

Myrmica host-ants limit the density of the ant-predatory large blue *Maculinea nausithous*

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Abstract Butterflies of the highly endangered genus *Maculinea* are parasites of red *Myrmica* ants. Prior to the adoption by *Myrmica* worker ants *Maculinea* caterpillars feed on a specific host plant. This field study aims to answer the question whether the density and distribution of the host plant *Sanguisorba officinalis* or the density of the host ant *M. rubra* limit the density of *M. nausithous* egg, larval and adult stage. We found that the density of *M. nausithous* egg stage and adult stage increased with the density of the host ant. The density of *M. nausithous* caterpillars was not associated with ant density or plant density. This study suggests that the density of *M. nausithous* is limited by the density of the host ant *M. rubra*. We conclude that habitat management for *M. nausithous* should focus on the maintenance of habitats that hold both resources, but that enable high densities of *M. rubra*. In addition, it is discussed why high densities of host ants might be more important in predatory than in cuckoo-feeding *Maculinea*.

Keywords Habitat conservation · *Myrmica rubra* · Spatial density-dependence

Introduction

Population density, i.e. the number of individuals per unit, often fluctuates in response to environmental variation (e.g. abundance of other species, climate change or habitats). The relative merits of density-dependent and density-independent processes in explaining population fluctuation have been widely debated (e.g. Nicholson 1933; Andrewartha and Birch 1954; Sinclair and Pech 1996; Daufresne and Renault 2006). Population density dependence has two facets: temporal (between generations) and spatial (within generation). The detection of density dependence is hindered by short temporal data sets (Woiwood and Hanski 1992), low test power (Pollard et al. 1987; Solow and Steele 1990), and spatial scale (Walde and Murdoch 1988). Ray and Hastings (1996) showed that appropriately scaled studies can effectively reveal density-dependence. In this study, spatial density dependence in the ant-parasitic butterfly *Maculinea nausithous* is analysed. Large blues of the genus *Maculinea* are of interest to ecologists and conservationists because they sequentially feed on specific host plants and specific host ants (e.g. Akino et al. 1999; Als et al. 2002; Thomas and Settele 2004). By measuring population density on small spatial scales we intend to answer the question whether the host plant or the host ant limit the density of this endangered butterfly.

Maculinea butterflies have evolved two strategies to exploit the resources of ant nests. After successful adoption by specific host ant species, predatory *Maculinea* like *M. nausithous* prey on the ant brood. If too many caterpillars are adopted into one host-ant nest, caterpillars experience scramble competition that can lead to high mortality rates among competing larvae (Thomas and Elmes 1998). The so-called cuckoo species, *M. alcon* and *M. rebeli*, are fed directly by the worker ants. Inside the ant nest, workers

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ants select a few caterpillars to nurture, leading to contest competition between caterpillars (Thomas et al. 1993).

A modelling approach on the cuckoo feeder *M. rebeli* suggested that the density of the host-plant and its spatial distribution should be key factors for the successful infestation of ant nests (Hochberg et al. 1994). The model predicted a close relationship between the density of host plants and the density of adult butterflies, with a positive correlation at low plant densities and a negative correlation at high plant densities. When plant density is high, the carrying capacity of the *Myrmica* host-ant is expected to be depressed and many ant nests might be supplanted by other *Myrmica* species (Elmes et al. 1996). Therefore, high plant densities should trigger an indirect interaction between plants and ants via *Maculinea*, a phenomenon called apparent competition (Holt 1977; Thomas et al. 1997). The validation of the model by Hochberg et al. (1994) confirmed the importance of host plant density and its spatial distribution for adult butterfly density (Elmes et al. 1996). Due to the strong density dependent mortality of caterpillars inside ant nests, predatory *Maculinea* should be more susceptible to high plant densities than *Maculinea* of the cuckoo type. This effect could be enhanced by clumping of the host-plant. Clumping is expected to create ant refuges in areas without host-plants and enhanced over-exploitation of ant nests in the remaining habitat.

Maculinea nausithous is listed in Annex II of the Habitats Directive (van Helsdingen et al. 1996) and vulnerable on the European Red List (van Swaay and Warren 1999). Despite of the long-standing interest in this species, we lack basic knowledge about resource limitation in *M. nausithous*. This study aims to fill this gap in order to facilitate efficient habitat management regimes: Does the density of *M. rubra* host ants or the density of *S. officinalis* host plants limit the density of *M. nausithous* stages? Does the distribution of *S. officinalis* affect the density of *M. nausithous*?

Materials and methods

Study system

Maculinea nausithous is univoltine with the main distribution in Mid-Europe and marginal populations in Spain, Turkey and Western Siberia (Wynhoff 1998). Females deposit their eggs into the inflorescences of the food-plant *Sanguisorba officinalis*. After the caterpillars have left the egg, the egg shell remains in the flower head and can be detected there until the flower head decays. Caterpillars feed for 2–3 weeks inside the flower heads on the developing seeds. Fourth-instar caterpillars leave the flower head, drop to the ground and are carried off by any *Myrmica* ant they encounter (Thomas et al. 1989).

However, in natural populations, successful development was observed in nests of *M. rubra* only (Thomas and Elmes 1998; Stankiewicz and Sielezniew 2002). The behaviour of adult *M. nausithous* is very closely associated to *S. officinalis*. Adult butterflies feed, mate and rest on the flower heads of the larval food plant.

Sanguisorba officinalis is a perennial, Eurasian plant growing on meadows and wetlands, but also on road verges and fallow lands (Hegi 1995). It is tolerant of frequent mowing, and in successional grasslands the number of shoots rapidly decreases with time while the number of flower heads per shoot increases.

Myrmica rubra (Formica: Formicidae) is a common holarctic red ant, that occurs in a variety of habitats (Seifert 1996). Colonies of *M. rubra* can split into several spatially separated nests that strongly differ in the number of queens and worker ants (Seppä and Pamilo 1995).

Research site, density measures, and inter patch distance

This field study was conducted in the Upper Rhine valley in South-western Germany around the city of Landau between 1 July and 10 August 2003 (Fig. 1). Thirty-four patches in the study area (20 km × 45 km) between the Rhine River and the Palatinate forest that were not mown 4 weeks before the onset of the flight period were investigated. We excluded one site where the closely-related *M. teleius* occurred, because young instar caterpillars are difficult to tell apart (Sliwinska et al. 2006). The size of a patch was defined by the area that was covered by the host plant *S. officinalis*. Ray and Hastings (1996) strongly recommend adjusting the scale of the study to the mobility of the species. Here, we used the same scale for adult butterflies and egg and larval stage, because the behaviour of adults is very closely associated to the food plant *S. officinalis*. The density of active *M. rubra* workers at baits was previously shown to be correlated with the density of *M. rubra* nests (Glinka and Settele 2005). Ant density was estimated using baits with sugar cubes and cake crumbs that were covered with a dark plastic pot. To achieve a random stratified manner of baiting the habitat patch was divided in corridors of 10 m width. Inside each corridor we walked a zig-zag-transect to distribute the baits. Random numbers between five and 15 were used to set the distance (measured in meters) between neighbouring baits. *Myrmica* workers forage up to 2 m from the nest (Elmes et al. 1998), so that a minimum distance of 5 m between baits was used to ensure independence of ant density measures at baits. Depending on the size of the patch, 16–53 baits were distributed (Thomas et al. 1989, Table 1). Due to the main foraging activity of *M. rubra* in the morning, baiting was started between 8 am and 11 am

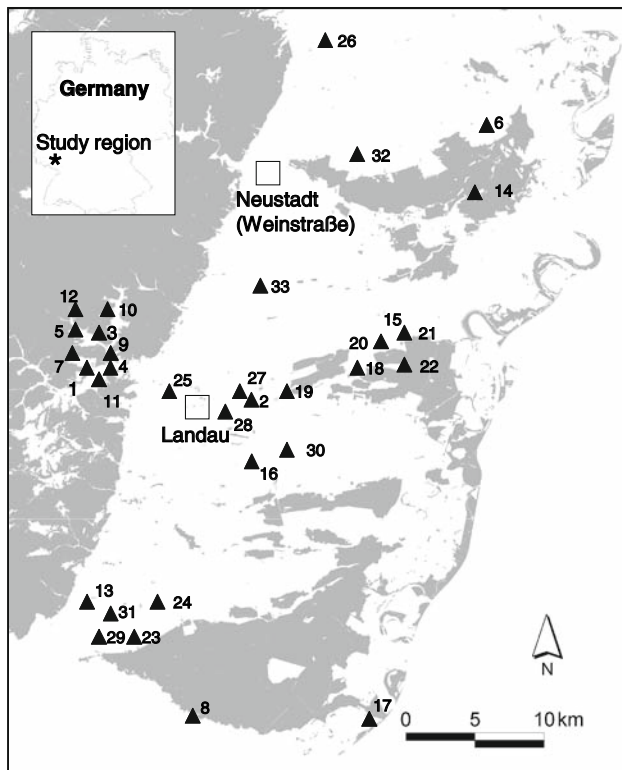


Fig. 1 Sample sites of *M. nausithous* stages in the Upper Rhine valley (South western Germany). Dark grey areas indicate forests; white areas are grasslands or areas used for vineyards and other forms of agriculture

and checked for ants 1–2 h later (Elmes et al. 1998; J.A. Thomas, pers. comm.). After removing the plastic pot we estimated the number of *M. rubra* at the baits using frequency classes (1–5 ants, 6–15, 16–35, 36–75, 76–160, >161). All *Myrmica* workers collected at the bait were stored in alcohol for identification in the laboratory (according to Wardlaw et al. 1998). Since the proportion of baits occupied by *M. rubra* workers correlated positively with the frequency of *M. rubra* workers per bait (Pearson correlation: $r^2 = 0.81$, d.f. = 33, $P < 0.0001$), the proportion of occupied baits was used as a measure for ant density in all statistical models. In a few cases, workers escaped from the bait. However, by using the presence/absence data of *M. rubra* at the bait, this inaccuracy might be negligible. Depending on the size of the patch, 16–50 stratified squares (2 m \times 2 m) were used to estimate the density of *S. officinalis* on each site. Inside each square we counted the number of shoots. The number of flower heads per shoot was estimated from 20 randomly chosen shoots throughout the habitat patch. To control for the size of flower heads, three randomly chosen flower heads per shoot were measured. The length of flower heads was measured from the basis to the top. In all statistical models the mean number of flower heads per square meter was used as a measure for host plant density. Butterfly density was

estimated for three different stages. Adult *M. nausithous* individuals were counted within transect walks during appropriate weather conditions (temperature: $>20^\circ\text{C}$). Transect walks covering the whole habitat patch were conducted between 10.00 am and 17.00 pm All individuals on the wing or on *S. officinalis* flower heads within an area of 2.5 m to each side were counted. Adults were counted three times during the flight period. From these three counts, the highest number of observed adults was divided by the patch area as a measure for butterfly density.

Egg density was calculated from a random collection of 40 *S. officinalis* flower heads per site that were dissected in the laboratory. The density of pre-adoption caterpillars was determined with a collection of flower heads from 20 randomly selected shoots of *S. officinalis*. Flower heads were stored at 23°C in Petri dishes. Caterpillars emerging from the flower heads were removed and counted every day. The flower heads containing the caterpillars were collected one week after the phenological peak of adult butterflies.

The distance between patches was measured from patch centre to patch centre to test for spatial autocorrelation of density measures (Kruess and Tschardtke 1994; Krauss et al. 2005).

Spatial distribution of *Sanguisorba officinalis*

To determine the dispersion of *S. officinalis* in each population the standardized Morisita index of dispersion was calculated:

$$Id = n \left[\frac{\sum x^2 - \sum x}{(\sum x)^2 - \sum x} \right] \quad (1)$$

where n is the sample size, and x is the number of shoots per square. The index by Smith-Gill (1962) who set out to improve Morisita's index by putting it on an absolute scale from -1 to 1 was used. This index is described as the best currently available since it is neither density nor sample size dependant (Krebs 1989).

Statistical analyses

Three separate multiple linear regression models were employed to investigate the effects of host-ant density, host plant density, and size of flower heads on the density of *M. nausithous* eggs, caterpillars, and adult butterflies. Response variables were log-transformed to achieve normal distribution of residuals (log ($y+1$); Crawley 2002). In a first step all variables were implemented in the maximal model. Non-significant terms ($P > 0.05$) were deleted step by step to obtain the minimal adequate model (Crawley 2002). Type-II sums of squares were calculated using ANOVA in

Table 1 Number of baits, number of baits with *M. rubra*, number of baits where *M. rubra* was the solely *Myrmica* species, and mean number of *S. officinalis* flower heads per square meter on each study site

Number of site	Site	# Baits	# Baits with <i>M. rubra</i>	# Baits solely <i>M. rubra</i>	# <i>S. officinalis</i> flower heads per m ²
1	Gräfenhausen-Ost	16	11	11	8.8
2	Offenbach-Süd	20	12	12	0.7
3	Gut Waldeck	25	10	9	16.8
4	Albersweiler	27	2	2	2.5
5	Eussertal –Ort	28	19	0	10.1
6	Schifferstadt	33	32	32	16
7	Gräfenhausen	34	15	15	37.3
8	Bienwaldmühle	37	4	4	5.3
9	Eußertal	38	27	26	8.7
10	Dernbach	40	13	13	3.5
11	Annweiler	41	17	16	11.3
12	Waltersbach	42	23	24	1.2
13	Oberotterbach	47	0	0	19.7
14	Haderwiesen	47	11	5	1.7
15	Lustadt	47	0	0	7.6
16	Rohrbach	48	0	0	2.3
17	Neuburg	49	11	10	4.1
18	Zeiskam-Mühle	49	5	4	2.1
19	Offenbach-Industrie	49	2	2	9.4
20	Zeiskam	49	5	5	4.1
21	Lachenmühle	49	26	26	3
22	Ludwigsmühle	49	3	3	1
23	Steinfeld	49	13	13	1.6
24	Schaidt	50	0	0	2.4
25	Reiterwiesen	50	5	0	1.5
26	Niederkirchen	50	23	23	4.7
27	Offenbach	50	34	34	0.3
28	Queichheim	50	15	15	8.4
29	Schweighofen	50	17	17	21.5
30	Herxheim	50	12	12	3.5
31	Ober-Otterbach-Ost	50	16	16	10.1
32	Hassloch	53	13	13	1.4
33	Venningen	53	24	21	12.9

For details see methods section

the R package ‘car’ in order to avoid order-dependency of variables in multiple regressions. The influence of food plant density and host ant density on the density of *M. nausithous* stages was also tested with simple linear regression analysis.

The impact of plant density and patch size on the frequency of *M. rubra* (proportion of occupied baits) was analysed separately using a generalised linear model (GLM) with quasi-binomial errors and a logit link function ($\ln(p/1-p)$). A simple linear regression was used to test the influence of patch size on the density of *S. officinalis* and to test the relationship between *M. nausithous* egg density and butterfly density. Mantel tests proofed for spatial

autocorrelation of the density of butterfly stages, food plant density, and host ant density of all patches (Mantel 1967). All models were performed with the software R v 2.0.1 (<http://cran.r-project.org/>).

Results

Spatial autocorrelation, plant distribution, ant density, and plant density

There was no correlation between the population density of any of the organisms and the geographical distance between

patches (Mantel tests: ant density, $r = 0.09$, $P = 0.14$; plant density, $r = 0.11$, $P = 0.15$; egg density, $r = 0.05$, $P = 0.20$; caterpillar density, $r = 0.02$, $P = 0.40$; adult butterfly density, $r = -0.04$, $P = 0.58$).

The mean value of Morisita’s index of dispersion across all sites indicated clumping of *S. officinalis* ($Id = 0.51 \pm 0.13$ SD). On just one site there was a uniform distribution and none of the sites showed a random Poisson distribution of *S. officinalis*. Therefore, plant dispersion was not included into the multiple regression models assuming an equal effect of clumping on the independent variables. When *M. rubra* was present at a bait ($N = 420$), it was the solely *Myrmica* species in 98% of the baits (Table 1). The proportion of baits occupied by *M. rubra* was neither affected by the density of *S. officinalis* (GLM: mean deviance = 13.0, $P = 0.30$), nor patch size (mean deviance = 2.1, $P = 0.16$). Also, the density of *S. officinalis* was not affected by patch size (linear regression: $r = 0.0003$, $P = 0.94$).

Population density of *M. nausithous* stages

The density of *M. nausithous* eggs positively correlated with ant density (Fig. 2 b, Table 2) and with the density of

butterflies (linear regression: $F_{1,32} = 6.2$, $P = 0.02$). The mean size of flower heads and the density of *S. officinalis* flower heads did not significantly influence the density of eggs (Table 2, Fig. 2a). There was no correlation between the density of caterpillars and the density of ants or plants (Fig. 2 c, d). Similarly, the density of caterpillars was not correlated with the size of flower heads, which was therefore removed from the model as a non-significant variable (Table 2). The density of butterflies was positively correlated with host-ant density, but there was no relationship between flower head density and butterfly density (Fig. 2e, f). The size of flower heads did not influence the density of butterflies (Table 2).

Discussion

The developmental stages of *M. nausithous* differed in their dependence on the ant and plant resources. While the density of eggs and adult butterflies correlated with the density of the host ant *M. rubra*, the density of caterpillars did neither correlate with the food plant *S. officinalis* nor with the host ant. Due to a lack of variation, the distribution of *S. officinalis* shoots was not implemented into regression analysis.

Fig. 2 Relationship between the density of *M. nausithous* stages and the density of the host plant *S. officinalis* (first column) and the host-ant *M. rubra* (second column). (a) relationship between egg density and plant density (linear regression: $r^2 = 0.12$, $P = 0.05$); (b) relationship between egg density and ant density (linear regression: $r^2 = 0.23$, $P = 0.005$); (c) relationship between caterpillar density and plant density (linear regression: $r^2 = 0.03$, $P = 0.30$); (d) relationship between caterpillar density and ant density (linear regression: $r^2 = 0.08$, $P = 0.10$); (e) relationship between adult density and plant density (linear regression: $r^2 = 0.0004$, $P = 0.91$); (f) relationship between adult density and ant density (linear regression: $r^2 = 0.27$, $P = 0.002$). Regression line is added if $P < 0.05$. Note: Two populations (7 & 13, see Table 1), where we did not find caterpillars are not shown in Fig. c and d because of the logarithmic scale

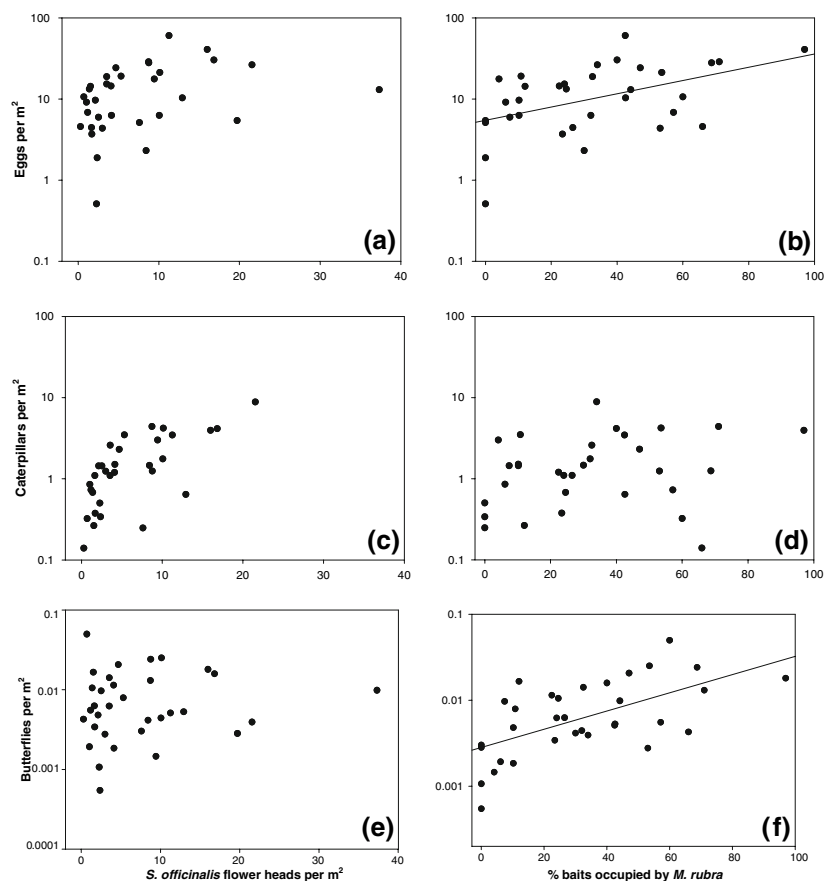


Table 2 Minimal adequate models (after stepwise deletion of predictor variables) analyzing the density of *M. nausithous* eggs (A), caterpillars (B) and adults (C). The maximal models contained

Dependant variable	Minimal adequate model			
	Predictor variable	F	P	% Variation
(A) Egg density	Ant density	8.9 _{1,31}	0.006	22.2
(B) Caterpillar density	Plant density	2.8 _{1,31}	0.10	8.4
(C) Butterfly density	Ant density	17.9 _{1,31}	0.0002	36.6

the variables host ant density (*M. rubra*), food plant density (*S. officinalis*), and size of flower heads of the food plant

Population density of *M. nausithous* stages

This study shows that the number of emerging *M. nausithous* butterflies depends on the density of the ant *M. rubra*. However, the egg-laying success of *M. nausithous* females may also depend on the density of suitable host plants as the slightly significant relationship between egg density and food plant density shows. The correlation between *M. nausithous* egg density and host ant density can hardly be explained by the butterflies' ability to locate host plants near to ant nests by means of ant odours (Musche et al. 2006). The number of eggs laid clearly depends on the density of adult butterflies, which was shown to be limited by the density of *M. rubra*. However, no correlation was found between *M. nausithous* caterpillars and host ant density. The competition among larvae for plant resources may lead to density dependent mortality on the flowerheads. This might be the reason for the absence of a correlation between the density of the host ant and the density of *M. nausithous* caterpillars. Cannibalism among competing caterpillars on the host plant is known for *M. arion* and was hypothesized for all *Maculinea* species (Thomas 1977). In contrast to *Maculinea* species of the cuckoo type, this field study indicates that the butterfly density of the predatory *M. nausithous* depends on the density of *M. rubra* on a given site.

Feeding strategy and population limitation

Adults of the cuckoo-feeder *Maculinea rebeli* were previously shown to be limited by the density of *Gentiana* host plants (Elmes et al. 1996). Predatory *Maculinea* are more destructive to ant nests than cuckoo feeders (Thomas and Wardlaw 1992). Consequently, feeding on the resources of the host enables higher growth rates than feeding on the host itself (Thomas and Elmes 1998). Although the average size of *M. rubra* nests exceeds that of any of the host-ants of the cuckoo feeders *M. alcon* and *M. rebeli*, smaller numbers of *M. nausithous* were found inside ant nests (Wardlaw and Elmes 1996; Thomas and Elmes 1998). Higher density of the host plant and the low efficiency of feeding inside the ant nest may lead to a limitation of the

predatory *M. nausithous* by the density of the host ant *M. rubra*. Consequently, this explains the absence of a negative correlation between host ant density and food plant density, i.e. the lack of apparent competition between *S. officinalis* and *M. rubra*.

The sites included in this analysis were not homogeneously managed and differed in size. While the majority of sites were hay meadows, some were mown every second year or even fallow land. However, the large number of replicates may compensate habitat variance. Patch size did not affect the density of *M. rubra* and *S. officinalis*. The relationship between patch size and *M. nausithous* density was not analysed because both variables are not independent in this analysis. If there was an effect of patch size on *M. nausithous*, we would expect to find this influence in the food plant density or host ant density.

Implications for conservation

Habitat conservation of *M. nausithous* is hampered by the fact that *M. rubra* and *S. officinalis* reach highest densities in differently managed habitats (Seifert 1996; Musche, unpublished data). Without mowing, succession will proceed by shrub invasion and a decrease of grassland species which is followed by a rapid decrease of *S. officinalis* (Musche et al. 2006; Musche, unpublished). However, *M. rubra* reaches highest densities in successional grasslands (Seifert 1996; Dauber and Wolters 2005). Concluding from our results we suggest that habitat management for the endangered *M. nausithous* should focus on the optimization of habitats that enable high densities of the host ant *M. rubra*. Depending on the productivity of the local site, mowing should be reduced to a level that prevents a strong increase of shrubs (and a decrease of *S. officinalis*). A network of habitat types covering different vegetation stages may be the best insurance for the maintenance of functioning *M. nausithous* metapopulations.

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