows that grasses and the dominant *Filipendula ulmaria* are concentrated at "bad" sites (codes 1 and 2 in Table 2).

Neither the abundance of *D. majalis* was correlated with the total coverage of herb layer ($r = 0.11$, $df = 1.13$, $p = 0.69$) nor the average total leaf area of *D. majalis* was significantly affected by the number of plant species at the site $r = 0.32$, $df = 1.13$, $p = 0.23$).

3.2. Effect of climatic conditions

The average total leaf area of *D. majalis* was significantly influenced by both Site and Year (ANOVA, $F = 7.26$, $p < 0.001$ and $F = 9.93$, $p < 0.001$, respectively). Effect of site was primarily connected with the type of its management and will be dealt with in Section 3.4. Effect of year reflects climatic conditions and is analyzed in Table 3. Most conspicuous is the highly significant ($p < 0.01$) positive correlation between May temperatures and total leaf area of the orchids. June precipitation was positively and May precipitation negatively associated with total leaf area of *D. majalis*. These correlations are, however, not significant probably because of the short duration of our observations (only 3 years).

3.3. Aspects of decline in the number of sites

The results of the inspections during 1995–1997 are shown in Table 4. Only about 1/3 of the known former sites still had populations and the absence of cultivation (mowing in this case), included in the "unknown" reasons for extinction and direct fertilisation were the most important reasons for extinction of the populations of *D. majalis* in the studied sites. Only 18% of all extant sites were larger than 0.5 ha, 35% of sites were mown and 44% of sites were waterlogged. The sizes of populations were considerably unbalanced, only 24% of populations consisted of more than 100 plants and 46% of populations consisted of less than 10 plants. The percentage cover of grasslands in a bioregion was significantly positively correlated with the number of extant sites in the bioregion ($r = 0.87$, $df = 1.4$, $p = 0.025$), but the percentage cover of arable land or forests were not.

3.4. Effect of management

The Tukey HSD test revealed that the average total leaf area was significantly the largest at the regularly mown sites Hr and Vr, followed by the site Mil, which was mown every other year and significantly lowest at unmown sites Sul, Ohr (Fig. 3). Total leaf area at unmown sites Su2 and Cak was smaller, but not significantly different from that at the site Mil.
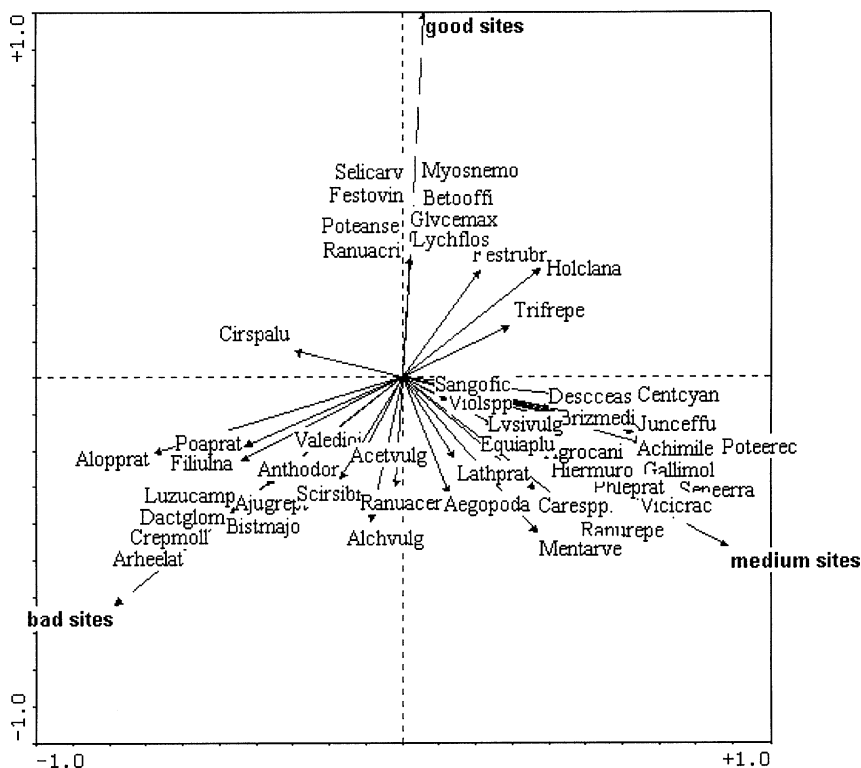
Fig. 2. Results of RDA; quality of 17 extant sites measured as the viability estimate (category defined in Table 2). *Legend*: bad sites, viability estimate 1 and 2; medium sites, viability estimate 3; good sites, viability estimate 4 and 5; Acetvulg, *Acetosa vulgaris*; Aegopoda, *Aegopodium podagraria*; Agrocani, *Agrostis canina*; Achimile, *Achillea milefolium*; Ajugrept, *Ajuga reptans*; Alchvulg, *Alchemilla vulgaris*; Alopprat, *Alopecurus pratensis*; Anthodor, *Anthoxanthum odoratum*; Arheelat, *Arhentherum elatius*; Avenflex, *Avenella flexuosa*; Betooffi, *Betonica officinalis*; Bistmajo, *Bistorta major*; Brizmedi, *Briza media*; Carespp, *Carex* spp.; Centcyan, *Centaurea cyanus*; Cirspalu, *Cirsium palustre*; Crepmoll, *Crepis mollis*; Dactglom, *Dactylis glomerata*; Descces, *Deschampsia cespitosa*; Equipalu, *Equisetum palustre*; Festovin, *Festuca ovinae*; Festrubr, *Festuca rubra*; Filiulma, *Filipendula ulmaria*; Galimolu, *Galium mollugo*; Glycemaxi, *Glyceria maxima*; Hiermuro, *Hieracium murorum*; Holclana, *Holcus lanatus*; Junceffu, *Juncuc effusus*; Lathprat, *Lathyrus pratensis*; Luzucamp, *Luzula campestris*; Lychflos, *Lychnis flos-cuculi*; Lysivulg, *Lysimachia vulgaris*; Mentarve, *Metha arvensis*; Myosnemo, *Myosotis nemorosa*; Phleprat, *Phleum pratense*; Poaprat, *Poa pratensis*; Poteanse, *Potentilla anserina*; Poteerec, *Potentilla erecta*; Ranuacer, *Ranunculus acer*; Ranuacri, *Ranunculus acris*; Ranurepe, *Ranunculus repens*; Sangofic, *Sanquisorba officinalis*; Scirsilv, *Scirpus silvaticus*; Selicarv, *Selinum carviflora*; Seneerra, *Senecio erraticus*; Trifrepe, *Trifolium repens*; Valedioi, *Valeriana dioica*; Vicicrac, *Vicia cracca*; Violspp, *Viola* spp.

Table 3
Correlation coefficients between average total leaf area of *D. majalis* and climatic variables: average monthly precipitations and average monthly temperature

Month	Precipitations	Temperature
April	−0.09	0.50
May	−0.88	0.99
June	0.81	0.56

Table 4
Percentage representation of reasons for extinction of *D. majalis*

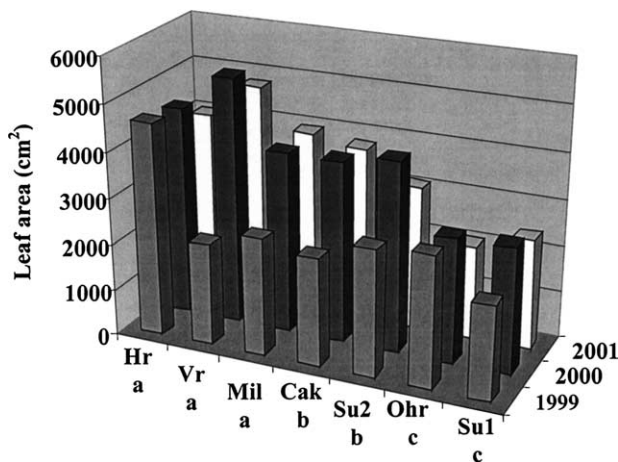| Reason for extinction	% of sites
Unknown	26
Destruction	8
Drainage	12
Fertilisation	20
Extant sites	34

Fig. 3. Total leaf area of *Dactylorhiza majalis* at the peak flowering time (mid May) in 1999–2001 at 7 studied sites. Sites mown every year are indicated by Hr, Vr, site mown every other year by Mil and un-mown sites by Cak, Ohr, Sul and Su2. Sites are ranked according to the total leaf area. The letters below the codes for sites are results of the Tukey HSD test (different letters = significant difference, $p = 5\%$).

Table 5
Rate of decline, r, of the number of individuals that appeared above ground from the initial cohort of 50 individuals per site at 7 sites during years 1999–2002

Management	Site	r
Mown every year	Hr	−0.19
	Vr	−0.13
Mown once in 2 years	Mil	−0.10
Unmown	Cak	−0.27
	Ohr	−0.20
	Sul	−0.33
	Su2	−0.35

Sites sorted according to the type of management.

The effect of management (mowing) is even more clearly seen from the analysis of the type of performance (flowering, vegetative, missing) during the years 1999–2002 presented in Table 5. The rate of decline of the number of plants that appeared above ground from the initial cohorts of 50 flowering individuals per site was similar for sites mown every year and mown once in 2 years, but was much larger at unmown sites (Table 5). The differences in the rates of decline of the number of plants that appeared above ground are also evident from Fig. 4, which – in addition – illustrates that the percentage of vegetative plants does not visibly reflect the type of management.
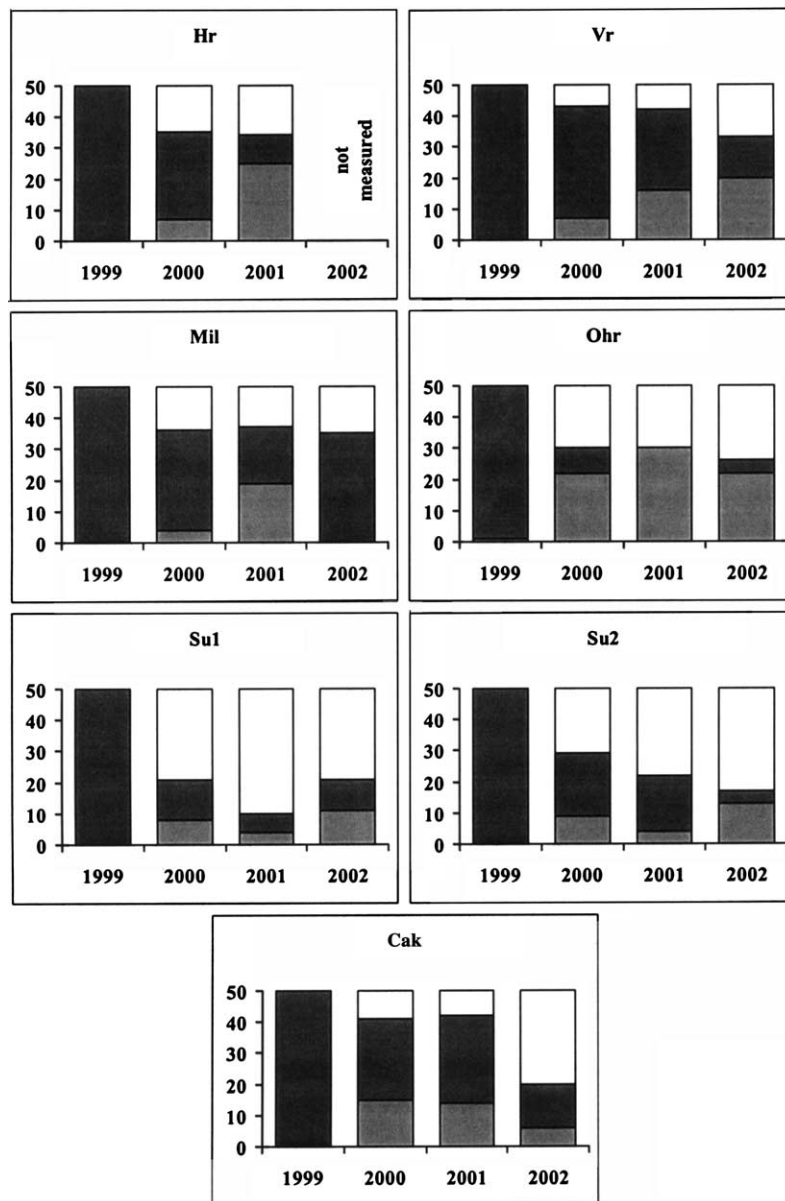

Fig. 4. Numbers of flowering (dark shaded columns), vegetative (lightly shaded columns) and missing (white columns) individuals from the initial cohort of 50 individuals of *Dactylorhiza majalis* at the peak flowering time (mid May) in various years and at various sites. Sites Hr and Vr are mown every year; site Mil is mown every other year and sites Cak, Ohr, Su1 and Su2 are unmown.

4. Discussion

4.1. Rate of decline in the number of sites

The proportion of extant sites found in this study is larger than that found in Moravia by Jatiová and Šmiták (1996). This may be because we based our selection of sites on relatively recent literature (from the 70s and 80s) and therefore the decline of occurrence of the species was not so dramatic, as the time period that passed between collection of the literature data and our research was relatively short. Before making any general conclusions, however, it is important to realize two points: (1) History of the species has to be seen as a continuous process of extinctions and colonisations within a metapopulation (Gilpin and Hanski, 1991) and therefore following only the decline of the number of sites starting from some initial "cohort" of historical sites is only one side of the coin (e.g., see historical pattern of *Himantoglossum hircinum* in England in Carey, 1998). Thus, the decline of the Moravian *D. majalis* populations from 1141 historical sites to 202 present ones (Jatiová and Šmiták, 1996) has to be accompanied by knowledge that many new sites have appeared in the meantime, so that the number of present sites equals 598. (2) Although the *absolute number* of extant *D. majalis* sites is not low, the *rate of their decline* is worrying. Thus, it is not only the present amount of, but also the temporal trend in the number of sites, which determines species "rarity" in terms of its conservation.

4.2. Reasons for decline in the number of sites

We found that the main reasons for decline of *D. majalis* were absence of mowing and intensive fertilisation (or washouts of fertilisers from fields nearby). Negative effect of modern agricultural management on the occurrence of orchid populations has been confirmed by several manipulative experiments (Dijk and Olff, 1994; Silvertown et al., 1994; McKendrick, 1996; Jersáková, 1996). Thus, our data confirm that these trends observed at the level of individual populations may significantly affect metapopulation dynamics of the species by negatively affecting the number of its extant sites.

Increased concentration of nutrients in soil is progressively manifested by visible changes in composition of the phytocoenosis. With increasing rate of eutrophication, competitively stronger nitrophilous species are taking over. Under regular fertilisation, however, phytocoenotic conditions in meadows favour grasses (Procházka, 1980). Total effect of nutrients is the result of a combination of direct or vegetation-mediated effects. Which of these is greater has not yet been unambiguously confirmed (Dijk and Olff, 1994). However,

there are positive correlations between orchid performance and abundance of herbs and negative correlations between orchid performance and abundance of grasses (Dijk and Olff, 1994). In our study, sites with low number of orchids, close to extinction, were especially characterised by prevalence of grasses. The majority of existing populations of *D. majalis* belonged to the community of sub-union *Calthion* of the order *Molinietalia* Koch 1926. This order includes grass or herbal stands of wet or moist sites, which are at least at the beginning of the vegetation season under the influence of groundwater or floodwater. These are all substitute communities after corresponding types of woods, i.e., after alder woods, floodplain forests, damp oak-hornbeam woods, etc.

The highly significant positive correlation between May temperatures and total leaf area of the orchids means that in May – when most of the leaf growth occurs in this species – high temperatures result in large leaf area. As high temperature is associated with a lot of sunshine, this is in accord with the heliophytic status of *D. majalis* and with the fact that this species performs better at mown sites, where vegetation from the previous year has been removed prior to the onset of *D. majalis* growth in early spring, thus allowing access of light for the growth of this species. These results, however, have to be taken with care, as our time series is very short – only three years.

The heliophytic status and low competitive abilities of *D. majalis* in nutrient-rich conditions mean that besides nutrient level, appropriate management is also vital for its survival. This is a general phenomenon, as many species of terrestrial orchids occur especially in secondary forest-free areas, meadows and pastures created by humans. Therefore, appropriate vegetation management of the site is essential for the orchid populations to persist (Willems and Lahtinen, 1997; Hutchings et al., 1998; Willems and Melser, 1998). Vegetation management, usually summer mowing and grazing, helps to maintain the relatively low-growing herbaceous vegetation that the orchids require (Bowles, 1983; Wheeler et al., 1998). Our results support this statement. We have found that mowing improves the performance of *D. majalis*, at least in yielding consistently larger individuals and lowering the rate of disappearance when the fate of a cohort of plants is followed. Thus, once sites are abandoned, they loose their orchid flora due to lack of traditional management and enhanced competition with surrounding vegetation (Silvertown et al., 1994; Sieg and King, 1995), mainly because of competition for light (Willems et al., 2001).

4.3. Conservation implications

Bearing the results presented above in mind, the recent trends in agriculture in central Europe render a

relatively optimistic prognosis for the future of *D. majalis* and other terrestrial orchid species living in wet meadows: Because of economic reasons, fertilisers are now applied only at intensively utilised meadows where no orchids can be found. Also drainage as a method of "improvement" of agricultural land is not being applied any more in the post-communist countries in central Europe, as the governments are aware of its negative consequences and ceased its financial support.

However, orchid populations seem to be still endangered indirectly by washouts from the fields, a factor with long-term and gradual effects, because of which no evident changes in biotope occur for a long time: the number of plants is gradually declining from year to year up to the extinction of population (Reinhard et al., 1991). Although *D. majalis* is considered to be capable of a relatively long resistance to increased nutrient level compared with other terrestrial orchid species (Procházka, 1980), it cannot survive high concentrations or permanently increased supply of nutrients for a long time, probably because it is overgrown by other species (Willems et al., 2001).

Maintenance of faunistically or floristically valuable sites is financed by governmental nature conservation authorities in the Czech Republic. They pay volunteer NGOs, farmers or professional organizations for performing proper management at the protected sites. However, the amount of money they can operate with is limited and not satisfactory for maintenance of all sites, which are worth protection. Therefore, also attractive *agricultural* subsidies should be made available to persuade farmers themselves to adopt the appropriate management of wet meadows.

The present system of agricultural subsidies in the Czech Republic does support management of meadows on poor soils. However, it does *not* distinguish sites according to their conservation value. Neither correct timing of mowing, nor proper management (reduction of fertilizer use) of sites adjacent to the valuable ones are made a necessary condition for obtaining the subsidies. Thus, there is no feedback on farmers, which mow or graze the meadows at the time convenient or economically profitable only for themselves, which is often the time when terrestrial orchids are in full bloom. Neither is there a penalty for those, who heavily fertilize fields adjacent to wet meadows. Being wet, these meadows are usually located below the fertilized fields and therefore collect washouts. This causes eutrophication and subsequent degradation of the wet meadows. Therefore, the system of agricultural subsidies should change towards more sensitive allocation of funds to those farmers who are ready to adopt the appropriate management of wet meadows and their surroundings. Since the Czech Republic is about to join the EU and the Common Agricultural Policy is about to change, it is extremely important that agricultural subsidies should be directed to protecting the remaining meadows and not to agriculturally improve them.

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