

# Resource use of specialist butterflies in agricultural landscapes: conservation lessons from the butterfly *Phengaris (Maculinea) nausithous*

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Received: 4 October 2011 / Accepted: 9 March 2012 / Published online: 22 March 2012  
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**Abstract** Most of the European grassland butterfly species are dependent on species rich grasslands shaped by low intensity farming. Conservation of these specialist species in agricultural landscapes relies on knowledge of their essential resources and the spatial distribution of these resources. In The Netherlands, the dusky large blue *Phengaris (Maculinea) nausithous* butterflies were extinct until their reintroduction in 1990. In addition, a spontaneous recolonization of road verges in an agricultural landscape occurred in 2001 in the southern part of The Netherlands. We analyzed the use of the essential resources, both host plants and host ants, of the latter population during the summers of 2003 and 2005. First we tested whether the distribution of the butterflies during several years could be explained by both the presence of host plants as well as host ants, as we expected that the resource that limits the distribution of this species can differ between locations and over time. We found that oviposition site selection was related to the most abundant resource. While in 2003, site selection was best explained by the presence of the host ant *Myrmica scabrinodis*, in 2005 it was more strongly related to flowerhead availability of the host plant. We secondly compared the net displacement of individuals between the road verge population and the reintroduced population in the Moerputten meadows, since we expected that movement of individuals depends on the

structure of their habitat. On the road verges, butterflies moved significantly shorter distances than on meadows, which limits the butterflies in finding their essential resources. Finally we analyzed the availability of the two essential resources in the surroundings of the road verge population. Given the short net displacement distances and the adverse landscape features for long-distance dispersal, this landscape analysis suggests that the *Phengaris* population at the Posterholt site is trapped on the recently recolonized road verges. These results highlight the importance of assessing the availability of essential resources across different years and locations relative to the movement of the butterflies, and the necessity to carefully manage these resources for the conservation of specialist species in agricultural landscapes, such as this butterfly species.

**Keywords** *Phengaris (Maculinea) nausithous* · *Myrmica* · Habitat management · Oviposition site selection · Host specificity

## Introduction

Most of the European grassland butterfly species are dependent on open grasslands rich in plant species, which are shaped by years of low intensity farming (Van Swaay 2002). These grasslands were common at the outskirts of almost all villages and cities, but nowadays in the North-west of Europe, they can only be found in nature reserves and along linearly shaped landscape elements, such as road verges, ditches and stream banks. This habitat reduction and fragmentation have led to a drastic decline in butterfly diversity, particularly among specialist species (Aviron et al. 2007; Blair and Launer 1997; Poschlod et al. 2005; Van Swaay 1990; Van Swaay et al. 2006; Wenzel et al.

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2006). The remaining patches with vegetation resembling the former extensively managed grasslands are usually inhabited by low numbers of generalist butterfly species while specialist species are rare (Duelli and Obrist 2003; Kivinen et al. 2008).

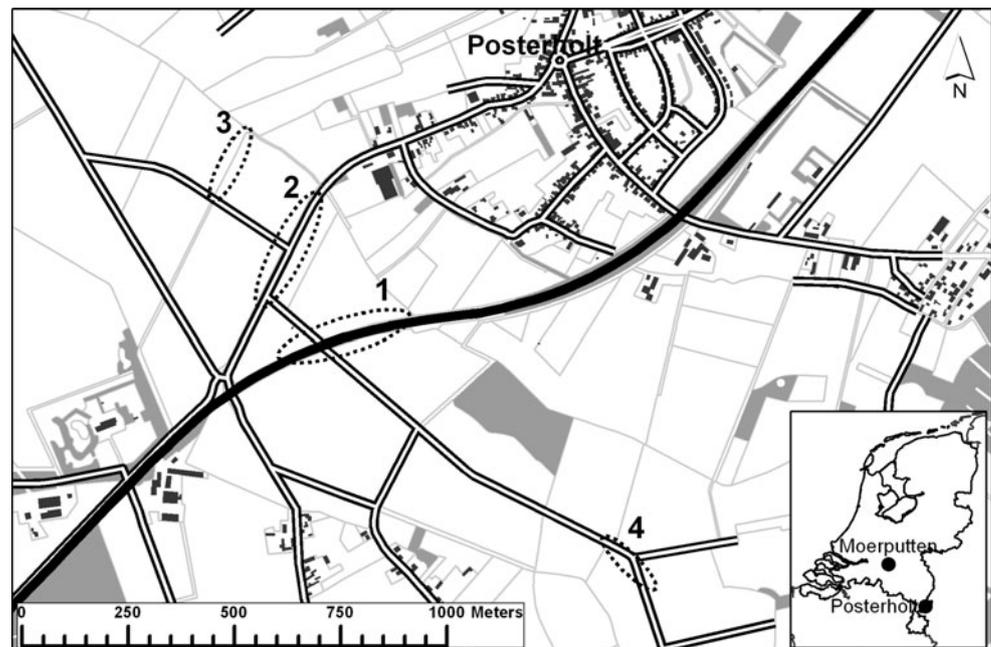
One of the few specialist butterfly species that can survive in small nature reserves and on linearly shaped landscape elements is the dusky large blue *Phengaris (Maculinea) nausithous* (European Union Habitats Directive App. II and IV, IUCN Red List of European Butterflies, Dutch National Red List; Van Swaay et al. 2011). In the southern parts of The Netherlands, this butterfly species used to be quite common on hay meadows and pastures. In the 1960s, population numbers declined sharply to be finally declared locally extinct in 1976 when the last population disappeared (Bos et al. 2006; Boeren et al. 2011). The butterflies were reintroduced in the center of the Netherlands in 1990 in the nature reserve Moerputten (Fig. 1, Wynhoff 2001; Wynhoff et al. 2008), originating from a Polish source population (Wynhoff 1998b). Independent from the reintroduction and rather unexpectedly, in 2001, a few individuals from small remnant stream bank populations across the border with Germany spontaneously recolonized several road verges close to the village of Posterholt in the south of the Netherlands, which is at a distance of about 90 km from the reintroduction site (Fig. 1; Wynhoff et al. 2005).

The conservation of rare species like this one relies strongly on a deep understanding of their essential resources and the spatial distribution of these resources (Dennis et al. 2006; Vanreusel and Van Dyck 2007; Van Langevelde and Wynhoff 2009). *P. nausithous* butterflies have a complex

life cycle in which they engage in multitrophic interactions with two host species, the plant *Sanguisorba officinalis* on which butterflies deposit their eggs and young larvae feed, and specific *Myrmica* ant species in which nests the latest instar caterpillars spend 10 months feeding on grubs and overwintering (Thomas 1984). Although the caterpillars of *P. nausithous* are adopted by all *Myrmica* ant species, the survival rate in the nests of different ant species varies (Thomas et al. 1989; Munguira and Martín 1999; Stanekiewicz and Sielezniew 2002; Tartally and Varga 2005; Tartally et al. 2008). It has been suggested that the preferred ant species for *P. nausithous* is *Myrmica rubra*, but in the absence of this ant species the caterpillars are found in *M. scabrinodis* nests (Pech et al. 2007; Tartally et al. 2008; Witek et al. 2008).

The evidence of selection of oviposition sites by this butterfly species based on plant and ant resources is controversial. There is some evidence indicating that females select sites based on vegetation characteristics regardless of the presence of host ant species (Thomas and Elmes 2001; Musche et al. 2006, Fürst and Nash 2010), whereas other studies suggest that *Phengaris* butterflies select for both resources (Van Dyck et al. 2000; Wynhoff et al. 2008; Van Langevelde and Wynhoff 2009; Van Dyck and Regniers 2010; Patricelli et al. 2011). It has been shown that oviposition site selection by this species depends on butterfly density: visits of adult butterflies to plots with the host plant but without the host ants especially occurred in years with high butterfly densities (Wynhoff et al. 2008). Due to differences in climate, management and the possible negative impact of the caterpillars on the nests of their host ants, densities of butterflies and host ant nests can vary

**Fig. 1** Location of four patches with the host plant *S. officinalis* for the study on *P. nausithous* next to the village of Posterholt (The Netherlands). On the small map the location of Moerputten and Posterholt in The Netherlands. *Black lines* main roads, *white lines* minor roads, *black areas* houses, *gray areas* forest, *white areas* agricultural fields



between years (Nowicki et al. 2009). The resource that limits oviposition site selection of this butterfly could therefore be different between areas and over time.

The extremely specialized interaction with both host plants and host ants imposes challenging restrictions for the survival of *P. nausithous* populations. Since the butterfly population has been able to survive in fragmented agricultural landscapes, such as those found in the area surrounding Posterholt, where both host plants and host ants are scarce and scatteredly distributed, we test whether the occurrence of butterflies during several years can be explained by both the presence of host plants as well as host ants. We compare the use of these essential resources of the spontaneously recolonized population with other studies on oviposition site selection of *P. nausithous*.

When movement along linear elements is limited to short distances, we also expect that individuals of expanding populations on spatially restricted habitat, like road verges, move differently, while searching for the essential resources as compared to individuals of populations on meadows (Van Langevelde and Grashof-Bokdam 2011; Hovestadt and Nowicki 2008). We compare net displacement data measured in Posterholt with the net displacement data of the reintroduced Moerputten population. Finally we analyze the surroundings of Posterholt to predict whether the spontaneously recolonized population could find their essential resources given the spatial distribution of these resources in the surroundings.

## Methods and materials

### Study area

The study area is located near the village of Posterholt (51° 08' 00"N, 6° 02' 00"E) within the valley of the river Roer, in the Limburg province of The Netherlands (Fig. 1). This area is at the margins of the distribution range of *P. nausithous* in Northwestern Europe (Wynhoff 1998a). The typical agricultural landscape is dominated by fields with fodder crops (mainly wheat and corn), pastures and small human settlements. After the new population of the butterflies at Posterholt was discovered in 2001, in the next 2 years we mapped all host plants, *S. officinalis*, in the nature reserves, road verges and stream borders up to a distance of 6,655 m from the recolonized site. This investigation included all sites where the butterfly species had been observed until its extinction in The Netherlands (Bos et al. 2006). In the consecutive years the population was monitored by transect counts and several mark-release-recapture (MRR) studies. We determined the availability of host ants at 1,023 plots of 1-m<sup>2</sup> around a single host plant or a group of host plants by using sugar

cubes as bait to attract ants. Sugar baits were placed on a concave glass covered by black plastic at the foot of a host plant during the morning hours and checked after 2 h. We kept the attracted ants in alcohol for later identification in the laboratory. Baits without ants were left in the field and were checked regularly every 2 h until the end of the day.

It appeared that the butterfly flight area was limited to road verges and banks of drainage canals that are covered with their host plant. We identified four patches with host plants (Fig. 1), 10–20 m wide and between 100 and 300 m long including the recolonized site and located within the expected dispersal range of the species (Van Langevelde and Wynhoff 2009). We sampled the small population of *P. nausithous* butterflies during their flight period between July and August in 2003 and 2005 using the MRR method. In 2003, weather conditions were comparatively warm for this region (mean temperature in July 18.8 °C, in August 19.3 °C), dry (July 57 mm, August 22 mm rainfall) and shiny (240 and 241 h of sunshine in July and August respectively). In contrast, the weather during the flight period of 2005 was cooler (mean temperature in July 17.7 °C, in August 16.2 °C), rainy (116 and 82 mm rainfall in July and August respectively) and with lower irradiance (July 163 h, August 193 h). These conditions depart from the long term average conditions in The Netherlands (period from 1971 to 2000) in July (17.4 °C, 70 mm rainfall, 201 sunshine hours) and August (17.2 °C, 62 mm rainfall, 198 h of sunshine).

### Flowerhead availability and ant species presence

Within the four selected host plant patches, we randomly distributed 1-m<sup>2</sup> plots (80 plots in 2003, with patch 1: 24 plots; patch 2: 22 plots; patch 3: 26 plots; patch 4: 8 plots; 77 plots in 2005, with patch 1: 35 plots; patch 2: 21 plots; patch 3: 14 plots, patch 4: 7 plots; Fig. 1). At the beginning of the flight period, we counted the total number of flowerheads present at the shoots of all host plants in each plot. We used the number of flowerheads as a measure for resource availability since the flowerheads provide a place for oviposition and are the main source of nectar for this butterfly species. We sampled the ants directly after the flight period of the butterflies when most caterpillars are still on the flowerheads. This reduces the effect of ant nest disturbance on caterpillar survival. The ants were baited with sugar cubes in the center of each plot in the same way as described above. In the analyses, we used all plots with *Myrmica* species present, but also the plots with other ant species and the plots without ants. In these latter categories caterpillars are expected to die because they are foraged upon or because they will not be found and adopted by the ants to survive the winter.

## Butterflies and oviposition

The MRR study allowed us to estimate population sizes during the flight season of both 2003 and 2005. On the four patches (Fig. 1), the butterflies were captured with a net and then marked with an individual code number using a fine-tipped Lumocolor overhead pen with permanent ink. After marking the butterflies were released immediately. For each butterfly captured, we measured and noted the GPS-coordinates. Sampling was conducted on 22 days in 2003 and 24 days in 2005 under appropriate weather conditions. In 2003, only during 4 single days in the flight period no butterflies were captured and marked, while in 2005 we were able to mark them on each day. An oviposition was recorded when a female not only touched the flowerhead with her abdominal tip but also squeezed the tip between the flowerbud and then froze to release the egg. In addition, in 2005, we collected 10–20 flowerheads in each plot and searched for egg remnants as an indirect evidence of oviposition. The flowerheads were collected after the caterpillars had left their host plant about 4 weeks after the end of the flight period. We estimated the minimal population size by Minimal Number Alive (MNA; Amler et al. 1999) and the total population size according to Jolly-Seber (Begon 1979).

## Butterfly net displacement

We used the GPS coordinates from the captures and recaptures to calculate the net displacement of a butterfly between captures. The data were analyzed to find differences of net displacement between years, gender and number of days between recaptures. In this analysis the data of the reintroduced population of *P. nausithous* in the nature reserve Moerputten in 1990 were included. This nature reserve consists of a central lake surrounded by tall beds of *Phragmites*, *Typha* and tall *Carex* species. Around these, moist forests are present nowadays where wet meadows used to occur when the area was still in agricultural use. On the outer borders of the nature reserve, partially within the forest, different types of grasslands are found, of which the hay meadows with a high abundance of *S. officinalis* are most important as habitat of *Phengaris* butterflies. For a detailed description of the Moerputten site see Wynhoff (1998b) and Wynhoff et al. (2008).

## Statistical analysis

We analyzed the data on resource use of the 2 years separately, because the weather conditions during the flight period and the butterfly population density were very different between the years. We checked the normality of the data by testing the residuals for using either a parametric or

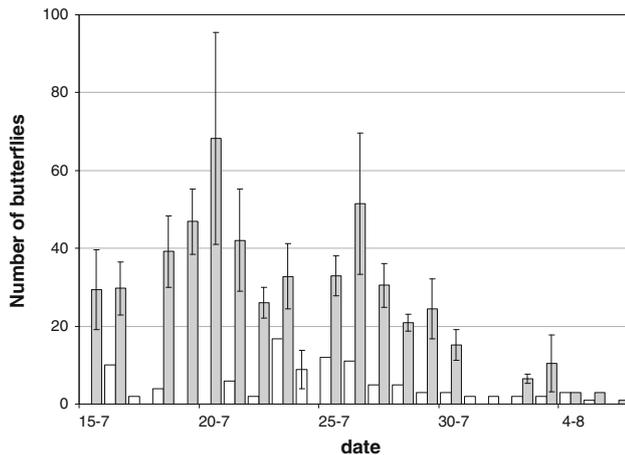
a non-parametric test. An Anova test was used to assess for differences in flowerhead availability between the plots occupied by different ant species, namely *M. rubra*, *M. scabrinodis*, *M. ruginodis*, a mix of *Myrmica* species, non-*Myrmica* species and ant free plots. A t-test or Mann–Whitney test was used to test for differences in flowerhead availability between years and between plots where butterflies and ovipositions were observed versus the plots where butterflies and ovipositions were not observed. The Kruskal–Wallis test was used to test whether the number of observed butterflies differed between plots occupied by these categories of ant species. We used logistic regressions to model oviposition site selection (i.e. probability of butterfly presence) and oviposition behavior (i.e. probability of oviposition presence) as a function of resource availability expressed as the number of flowerheads and the presence or absence of the different ant species for each year separately. The mean net displacement of the butterflies was analyzed using a General Linear Model (GLM) with a pairwise comparison according to the Sidak post hoc test (Field 2005). In this analysis the number of days in between capture and recapture was taken as covariable.

## Results

In 2003, 38 individuals (sex ratio males:females = 0.41) of *P. nausithous* were marked, of which 41.0 % were recaptured. In 2005 the population was larger. We captured 89 butterflies (sex ratio males:females = 0.71) and achieved a recapture of 68.5 %. The estimated population size of *P. nausithous* in 2005 was approximately 160 butterflies, almost three times larger than in 2003 with 54 individuals. In 2003, the total number of butterflies during the whole flight period was not much higher than the minimal population size of 48 butterflies. This indicates that not many butterflies have escaped our attention. In 2005, even though more than half of the marked individuals have been recaptured at least once, the estimated total population size was higher than the minimal population size of 100. The within-season daily population size dynamics is presented in Fig. 2. In both years the butterflies were observed only in patches 1 and 2 (Fig. 1).

## Flowerhead and host ant availability

We found three *Myrmica* ant species in the 1-m<sup>2</sup> plots: *M. rubra*, *M. scabrinodis* and *M. ruginodis* (Table 1). In 2005, there were fewer plots with ant species present than in 2003. This was especially the case with *M. rubra*. In general, plots with *M. ruginodis* or with a mix of *Myrmica* species appeared to be quite rare. The most common non-*Myrmica* ant species was *Lasius niger*.



**Fig. 2** Daily population size of *P. nausithous* in the flight period of 2003 (white bars) and 2005 (gray bars) at the Posterholt site in The Netherlands. The daily population size was estimated according to Jolly Seber. Error bars represent the standard errors

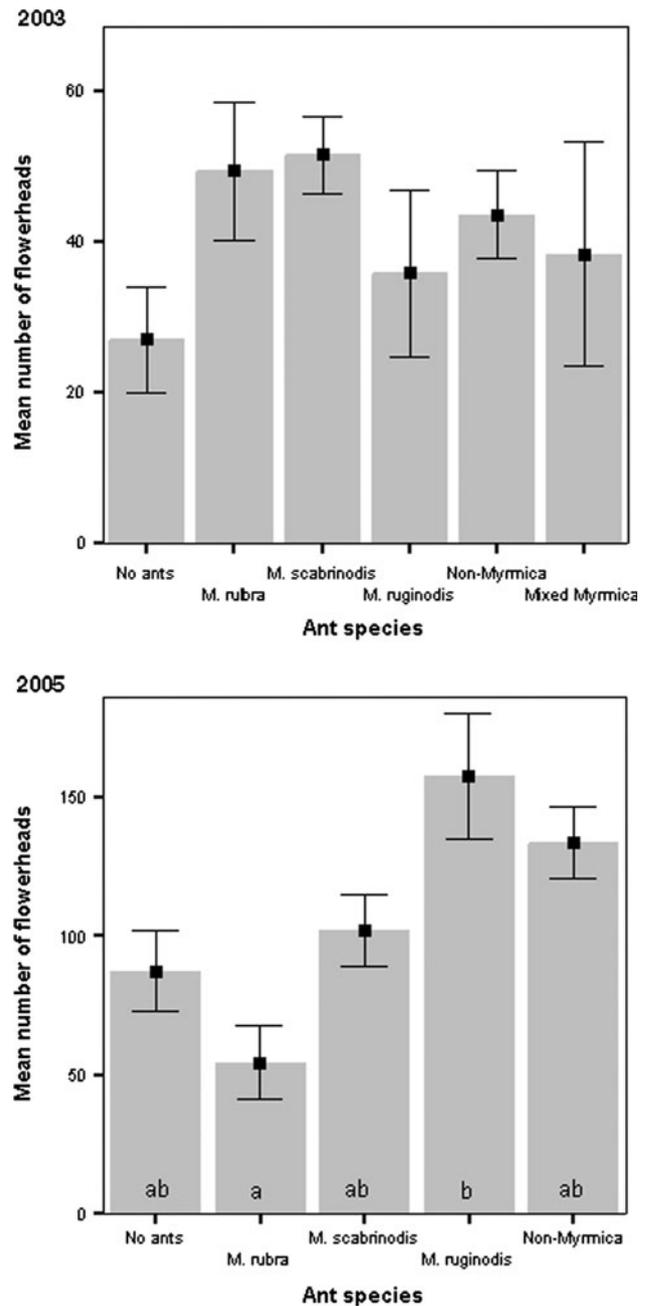
**Table 1** Ant species distribution at the Posterholt location in 2003 and 2005 (N: Number of plots and % of total)

Ant species	2003		2005	
	N	%	N	%
No-ants	14	17.5	25	32.4
<i>M. rubra</i>	18	22.5	11	14.3
<i>M. scabrinodis</i>	20	25.0	20	26.0
<i>M. ruginodis</i>	8	10.0	2	2.6
Non-Myrmica	17	21.3	19	24.7
Mix-Myrmica	3	3.8	–	–
Total	80	100.0	77	100.0

The mean number of flowerheads per plot in 2005 (mean number of flowerheads  $\pm$  SE:  $94.54 \pm 6.16$ ) was almost twice as high as in 2003 (mean number of flowerheads  $\pm$  SE:  $44.70 \pm 2.68$ ,  $t = -7.423$ ,  $p < 0.001$ ). In 2003 the flowerhead availability was equally distributed between the different ant species groups (Anova:  $F_{5,69} = 1.219$ ,  $p = 0.310$ , Fig. 3). In 2005, there was a significantly lower number of flowerheads in the plots with *M. rubra* and a significantly higher number of flowerheads in the plots with the ant *M. ruginodis*, whereas the other groups did not differ in number of flowerheads (Anova:  $F_{4,71} = 1.219$ ,  $p = 0.008$ , significant differences between groups according to the Sidak post hoc test are indicated by letters).

Oviposition site selection

In 2003 the butterflies were observed in 22 plots (27.5 %,  $n = 80$ ). The mean number of flowerheads in the occupied plots was not significantly higher when compared to the



**Fig. 3** The distribution of flowerheads of *S. officinalis* over the different ant species in 2003 and 2005 at the Posterholt location. Data were collected from 80 plots in 2003 and 77 plots in 2005 within four patches (Fig. 1). Error bars represent the standard errors of the mean. Letters indicate significant differences

plots where no butterflies were seen (t test on log-transformed number of flowerheads:  $t = -1.295$ ,  $df = 73$ ,  $p = 0.199$ ). The total number of butterflies counted on plots with *M. scabrinodis* was significantly higher when compared to the plots with other ant species (Kruskal–Wallis test:  $\chi^2_{\text{number of butterflies}} = 11.175$ ,  $p = 0.048$ ,  $n = 80$ ). In a logistic regression analysis the oviposition site selection, expressed as the probability of observing a

**Table 2** Results of the logistic regression analyses of the presence and absence of *P. nausithous* in 2003 and 2005

Year	2003				2005			
Number of cases	80				77			
% predicted correctly	72.5				71.1			
Variable	$\beta_i$	SE	Wald	Sig.	$\beta_i$	SE	Wald	Sig.
Constant	-1.838	0.437	17.647	<0.001	-1.117	0.468	5.682	0.017
Ant presence <i>M. scabrinodis</i>	1.162	0.557	4.349	0.037				
Ant presence Non <i>Myrmica</i> species	1.157	0.539	4.604	0.032				
Number of flowerheads					0.012	0.004	8.115	0.004

It was tested whether the ant species and the number of flowerheads had an effect on the probability of observing butterflies. Only factors with significant effect are presented. The regression coefficients ( $\beta$ ), their standard errors (SE), the Wald-statistics and their significance levels are given. The probability of observing a butterfly is given by  $e^{\text{regression equation}}/(1 + e^{\text{regression equation}})$

butterfly in a plot, showed to be positively related to the presence of the ant *M. scabrinodis* and the non-*Myrmica* ants. These factors correctly predict 72.5 % of the observations (Table 2).

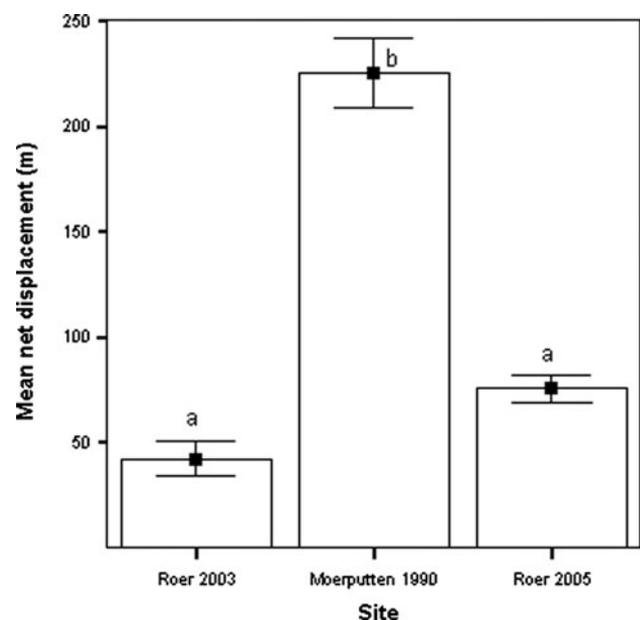
In 2005 the butterflies occupied 40 plots (51.9 %,  $n = 77$ ). This year, butterflies were present in plots with a significantly higher flowerhead availability compared to the plots where butterflies were absent (Mann–Whitney test:  $Z = -3.123$ ,  $p = 0.002$ ,  $n = 77$ ). Interestingly, we found no significant influence of the ant species on the presence and absence of the butterflies in our plots during this second year. The total number of butterflies showed to be equally distributed over the different ant species groups (Kruskal–Wallis test:  $\chi^2_{\text{number of butterflies}} = 8.911$ ,  $p = 0.063$ ,  $n = 77$ ). The logistic regression analysis of the oviposition site selection in 2005 showed that the habitat selection was only positively related to the number of available flowerheads. This factor predicts 71.1 % of the observations correctly (Table 2).

#### Oviposition behavior

In 2003, oviposition was observed on 5 plots (6.3 %,  $n = 80$ ) and in 2005 on 14 plots (18.2 %,  $n = 77$ ). In both years there was no significant difference in the number of flowerheads between the plots where oviposition was observed and the plots with no oviposition (for 2003:  $t$  test on log transformed number of flowerheads,  $t = 0.659$ ,  $df = 73$ ,  $p = 0.516$ ; for 2005: Mann–Whitney test:  $Z = -1.219$ ,  $p = 0.223$ ,  $n = 77$ ). The logistic regression analyses for the years 2003 and 2005 also showed that the oviposition behavior, expressed as the probability of observing oviposition in a plot, was not related to the flowerhead availability or the ant species distribution. These results were confirmed when the regressions for the presence and absence of oviposition were run only on the plots where butterflies have been present.

#### Mean net displacement

In 2005, the distance between butterfly captures was larger, though not significantly different from 2003, whereas the reintroduced butterflies on the meadows of the Moerputten flew much longer distances (GLM,  $F_{2,264} = 35.931$ ,  $p < 0.001$ , Fig. 4). Male and female butterflies did not differ in the mean net displacement between captures ( $F_{1,264} = 0.206$ ,  $p = 0.65$ ). We found no interaction between sex and site ( $F_{2,264} = 0.164$ ,  $p = 0.849$ ). The distance between captures increased with the number of days in between ( $F_{1,264} = 13.158$ ,  $p < 0.001$ ).

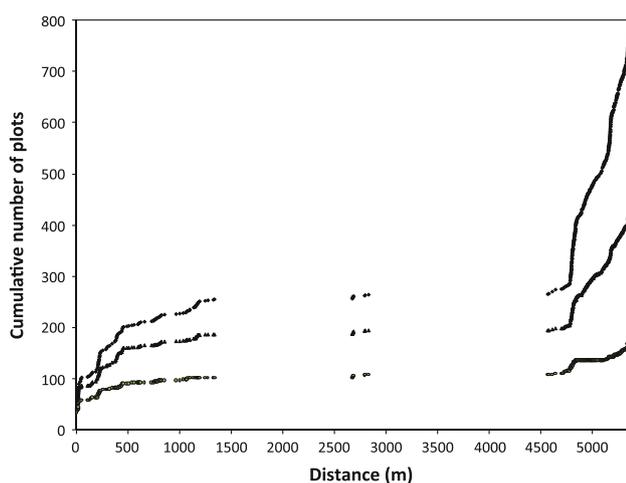


**Fig. 4** Mean net displacement of marked individuals of *P. nausithous*. Roer 2003 and Roer 2005: the Posterholt population in 2003 and 2005 resp., Moerputten 1990: the reintroduced population in the nature reserve Moerputten in 1990. Error bars represent the standard errors of the mean. Letters indicate significant differences

In 2005, only 10 % of the marked butterflies captured in one patch were recaptured in another patch. The mean net displacement distance was  $75 \pm 6$  m and the maximum net displacement was as far as 375 m (Jansen et al. 2006). In 2003 the mean net displacement was even less:  $43 \pm 8$  m. The two smaller patches at the Posterholt location where no *P. nausithous* butterflies were observed were within the mean net displacement range measured in the reintroduced Moerputten population ( $226 \pm 16$  m) and therefore within the measured net displacement range of the species. Mean net displacement values obtained by MRR studies underestimate dispersal distance and dispersal rate due to the method itself (Hovestadt et al. 2011). Even when taking that into consideration, the estimated values for the Posterholt population are low (Nowicki et al. 2005c).

#### Resource availability at landscape scale

We found ant species in only 45 % of the investigated plots ( $n = 1,023$ ) with (groups of) host plants in the landscape around Posterholt. 67 % of these plots were occupied by a *Myrmica* species. The most abundant host ant species in these plots was *M. rubra* (35 %), while *M. scabrinodis* (19 %) and *M. ruginodis* (11 %) were quite rare. At the patches where we found *P. nausithous*, both density and diversity of *Myrmica* ants was high while not more than 35 % of the plots were occupied by the potential predator *L. niger*. At locations without *P. nausithous*, less ant species were found. Sometimes *L. niger* was the dominating species, but we also found that *M. rubra* or *M. ruginodis* comprised most of the local ant fauna. Figure 5 shows that with increasing distance from the population at Posterholt,



**Fig. 5** Sites with *S. officinalis* at the distance to the Posterholt population of *P. nausithous*. Highest line Plot with only *S. officinalis*, middle line plot with *S. officinalis* and ants of any species, lowest line plot with *S. officinalis* and *Myrmica* ants

only a limited number of plots contained the two essential resources for the butterflies.

#### Discussion

Specialist butterflies, such as *P. nausithous*, have to make choices on where to go for nectar and on which host plants to deposit their eggs in order to ensure high survival of their offspring, preferably in nests of their host ant species. The availability and the distribution of these essential resources are expected to influence the butterfly behavior. When both resources are abundant butterflies are more likely to be found in plots with both host plants and ants, whereas when a specific resource is limited and competition for it is high, butterflies might be forced to stay also in plots with only one resource (Wynhoff et al. 2008). We found that the flowerhead availability and the presence of the ant *M. scabrinodis* were both important factors in determining the distribution of *P. nausithous* butterflies. The availability of these resources differed between the 2 years of the study and this seemed to have affected the oviposition site selection made by the butterflies; 2003 was a dry year with relatively low host plant flowerhead availability and high ant presence, while 2005 had relatively high flowerhead availability and low ant presence. In addition, in 2005 the population size of *P. nausithous* with approximately 160 butterflies was almost three times as high as in 2003. In our analysis, oviposition site selection defined in terms of the probability that a butterfly was present, seems to be best explained by the most abundant resource: in 2003 site selection was explained by the presence of the ant *M. scabrinodis*, while in 2005 site selection was positively influenced by the number of host plant flowerheads. These site selection changes are found only in relation to butterfly distribution since during the 2 years we found no influence of the two resources on the oviposition behavior which may have been prevented by the low number of observations.

Most *Phengaris* species show geographical differences in host ant specificity (Als et al. 2002, 2004; Steiner et al. 2003; Stankiewicz et al. 2005). In contrast *P. nausithous* is dependent on only *M. rubra* in most of Europe, with some populations at the edge of the butterfly distribution area using *M. scabrinodis* as a single host (Munguira and Martín 1999; Tartally et al. 2008; Witek et al. 2008). While for the reintroduced population in the centre of The Netherlands a relation with *M. rubra* could be shown (Wynhoff et al. 2008, Van Langevelde and Wynhoff 2009), we were not able to confirm this for the Posterholt population. It is possible that this is due to the low occurrence of the typical host ant species at the study site. The population might survive in the nests of the second best host ant species,

namely *M. scabrinodis*, with a reduced survival probability for the caterpillars (Thomas et al. 1989). Unfortunately, we do not have information about the local host ant specificity of the nearby German populations. Populations in the Westerwald region (appr. 100 km from Posterholt) are more numerous on sites with more *M. rubra* ants captured on baits (Dierks and Fischer 2009), indicating that this is most likely the most important host ant. It is only possible to collect data about this by excavating the ant nests in the beginning of the flight period in search for pupae, which is highly undesirable in our small, spontaneously recolonized population.

The Posterholt population is rather small in comparison with other populations of this butterfly species (Binzenhöfer and Settele 2000; Nowicki et al. 2005a). In the published literature only a few sites are known which host populations smaller than 150 butterflies during the entire flight period, but these occur on meadows and not on road verges (Nowicki et al. 2005b). Usually, populations are larger. Nowicki et al. (2005a) describes a metapopulation of the species consisting of more than 50 local patches where all together more than 50.000 butterflies thrive. Although the Posterholt population might be small, it is the largest population within a circle of at least 50 km. During several field visits to the neighboring populations in Germany, we never found more than 7 butterflies on the same location. Due to the lack of data it is not possible to estimate a reliable population size, but is obvious that the number of butterflies in the German populations is below that of the Dutch population (Boeren et al. 2011). Clearly, the Posterholt population is not a sink population connected to another site with a high number of butterflies that might feed this small population with dispersing individuals. Since the nearest populations are at distances of 5,500 and 6,300 m, they are within the dispersal range of the species. However, for a regular exchange of individuals the distances are probably too large (Van Langevelde and Wynhoff 2009; Hovestadt et al. 2011).

The distribution of the essential resources for these butterflies can only be found along the linearly shaped landscape elements, mainly road verges. We found that the butterflies of the Posterholt road verge population move over only very short distances compared to individuals of the reintroduced population in the meadows of the Moerputten nature reserve, based on net displacement distances derived from our MRR studies. Hovestadt and Nowicki (2008) also found that similarly obtained net displacement distances for the butterfly species *Phengaris teleius* are site specific, most likely because of differences in habitat patch heterogeneity. In contrast, the average distances of movements were several 100 m in populations that were at least ten times larger than the Posterholt road verge population and occurred in large extended habitats (Settele 1998;

Binzenhöfer and Settele 2000; Stettmer et al. 2001). If the butterflies from the studied patches 1 and 2 would move as far as those in the Moerputten nature reserve, they would have been able to also colonize patches 3 and 4, where both resources are available. These findings support the hypothesis that populations in linearly shaped habitat suffer from low dispersal rates which might result in small local populations with high extinction risk (Van Langevelde and Grashof-Bokdam 2011). The Posterholt population did indeed not colonize more patches at close distance, such as patches 3 and 4. Nowicki et al. (2005a) also reports such very high site fidelity. This high site fidelity may cause serious problems in the conservation of the species, especially when its habitat is highly fragmented and restricted to linearly shaped landscape elements (Van Langevelde and Wynhoff 2009; Van Langevelde and Grashof-Bokdam 2011). Our results suggest that the road verge population might be limited in their movements due to the shape of their habitat. If so, mobility is a landscape-specific trait rather than being defined only by species characteristics.

In the surroundings of the Posterholt population, it appeared that dispersing butterflies have to bridge two large gaps without any of the resources in between suitable plots (Fig. 5). The meadows where the historical populations of *P. nausithous* used to occur have lost both their species rich vegetation and their diverse ant communities. This makes them unsuitable as habitat for the butterflies, even though the sites are now protected within the borders of nature reserves. Given the short net displacement distances and the adverse landscape features for long-distance dispersal, this landscape analysis suggests that the *Phengaris* population at the Posterholt site is trapped on the recently recolonized road verges. The historical meadow habitat is currently completely disappeared and even within nature reserves no sites were found for the species to colonize. Future population growth of *P. nausithous* in the Posterholt area could be achieved by increasing nest densities of the different host ant species (Anton et al. 2008) as this seems to be a limiting resource in some years. In addition, potential habitat could be expanded by promoting areas with host plants. Until severe management activities to reestablish habitat with a high density of host plants and host ants have been taken place, no other locations than road side verges and stream side vegetation will be available for the butterflies. By adjusting the management and mowing regime of the road verges and drainage canals where this butterfly occurs, and with the help of agri-environmental schemes, in the surrounding borders of agricultural fields, both host plant densities as well as nest densities of the different host ant species could be increased and refuge areas for the ants can be created (Johst et al. 2006; Grill et al. 2008; Nowicki et al. 2007).

Nowadays, linearly shaped elements in the agricultural landscape are frequently mown and have a rather short vegetation height. Less frequent management schemes allowing the growth of taller vegetation provide butterflies and ants with shelter and food resources (Wynhoff et al. 2011). They can facilitate the dispersal of specialist butterflies and other species along these landscape elements (Söderström and Hedblom 2007). Due to their low edge-area ratio, however, linearly shaped landscape elements have a high sensitivity to disturbances due to land use. Specialist species such as these butterflies occurring only on such landscape elements, like road verges, are especially vulnerable for these disturbances. Nonetheless, if a network of a high density of interconnected landscape elements with suitable habitat is available, a high persistence for *P. nausithous* populations can be achieved. Nearby nature reserves should also be included in this network. Eventually the expansion of this patchy habitat network will connect the Dutch and German *P. nausithous* populations, creating a metapopulation throughout the whole Roer valley.

**Acknowledgments** We thank Dutch Butterfly Conservation and Wageningen University for facilitating this work. Jan Boeren, Jacqueline King and Mark Grutters assisted with the fieldwork. Rebekka Eckelboom introduced us to the German sites. Nicolien Peet identified the ants. M.H. thanks the Dutch NWO Meervoud programme 836.05.021.

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