

An individual based model for the conservation of the endangered Large Blue Butterfly, *Maculinea arion* (Lepidoptera: Lycaenidae)

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Abstract

European populations of the Large Blue Butterfly *Maculinea arion* have experienced severe declines during the 20th century, especially in the northern part of the species' range. This endangered lycaenid butterfly needs two resources for development: flower buds of specific plants (*Thymus* spp., *Origanum vulgare*), on which young caterpillars briefly feed, and red ants of the genus *Myrmica*, whose nests support caterpillars during a prolonged final instar. In order to improve understanding of those mechanisms that are most influential to population dynamics of the butterfly, we developed a stochastic population model. This individual based model implements three main biological components relevant for population dynamics of the butterfly: (i) life on the initial host plant, (ii) adoption of the caterpillars by host ants, and (iii) life of the caterpillars within host ant nests. The model explicitly describes the spatial distribution and abundance of the butterfly, the foodplant and the host ant. Life-history parameters of the butterfly were derived from literature. Habitat characteristics such as area size, *Thymus* cover, density of host ant nests and proportion of adoption by non-host *Myrmica* ant species were obtained from a population of *M. arion* in the Swabian Jura (Baden-Württemberg, Germany). The model was successfully tested on results from studies of this natural population. A highly significant correlation between the number of individuals marked in the field and the number of individuals predicted by the model was found. A sensitivity analysis was used to test and assess general conservation measures for the Swabian population and the species in general. The Monte Carlo simulations clearly indicate that the density of host ant nests and the proportion of caterpillars adopted by non-host ant *Myrmica* is more critical for the survival of the butterfly than the density of its initial foodplants. A population inhabiting an area of 1 ha is likely to be regarded as safe for the next 50 years under the following conditions: *Thymus* cover should not fall below 5%, the proportion of adoption of caterpillars by host ants should be greater than 20%, and a minimum nest density of host ants greater than 500 per ha should be assured. Maintenance or re-establishment of grazing or mowing was successfully tested as a suitable conservation measure for declining *M. arion* populations. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: *Maculinea arion*; *Myrmica sabuleti*; Individual based model; Extinction risk; Conservation biology

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1. Introduction

The Large Blue Butterfly *Maculinea arion* (Linnaeus, 1758) is a palaeartic, obligatory myrmecophilous butterfly. All over Europe, it experienced severe declines during the 20th century, especially in the northern part of the species' range (Wynhoff, 1998). Most populations have disappeared as a result of habitat destruction and habitat deterioration. Habitat changes with changes in agricultural techniques, such as increases in mowing frequency, intensification of grazing or, alternatively, abandonment. In the UK, about 50% of *M. arion* extinctions were caused by serious deterioration of habitat by intensive agriculture. The remaining extinctions resulted from the abandonment of sites by farmers, leading to an increase in vegetation height and cover and a subsequent rapid loss of the host ant *Myrmica sabuleti* Meinert, 1860 (Thomas, 1995a).

The Large Blue Butterfly has been subject to more specific conservation measures during the past century than almost any other insect species in the world. The history of *M. arion*'s conservation is reviewed by Thomas (1980, 1989, 1995a). Long-term studies performed in the UK identified and quantified factors influencing natality, dispersal and mortality throughout the life cycle of the butterfly. They also revealed the main factors controlling populations of *Thymus* spp. on which young caterpillars briefly feed, and those controlling red ants in the genus *Myrmica*, whose nests support caterpillars during a prolonged final instar (Thomas, 1980, 1993, 1995b; Thomas et al., 1989; Thomas and Wardlaw, 1990, 1992). Thomas et al. (1998) recorded sward structure, foodplant distribution and the distribution and density of *M. sabuleti* on 26 sites in five regions of Europe during the adult flight period. They were able to define the niche breadth and optimum habitat for *M. arion*, its foodplants *Thymus* spp. and *Origanum vulgare* and its primary host ant *M. sabuleti* across Europe. The niches of the host ant and to a lesser extent the niche of both potential initial foodplants becomes much narrower towards the edge of *M. arion*'s range. Generally, the niche of either foodplant was much broader than the niche of any *Myrmica* species (Thomas et al., 1998;

Elmes et al., 1998). Therefore, niche availability of the primary host ant is considered to be restricting the dynamics of *M. arion* populations more severely than the niche requirements of either foodplant. This intensive ecological research revealed that the key to conserving *M. arion* is to manage sites to encourage high densities of *M. sabuleti* to co-exist with *Thymus* or any other suitable initial foodplant (e.g. *Origanum*). This suggestion was already tested at one site in the UK, near the northern limit of the range of *M. arion* (Thomas et al., 1998). During a 20-year period sward height was reduced from 20 to 0.5 cm by re-establishment of regular heavy grazing. The most thermophilous species, *M. specioses*, colonised the managed site during this period and the proportion of the host ant *M. sabuleti* increased from 7 to 86% relative to all *Myrmica* ant species that were recorded at the site (*M. ruginodis*, *M. scabrinodis*, *M. sabuleti*, *M. schencki* and *M. specioses*). This shift towards warmth-loving species of *Myrmica* was accompanied by a sharp decline of *M. scabrinodis* and *M. ruginodis* both preferring cooler microclimates.

In view of the need for species conservation, population models help to provide insights into the ecologies of species by identifying and quantifying key parameters for their survival (Wolff, 1994; McCarty, 1996; Berger et al., 1999; Griebeler and Gottschalk, 2000a,b; Jager, 2001; Cromsigt et al., 2002; Mooij et al., 2002). Models also help to test and assess practical conservation measures. A model has already assisted our understanding of the ways in which another *Maculinea* butterfly, *M. rebeli*, depends upon the spatial distribution and abundance of its initial foodplant, the gentian *Gentiana cruciata* and its *M. schencki* host ant (Hochberg et al., 1992, 1994; Clarke et al., 1998). The model was initially calibrated for a large site in the Spanish Pyrenees, but has also been successfully tested on 12 French sites and another in Spain.

M. rebeli caterpillars mimic ant larvae and thus induce *M. schencki* workers to feed them directly with regurgitations, trophic eggs (unfertilised eggs of the host ant that are normally used as food for ant larvae) and prey (Elmes et al., 1991). Individual *M. rebeli* caterpillars have inherently differ-

ent growth rates, and are also fed selectively by worker ants (Elmes et al., 1991). As a result, only the smallest die when more caterpillars are adopted than can be supported by the nest, i.e. they exhibit contest competition (Hochberg et al., 1992). In contrast, *M. arion* are predators of the ant-brood and are hence subject to scramble-competition. Therefore, *M. arion* is expected to be more prone to overexploitation of host ant nests, to have stronger fluctuations in population densities and to be more susceptible to local extinction than *M. rebeli* (Clarke et al., 1998).

This paper describes the development and use of a spatial simulation model for the *Maculinea arion*–*Myrmica* host ant species–*Thymus pulegiodes* system. The model is related to the model developed by Clarke et al. (1998) for *M. rebeli*. It is used to explore interactions between the species involved, to derive key processes in the life cycle of the species, to estimate the extinction risk of a natural population and assess conservation measures.

2. Material and methods

2.1. Biology of the *Maculinea*–*Thymus*–*Myrmica* system

As with all *Maculinea* butterflies, *M. arion* is univoltine. Adults usually fly for about 4 weeks in July or August. Each female butterfly lays a clutch of one egg about 60 times per generation on flower buds of specific plants. They prefer *Thymus* for oviposition and *Origanum* is frequently used in the absence of thyme. A high proportion of eggs hatch about 1 week after being laid (Thomas et al., 1991). Young caterpillars feed on buds for about 3 weeks, although they are cannibalistic during their first instar (Thomas, 1977).

Occasionally, within this time, caterpillars are parasitized by *Trichogramma* species (Thomas et al., 1991). Caterpillars acquire only about 1% of their ultimate biomass during their life on the plants (Thomas, 1977). They then moult for the third and final time, drop to the ground where they await discovery by *Myrmica* workers, or die within the next 2 days if they are beyond the

foraging range of an ant colony (Thomas, 1977; Thomas et al., 1989). Curiously, adult *Maculinea* cannot detect *Myrmica*, and place their eggs more or less randomly on plants growing both beyond and within the foraging ranges of these ants (Thomas et al., 1989). Even though workers from most species of *Myrmica* take the caterpillar back to their nests with equal success, caterpillars survive almost exclusively within nests of *M. sabuleti* (Elmes et al., 1998). Within the nests, caterpillars mimic an ant larva in its final instar. They are obligate predators of *Myrmica* larvae. It is estimated that 230 of the largest available larvae, and a minimum nest size of 354 *M. sabuleti* workers, is needed to support a single butterfly.

Therefore, many caterpillars die in ant nests if they are too small (Thomas and Wardlaw, 1992). Mortality of caterpillars is 2.8 times higher in nests that have queen ants present compared with queenless nests (Thomas and Wardlaw, 1990). After the caterpillars have exploited ant nests for about 10 months, butterflies finally emerge from pupae.

2.2. Study area

In 1992, 1994 and 1995 detailed studies in the Swabian Jura (Baden-Württemberg, Germany) were performed on *M. arion* at ‘Jungingen’ (Fig. 1; Pauler et al., 1995; Pauler-Fürste et al., 1996). The goal of this investigation was to identify and quantify key parameters that are important for the viability of *M. arion* in south-west Germany. The authors focused on habitat quality, population ecology, mobility and area requirement of the Large Blue Butterfly. The chosen study site consisted mainly of semi-dry grassland that is used as pasture to different degrees. The site was characterised by variably exposed slopes of white and brown Jura (630–700 m a.s.l.). Fig. 1 shows a schematic representation of this study site and presents the location of the eight test areas. Within two of the areas (NSG Beuren and geplantes NSG Kirchenköpfe) different vegetation types were found. *Thymus*-cover at each area was determined according to Braun-Blanquet (1951). Table 1 summarises habitat characteristics of the areas.

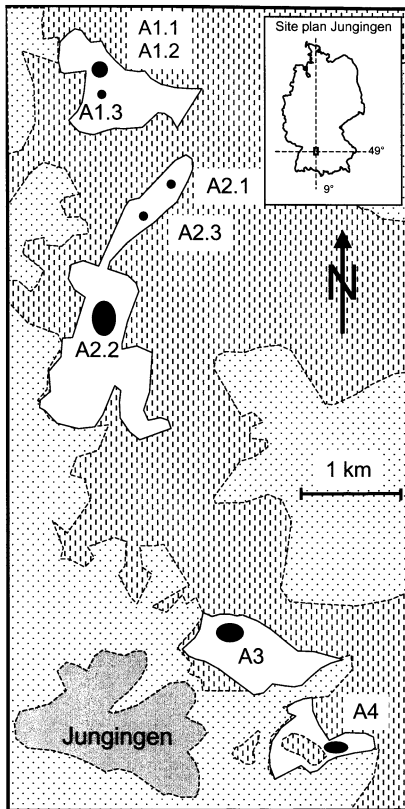


Fig. 1. Schematic map of the eight areas at 'Jungingen' studied by Pauler et al. (1995), Pauler-Fürste et al. (1996). (1) NSG Beuren; (2) geplantes NSG Kirchenköpfe; (3) Köhlberg-südhang; (4) NSG Bürgle. Habitat characteristics of study areas are summarised in Table 1. White denotes dry grassland, grey the village 'Jungingen' and black the study areas. Dotted areas are meadows or farmland and dashed areas are forest.

2.3. The model

In order to estimate population vulnerabilities of *M. arion* at 'Jungingen' and gain better insights into the species' ecology, we developed a stochastic spatial individual based model. This model consists of two submodels: (1) a habitat model that describes characteristics of the area inhabited by the butterfly and (2) a population dynamical model that determines the fate of *M. arion* individuals and simulates life-history events. Fig. 2 shows the life cycle of an individual in the model and the cycle's dependence on life-history and

habitat parameters. Model parameters are summarised in Table 2.

2.3.1. Habitat model

Each modelled area of a given size S consists of a grid of square cells, with each cell equalling an area of 1 m^2 . This unit was chosen in accordance with the foraging area of *M. sabuleti* workers and the maximal density of ant nests observed by Elmes and Wardlaw (1982). In each simulation a constant number of host ant nests 'A' is randomly distributed in the grid so that none of the cells contains more than one nest. According to the degree of *Thymus*-cover T_C that is assumed for a modelled area a proportion of cells is randomly selected where the host plant is abundant. Additionally, a total number of flower buds per square cell T_B has to be chosen for cells where *Thymus* plants are present. In contrast to the host ants, we do not explicitly model the spatial distribution of non-host *Myrmica* ants that also adopt the caterpillars. We only assume that a constant proportion of caterpillars are adopted by other non-host *Myrmica* $\Phi_{\text{other Myrmica}}$ and that caterpillars do not survive within the nests of these non-host ants. In conclusion, habitat characteristics of an area are defined by *Thymus*-cover T_C , the total number of flower buds per cell T_B , the number of host ant nests A , the proportion of caterpillars that are adopted by other non-host *Myrmica* species $\Phi_{\text{other Myrmica}}$ and area size S . These input parameters of the model have to be estimated in field to apply our model to a natural population.

2.3.2. Population dynamics

The length of one time step for the model was chosen as one generation of *M. arion*. Each generation starts with oviposition. Each female butterfly lays a clutch of one egg 60 times per generation (Thomas, 1989; Thomas et al., 1991), so given a 1:1 sex ratio the model treats each butterfly as laying λ ($= 30$) eggs (Hochberg et al., 1992). For each egg laid, a grid cell that is covered by *Thymus* is randomly selected as well as a flower bud chosen for oviposition (Thomas et al., 1989). Eggs that develop to caterpillars are randomly selected with a constant probability $\Phi_{\text{egg hatching}}$ ($= 0.9$, Thomas et al., 1991). Caterpillars are

Table 1
Habitat characteristics of the areas studied by [Pauler et al. \(1995\)](#), [Pauler-Fürste et al. \(1996\)](#)

Area	Site	Area size (ha)	Inclination	Type of land use	Vegetation type	<i>T. pulegioides</i> (%)	<i>Myrmica</i> species	Nest density per 100 m ²
A1.1	NSG Beuren	2	SW, SE	Mowing every 2 years up to once a year	1a	< 5	<i>M. sabuleti</i>	17
A1.2	NSG Beuren	2	W	Mowing every 2 years up to once a year	1a	< 5	<i>M. scabrinoides</i> <i>M. sabuleti</i>	11 9
A1.3	NSG Beuren	1	SW	Mowing every 2 years up to once a year	1b	10	<i>M. scabrinoides</i> <i>M. rubra</i> <i>M. sabuleti</i>	1 21 32
A2.1	2 geplantes NSG Kirchenköpfe	1	SW	Fortnightly grazing	2a	8	<i>M. scabrinoides</i> <i>M. schencki</i> <i>M. sabuleti</i>	2 1 35
A2.2	Geplantes NSG Kirchenköpfe	10	SW	Weekly grazing	2b	30	<i>M. rubra</i> <i>M. schencki</i> <i>M. sabuleti</i>	18 1 20
A2.3	Geplantes NSG Kirchenköpfe	1	W	Daily grazing	2b	30	<i>M. sabuleti</i>	13
A3	Köhlberg Südhang	7	NW	Annual grazing	3	< 5	<i>M. scabrinoides</i> <i>M. scabrinoidis</i> <i>M. rubra</i>	13 36 44
A4	NSG Bürgle	1	SW	Grazing every 2 years up to once a year	4	1	<i>M. rubra</i>	64

1a: Gent. K./Mesobr., dense and tall vegetation, open soil; 1b: Gent. K./Mesobr., sparse and tall vegetation, open soil; 2a: Gent. K./Mesobr., dense and short vegetation, open soil; 2b: Gent. K., sparse and short vegetation, open soil; 3: moist grassland with extensive grazing; 4: ruderal (thistle), shrub succession, *O. vulgare* frequent, open soil. Mesobr.: Mesobrometum; Gent. K.: Gentiano Kolerietum. The cover of *T. pulegioides* and *O. vulgare* was determined according to [Braun-Blanquet \(1951\)](#).

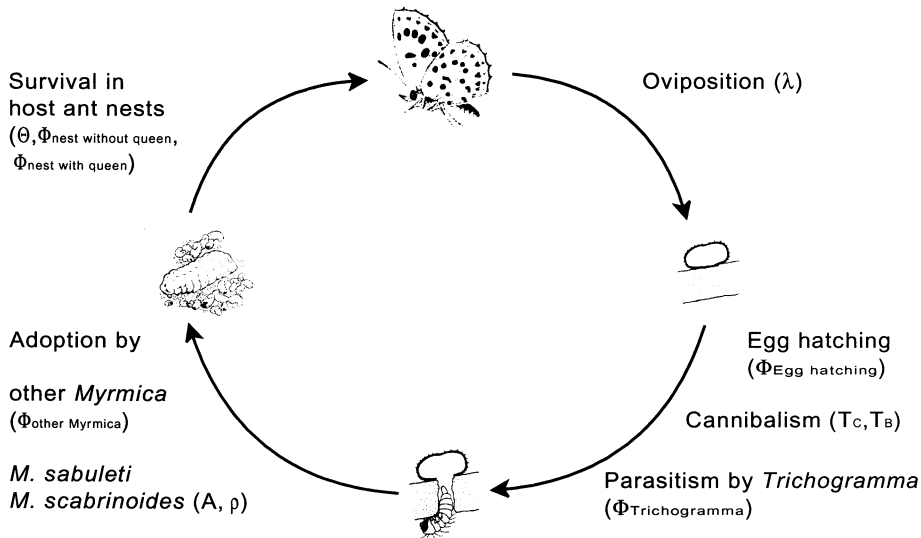


Fig. 2. Life cycle of an individual in the model and its dependence on life-history and habitat parameters (see also Table 2) (adapted from Thomas and Wardlaw, 1990; Thomas et al., 1991).

cannibalistic during their first instar (Thomas, 1977). Therefore, if two or more caterpillars feed by chance on the same flower bud all but one of them die in our model. In nature, caterpillars may be parasitized by *Trichogramma* species with an average probability of 0.053 (Thomas et al., 1991). Caterpillars survive this parasitism in our model with the probability $\Phi_{Trichogramma}$ ($= 0.947$). Surviving caterpillars await discovery by *Myrmica* workers. Since we assume that a constant proportion of the caterpillars is adopted by other non-host *Myrmica* ($\Phi_{other\ Myrmica}$), each of the caterpillars randomly dies in our model with the probability $\Phi_{other\ Myrmica}$. The surviving caterpillars are only adopted by their host ant if the cell where they await discovery resides in the foraging area of at least one ant colony or a cell that is inhabited by the host ant, respectively. We assume that workers forage up to a distance ρ ($= 2$ m, Thomas, 1990) from the centre of the cell that is colonised by the host ant. If there is more than one nest that may adopt a caterpillar, one of these potential target nests is randomly selected to take up the caterpillar. Thomas and Wardlaw (1990, 1992) found in their field studies that many caterpillars die in nests of their correct host *M. sabuleti*. Mortalities were 2.8 times greater in nests

that had a queen present compared with queenless nests and only one third of wild *M. sabuleti* nests ($\Phi_{queenless\ nests}$) lacked a queen (Thomas and Wardlaw, 1990). In another study, Thomas and Wardlaw (1992) estimated the survival of wild *M. arion* caterpillars adopted at different densities into *M. sabuleti* nests. Unfortunately, they did not state the fraction of examined nests where queens were present. In our model, caterpillars survive to pupate in the following way. First, we determine the number of caterpillars that are present in each nest. Then we decide with the probability θ ($= 1/3$) whether the nest is queenless or not. According to this decision either the mean survival rates $\Phi_{nest\ without\ queens}$ or $\Phi_{nest\ with\ queens}$ (Table 2) are used to model individual survival of caterpillars in host ant nests. These rates were derived from the survival rates of adopted caterpillars given in Thomas and Wardlaw (1992), (Fig. 4 in their paper). We assumed that one third of the nests studied by these authors was queenless and that survival was 2.8 times higher in queenless nests than in those with queens. This seems likely since the proportion of queenless nests is corroborated by Elmes and Wardlaw (1981) in a number of studies that were performed at different geographical sites. Effects of the butterflies on the

Table 2
Model parameters

Parameter	Meaning	Value
S	Area size (ha)	Site dependent
A	Density of host ant nests per ha	Site dependent
T_C	<i>Thymus</i> -cover	Site dependent (%)
T_B	Number of flower buds per m ²	Site dependent
$\Phi_{\text{other } Myrmica}$	Proportion of adoption of caterpillars by incorrect host ants	Site dependent (%)
λ	Number of eggs laid per adult	30 = 60/2 (Thomas, 1989)
$\Phi_{\text{egg hatching}}$	Egg survival	0.9 (Thomas et al., 1991)
$\Phi_{\text{Trichogramma}}$	Survival from parasitism by <i>Trichogramma</i>	0.947 (= 1–0.053, Thomas et al., 1991)
ρ	Foraging distance of <i>M. sabuleti</i> workers	2 (m) (Thomas, 1990)
θ	Proportion of queenless nests	1/3 (Thomas and Wardlaw, 1992)
$\Phi_{\text{nest without queens}}(n)$	Survival of caterpillars that are adopted at different numbers n into queenless host ant nests	$\Phi_{\text{nest without queens}}(1) = 0.45$ $\Phi_{\text{nest without queens}}(2) = 0.23$ $\Phi_{\text{nest without queens}}(3) = 0.11$ $\Phi_{\text{nest without queens}}(4) = 0.05$ $\Phi_{\text{nest without queens}}(5) = 0.03$ $\Phi_{\text{nest without queens}}(6) = 0.01$ Otherwise $\Phi_{\text{nest without queens}}(n) = 0$ (according to Thomas and Wardlaw, 1992)
$\Phi_{\text{nest with queens}}(n)$	Survival of caterpillars that are adopted at different numbers n into host ant nests with queens	$\Phi_{\text{nest with queens}}(1) = 0.16$ $\Phi_{\text{nest with queens}}(2) = 0.08$ $\Phi_{\text{nest with queens}}(3) = 0.04$ $\Phi_{\text{nest with queens}}(4) = 0.02$ $\Phi_{\text{nest with queens}}(5) = 0.01$ Otherwise $\Phi_{\text{nest with queens}}(n) = 0$ (according to Thomas and Wardlaw, 1992)

dynamics of the host ant population such as the dissolution of individual nests are neglected in the model. A complete definition of the population model of *M. arion* is given in the [Appendix A](#).

2.4. Computer simulations

We implemented our individual based model as a Monte Carlo simulation. We carried out a series of simulation experiments to determine model sensitivity, to assess the extinction risk of the population living at ‘Jungingen’ and estimate the impact of potential conservation measures. In each simulation experiment, we calculated mean population size and extinction probability over a period of 50 years. These output parameters were always based on 10 000 independent simulation runs.

2.4.1. Model sensitivity

We conducted a sensitivity analysis of our model to test how model predictions would change if there were errors in parameter estimation. All simulations were run for a single population and were initialised with 20 butterflies. We always assumed an area size S of 1 ha according to area A2.3.

We assume in our model that parameters λ , $\Phi_{\text{egg hatching}}$, $\Phi_{\text{Trichogramma}}$, ρ and θ (Table 2) are not dependent on the site. To study the influence of errors in estimates of these parameters on the model’s predictions, we varied systematically the value assumed for each of these parameters while holding the remaining parameter values constant. For the habitat characteristics of the area, we chose in this investigation the following setting

$A = 1300$, $\Phi_{\text{other Myrmica}} = 50\%$, $T_C = 30\%$ and $T_B = 150$. These values were observed at area A2.3 (Table 2, Pauler-Fürste, personal communication). The remaining parameter values were chosen according to Table 2.

Thymus cover, host ant density and the proportion of caterpillars that are adopted by other *Myrmica* are essential factors for the conservation of *M. arion*. These habitat characteristics can be influenced directly by conservation measures, e.g. by regular heavy grazing (Thomas, 1990; Thomas et al., 1998). To estimate the impact of conservation measures that are based on changing these characteristics of a site, we performed two further analyses for an area of 1 ha. First, *Thymus* cover T_C and the number of host ant nests A were simultaneously changed assuming that 50% of caterpillars are adopted by other *Myrmica* $\Phi_{\text{other Myrmica}}$ (A2.3 in Table 1). Next, the number of host ant nests and the proportion of caterpillars that are adopted by other *Myrmica* were simultaneously changed assuming that *Thymus* cover T_C is 30% (A2.3 in Table 1). In both analyses, T_B was set to 150 flower buds per m^2 according to area A2.3 and the remaining model parameters were chosen as given in Table 2.

2.4.2. Estimation of the extinction risk of the total population at site 'Jungingen'

Pauler et al. (1995) and Pauler-Fürste et al. (1996) examined movement patterns and mobility of the total population at 'Jungingen' in 1992, 1994 and 1995. In 1992, they did not observe any exchange between neighbouring study areas. None of the 166 marked individuals was recaptured in another area. In 1994 and 1995 they recorded only three movements into neighbouring areas (from A2.2 to A3, A2.2 to A2.1 and A2.3 to A1.3). They concluded that adult butterflies are very sedentary and corroborated several authors (Elmes and Thomas, 1987a,b; Thomas, 1989; Weidemann, 1995). To estimate the extinction risk of the total population at 'Jungingen', we examined the scenario that each of the eight areas is inhabited by a single closed population and thus neglected possible minor migration between areas.

Elmes et al. (1998) more recently reported that the ant species *M. scabrinodis* is a secondary host

of *M. arion*. In order to take this observation into consideration, we examined two situations at 'Jungingen': (1) caterpillars are only adopted by their primary host *M. sabuleti*, and (2) caterpillars are adopted by either the primary host *M. sabuleti* or the secondary host *M. scabrinodis*. In both situations, for each area, habitat characteristics were chosen according to Table 1. The simulation of each area was started with the number of individuals that were marked at this area in 1992 (Pauler et al., 1995). However, there were two exceptions from this procedure. In the field study, areas A1.1 and A1.2 were treated as one area. Therefore, we halved the number of individuals marked and initialised each of both areas with the number obtained. Unfortunately, in 1992, area A1.3 was not examined. In this case the simulation was initialised with ten adult butterflies. All input parameters of the simulations are summarised in Table 3. Values assumed for the remaining model parameters are given in Table 2.

3. Results

3.1. Model sensitivity

Fig. 3 shows the results of the sensitivity analysis of model parameters λ , $\Phi_{\text{egg hatching}}$, $\Phi_{\text{Trichogramma}}$, ρ and Θ . In this figure, the most sensitive parameters to errors in parameter estimation are the number of eggs laid per adult λ and the proportion of queenless nests Θ . Increasing the value of λ resulted in an exponential decrease in the extinction probability ($R = 0.999$) and in a hyperbolically increasing mean population size ($R = 0.956$). In contrast, the extinction probability was not affected by an increase in Θ (with respect to the precision generated by 10 000 Monte Carlo simulation runs), whereas the mean population size increased linearly with an increasing number of queenless nests ($R = 0.988$). Within the possible interval of Θ ([0,1]) the mean population size was tripled.

For $\Phi_{\text{egg hatching}}$, $\Phi_{\text{Trichogramma}}$ or ρ , the extinction probability was not influenced by a change in the parameter value (with respect to the precision generated by 10 000 Monte Carlo simulation runs).

Table 3
Values of input parameters to estimate the extinction risk at ‘Jungingen’

Area	S (ha)	T_C (%)	T_B	N_0	Survival in <i>M. sabuleti</i> nests		Survival in <i>M. sabuleti</i> or <i>M. scabrinodis</i> nests	
					A	$\Phi_{\text{other Myrmica}}$ (%)	A	$\Phi_{\text{other Myrmica}}$ (%)
A1.1	2	1	10	4	1700	39.3	2800	0
A1.2	2	1	10	4	900	71.0	1000	67.7
A1.3	1	10	50	10	3200	8.5	3400	2.9
A2.1	1	8	40	18	3500	35.2	3500	35.2
A2.2	10	30	150	97	2000	0	2000	0
A2.3	1	30	150	2	1300	50	2600	0
A3	7	1	10	38	0	100	3600	55
A4	1	1	10	0	0	100	0	100

We assumed that each of the eight areas is inhabited by a single closed population. For each area, size S , *Thymus* cover T_C , number of flower buds T_B and initial population size N_0 are shown. Host ant density A and proportion of adoption of caterpillars by incorrect host ants $\Phi_{\text{other Myrmica}}$ are presented for the two situations of adoption mentioned in the text. For both situations, the remaining model parameters were set according to Table 2.

However, the mean population size increased hyperbolically with an increasing egg survival probability $\Phi_{\text{egg hatching}}$ ($R = 0.947$), an increasing probability of survival from parasitism by *Trichogramma* $\Phi_{\text{Trichogramma}}$ ($R = 0.974$) and an increasing foraging distance of workers ρ ($R = 0.938$).

Fig. 4 presents the change in extinction probability and mean population size in relation to *Thymus* cover T_C and number of host ant nests A . Both parameters can directly be influenced by conservation measures (Thomas, 1990; Thomas et al., 1998). Extinction probability and mean population size were more strongly influenced by the number of host ant nests than by *Thymus* cover (Fig. 4). For a constant number of ant nests, the extinction probability decreased hyperbolically with increasing values for *Thymus* cover (Fig. 4a; worst fitting found for $A = 200$, in this case $R = 0.841$). The minimum extinction probability was reached at about 5% for all studied numbers of host ant nests. The extinction probability also decreased hyperbolically with an increasing number of ant nests for constant *Thymus* cover (Fig. 4a; worst fitting found for $T_C = 10\%$, in this case $R = 0.864$). The mean population size increased hyperbolically with an increasing *Thymus* cover (Fig. 4b; worst fitting found for $A = 200$, in this case $R = 0.935$) for a constant number of ant nests. For all studied numbers of ant nests, the maximal

mean population size was approximately reached at 20% *Thymus* cover (Fig. 4b). In contrast, for a constant value of *Thymus* cover the mean population size increased linearly with an increasing number of ant nests (Fig. 4b; worst fitting found for $T_C = 100\%$, in this case $R = 0.999$).

The relation between the number of host ant nests A and the proportion of adoption of caterpillars by correct host ants ($100 - \Phi_{\text{other Myrmica}}$) and the extinction probability and mean population size, respectively is shown in Fig. 5. Both an increase in the number of ant nests and an increase in the proportion of adoption of caterpillars by correct hosts result in a rapid decrease in the extinction probability (Fig. 5a). The studied population is not endangered if $(100 - \Phi_{\text{other Myrmica}})$ is greater than 20% (Fig. 5a). For a constant number of host ant nests, the dependence of the mean population size on the proportion of adoption of caterpillars by the correct hosts is characterised by a function that has an optimum (Fig. 5b). In contrast, for a constant proportion of adoption of caterpillars by the correct hosts, the mean population size increases linearly with an increasing number of host ant nests (Fig. 5b; worst case of fitting found for $100 - \Phi_{\text{other Myrmica}} = 10\%$, in this case $R = 0.986$).

In conclusion, the simulation results concerning habitat characteristics that can directly be influ-

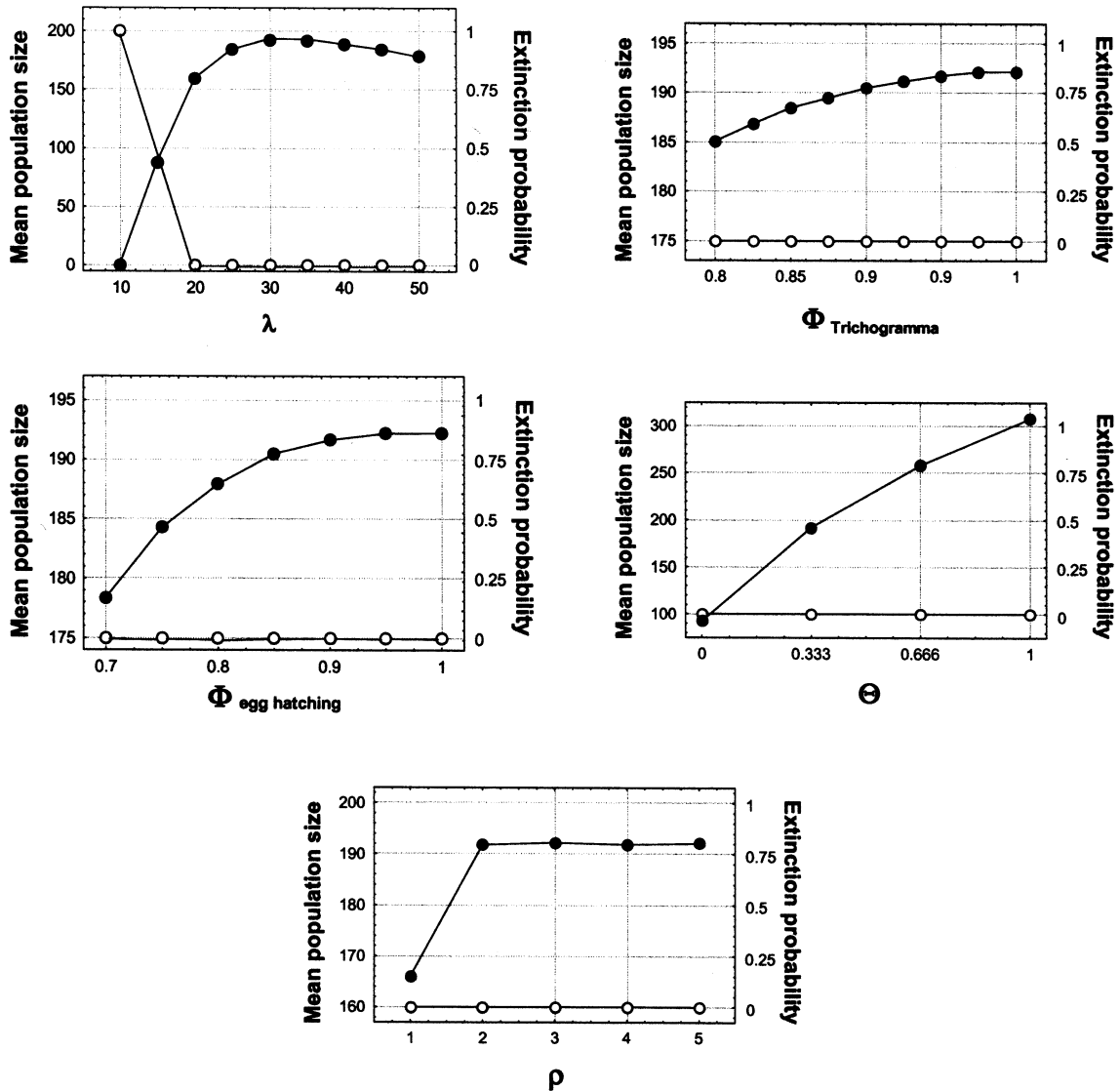


Fig. 3. Sensitivity analysis of model parameters λ , $\Phi_{\text{egg hatching}}$, $\Phi_{\text{Trichogramma}}$, ρ and Θ . Estimated extinction probabilities (open circles) and mean population sizes (filled circles) are shown in relation to the values assumed for each of the following parameters: number of eggs laid per adult λ , egg survival $\Phi_{\text{egg hatching}}$, survival of parasitism by *Trichogramma* $\Phi_{\text{Trichogramma}}$, foraging distance of *M. sabuleti* workers ρ , and proportion of queenless nests Θ . Only one of the studied model parameter values was systematically varied in each graph. For each studied model parameter, the remaining parameter values were chosen according to Table 2. Habitat characteristics were always set in accordance with area A2.3. Simulations were initialised with 20 butterflies.

enced by conservation measures (Figs. 4 and 5) suggest that a population inhabiting an area of 1 ha is likely to be regarded as safe for the next 50 years under the following conditions: *Thymus* cover should not fall below 5% (Fig. 4a), the

proportion of adoption of caterpillars by host ants should be greater than 20% (Fig. 5a), and a minimum nest density of host ants greater than 500 per ha should be assured (Fig. 4a, Fig. 5a).

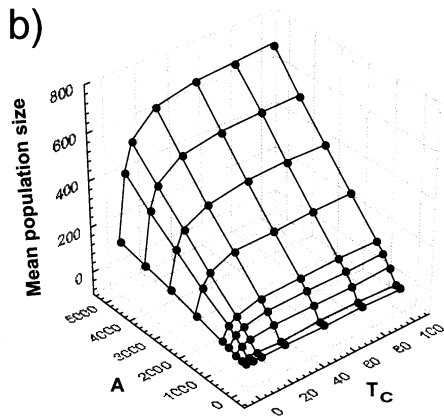
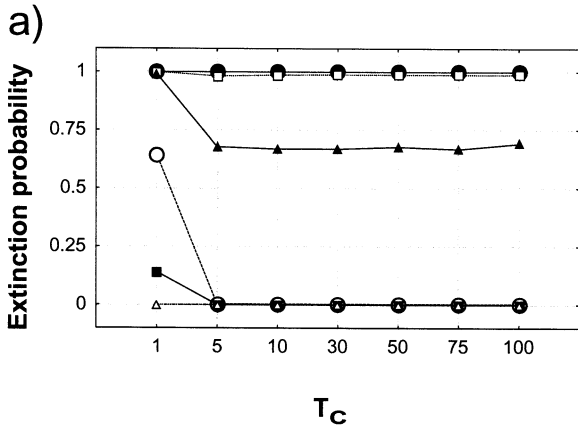


Fig. 4. Sensitivity analysis of model parameters T_C and A . Estimated extinction probabilities (a) and mean population sizes (b) are shown in relation to the values assumed for *Thymus* cover T_C and density of host ant nests per ha A . Filled circles represent 100, open squares 200, filled triangles 300, open circles 400, filled squares 500, and open triangles ≥ 750 host ant nests per ha. The proportion of caterpillars adopted by incorrect host ants $\Phi_{\text{other Myrmica}}$ was set to 50%. Area size S was 1 ha. Site independent parameters were chosen according to Table 2. Simulations were initialised with 20 butterflies. The presented simulation results show that the abundance of *Thymus* should not fall below 5% cover to ensure good conditions for the butterfly (a). Adding extra *Thymus* is not mandatory because it does not further decrease the extinction probability of the population but its mean population size still increases while increasing *Thymus* cover values that are below 20% (b).

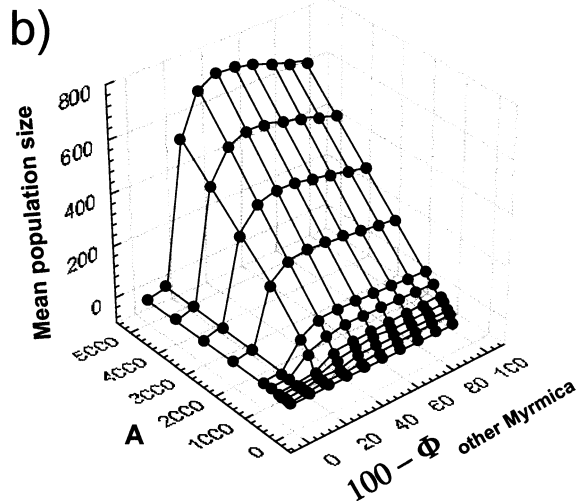
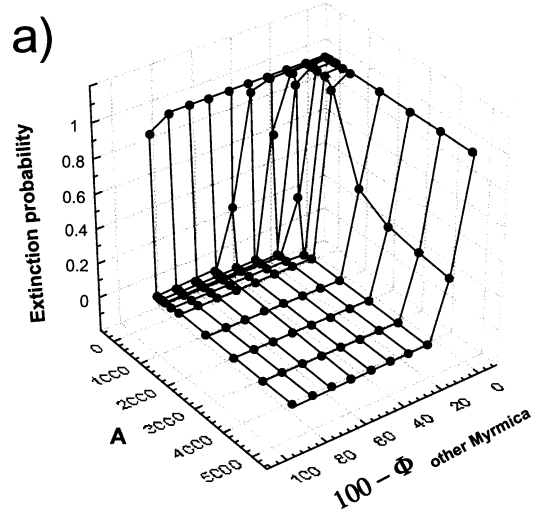


Fig. 5. Sensitivity analyses of model parameters A and $\Phi_{\text{other Myrmica}}$. Estimated extinction probabilities (a) and mean population sizes (b) are shown in relation to the values assumed for density of host ant nests per ha A and proportion of adoption of caterpillars by incorrect host ants $\Phi_{\text{other Myrmica}}$. *Thymus* cover T_C was set to 30%. Area size S was 1 ha. Site independent parameters were chosen according to Table 2. Simulations were initialised with 20 butterflies. The shown simulation results suggest that a population should not be endangered if the proportion of host ant adoption is greater than 20% and the nest density of host ants is greater than 500 per ha. Such conditions ensure a small extinction probability (< 0.01).

3.2. Vulnerability of the total population at site 'Jungingen'

Table 4 summarises for each area the estimated extinction probabilities and mean population sizes under the two studied situations of host adoption. To test whether our model works correctly for the total population at 'Jungingen', we compared the population sizes generated by our model and the number of individuals marked at each area. Population size estimates were not available for all studied areas. Recaptures of marked individuals were in most areas too low to perform the appropriate calculations to estimate population size (Pauler et al., 1995; Pauler-Fürste et al., 1996). Nevertheless, the times spent on the areas were equal and thus the number of marked individuals in an area is expected to be proportional to population size. For the situation that caterpillars are only adopted by their primary host ant *M. sabuleti*, we found no correlation between the number of marked individuals at the areas and the predicted mean population size (Spearman $R = 0.493$, $P = 0.321$, areas A1.1 and A1.2 were treated as one area). However, a high correlation was found in the situation that caterpillars were either adopted by the primary host *M. sabuleti* or the secondary host *M. scabrinodis* (Spearman $R = 0.943$, $P < 0.005$; areas A1.1 and A1.2 were again treated as one area). In either situation, none of the populations inhabiting each of the areas A1.1 through A2.3 was endangered. The extinction probability of all these populations was very small (< 0.01 , Table 4). Therefore, under constant conditions of habitat quality the total population at site 'Jungingen' is likely to be regarded as safe for the next 50 years.

4. Discussion

4.1. Model sensitivity and general implications for species conservation

With respect to vulnerability of the butterfly *M. arion*, the most critical parameters are number of eggs laid per adult λ , proportion of queenless nests Θ , *Thymus* cover T_C , density of host ant nests A

and the proportion of caterpillars adopted by other non-host *Myrmica* $\Phi_{\text{other Myrmica}}$. The remaining parameters are of intermediate to low sensitivity, only having an effect if errors in estimates are strong. This suggests that moderate site-dependent variation in parameters $\Phi_{\text{egg hatching}}$ and $\Phi_{\text{Trichogramma}}$ will not strongly influence the predictions of our model. Habitat characteristics T_C , A and $\Phi_{\text{other Myrmica}}$ are critical key parameters that may be influenced by conservation measures (Thomas, 1990; Thomas et al., 1998).

Our model suggests that the abundance of *Thymus* should not fall below 5% cover to guarantee good conditions for the butterfly (Fig. 4a). Adding extra *Thymus* is not mandatory since this conservation measure does not further decrease the extinction probability of a population (Fig. 4a) but its mean population size will still increase while increasing *Thymus* cover values that are below 20% (Fig. 4b). This observation is in contrast to the results obtained for the butterfly *M. rebeli* by Clarke et al. (1998). For low densities of the larval foodplant (< 1000 plants per ha), these authors found a close relationship between the egg density which is proportional to adult density and the density of the larval foodplant, the gentian *G. cruciata*. In contrast to *Thymus* plants, which are evenly distributed at 'Jungingen', gentians tend to be very strongly aggregated at low densities. At high densities gentians are also evenly distributed across an area. When foodplants are evenly distributed throughout a site, all host ant nests tend to be impacted to roughly the same extent by *Maculinea* caterpillars. Due to the clumping of gentians at low densities the total sustainable capacity of ant nests is not most efficiently used by *M. rebeli*. Thus, an increase in the gentian density fills the gaps between existing plants, increases remarkably the number of host ant nests used by *M. rebeli* caterpillars and these two processes together result in an increase in the abundance of the butterfly. However, if the gentian density further increases none host ant nest is safe for exploitation by *M. rebeli* and this leads to a dramatic fall in the size of the butterfly population. The latter effect was found by Clarke et al. (1998) but it is not observable in our simulations since the predator-prey interaction

Table 4
Simulation results of the extinction risk of the populations at ‘Jungingen’

Area	(a) Survival in <i>M. sabuleti</i>			(b) Survival in <i>M. sabuleti</i> or <i>M. scabrinodis</i> nests			Number of marked individuals
	Extinction probability	Population size	Population density per ha	Extinction probability	Population size	Population density per ha	
A1.1	0.000	111.064	57.032	0.000	103.409	51.705	4
A1.2	0.008	49.697	24.849	0.007	47.137	23.569	4
A1.3	0.000	396.286	396.286	0.000	411.204	411.204	–
A2.1	0.000	447.833	447.833	0.000	447.833	447.833	18
A2.2	0.000	2550.229	255.023	0.000	2550.229	255.023	97
A2.3	0.000	191.533	191.533	0.000	331.117	331.117	2
A3	1.000	0.000	0.000	0.000	799.881	114.269	38
A4	1.000	0.000	0.000	1.000	0.000	0.000	0

We assumed that each of the eight areas is inhabited by a single closed population. Estimates of extinction probability, mean population size and density per ha are presented for two situations of host ant adoption mentioned in the text. Furthermore, the number of butterflies marked in this area during the field study of [Pauler et al. \(1995\)](#) is shown for each area. In this study, areas A1.1 and A1.2 were treated as one area and area A1.3 was not examined. There is no correlation between the number of marked individuals and the predicted population size in case (a) but a high correlation ($R = 0.943$, $P < 0.005$) in case (b).

between *M. arion* and its host ant is neglected in our model.

Regardless of the local climate, the niche breadth of the primary host ant *M. sabuleti* is much narrower than the niche breadth of *Thymus*. It is much more affected by latitude, altitude and climate than the niche of the initial foodplant (Thomas et al., 1998). Nest densities of host ants, furthermore, are influenced by competition with other *Myrmica* ants (Levings and Traniello, 1981) whose niches overlap with the niche of *M. sabuleti* (Thomas et al., 1998). Therefore, nest densities of host ants and non-host *Myrmica* cannot be changed independently of each other in the field. Our simulation results suggest that a population should not be endangered if the proportion of caterpillar adoption by the correct host ant is greater than 20% and the minimum nest density of host ants is greater than 500 per ha (Fig. 5a). Thomas (1990) stated that a 'safe' population of 400–1000 adult *M. arion* could be theoretically supported by 1 ha of ground, given ideal habitat (at least 2500 *M. sabuleti* nests). The results of our sensitivity analysis corroborate his field observation. Our model predicts approximately 400 adults for a habitat of size 1 ha, 30% *Thymus* cover, 2500 *M. sabuleti* nests and at least 20% host ant adoption (Fig. 5b).

The dependence of the mean population size on the proportion of adoption of caterpillars by the correct host ant for a constant number of host ant nests is characterised by a function that has an optimum (Fig. 5b). This results from scramble competition of caterpillars in ant nests (Clarke et al., 1998) that causes a decrease in the survival probability of a caterpillar with an increasing number of caterpillars in the nest. If the proportion of adoption by the correct host ant is low, only a few caterpillars are adopted and mean survival rate of these adopted individuals is high. With an increasing proportion of adopted caterpillars the mean number of caterpillars adopted per nest will exceed one and thus, the survival probability of each caterpillar will decrease (Table 2). The latter effect results in a decrease in the mean population size for high values of host ant adoption (Fig. 5b).

In conclusion, our simulation results support the effect of conservation measures that were implemented in the UK after intensive ecological research (Thomas, 1980, 1993, 1995b; Thomas et al., 1989; Thomas and Wardlaw, 1990, 1992).

4.2. Vulnerability of the total population at 'Jungingen'

We found in our simulations that the total population at 'Jungingen' is likely to be regarded as safe for the next 50 years if habitat quality will not change. This result was independent of the assumption made for caterpillar adoption and the neglect of migration between the eight areas inhabited by the butterfly. The latter process is expected to further decrease the extinction risk of spatially structured populations. Area A2 is the most important for the persistence of the 'Jungingen' population. It shows the highest densities of *M. arion* (Table 4). High densities of the butterfly are bound to a high abundance of *Thymus* and a high abundance of *Myrmica* host ant colonies. These conditions are maintained at area A2 by grazing at short intervals (Table 1, Pauler et al., 1995). Extensive grazing by sheep and goats or extensive mowing has already caused a low abundance of the butterfly in area A1, A3 and A4 (Pauler et al., 1995). Swards of low height are warmer in general and thus are more favourable for the warmth-loving host ant than swards with high vegetation. Extensive grazing or mowing increases mean vegetation height of the grassland and causes a decrease in host ant abundance due to the resulting less favourable climatic conditions for the host ant. Moreover, grazing increases *Thymus* cover. Sheep and goats avoid to graze *Thymus* due to the essential oils of the plants. The plants themselves benefit from the gain in light caused by an overall decrease in vegetation height that is caused by grazing and mowing. Large-scale abandonment of grazing or mowing could quickly lead to a reduction in the abundance of *M. arion*. In the UK, abandonment of pasture during the 1980s led to a rapid decline in the abundance of the host ant *M. sabuleti* followed by the extinction of the Large Blue Butterfly (Thomas, 1980). Grazing or mowing also maintains habitat require-

ments of *M. arion* at ‘Jungingen’ (Pauler et al., 1995; Pauler-Fürste et al., 1996). Consequently, future land use developments at ‘Jungingen’ and in the region have to be monitored carefully to ensure survival of *M. arion*.

Elmes et al. (1998) noted that a trivial number of adult butterflies emerge from secondary host nests and that in some populations this could be important for long-term survival. In our simulations, adding adoption of caterpillars by its secondary host ant *M. scabrinodis* resulted in better estimations of the abundance of *M. arion* at ‘Jungingen’. Especially, for area A3 that shows low *Thymus* cover and absence of *M. sabuleti*, the prediction of the population size became much better if the secondary host ant was considered. The niche preference of *M. scabrinodis* is characterised by medium to high values of soil moisture and medium values of soil temperature. Such conditions are suboptimal for the primary host ant *M. sabuleti* which prefers warmer and drier soils (Elmes et al., 1998). The importance of suboptimal habitats for the survival of other species was demonstrated in several field studies (Dobkin et al., 1987; Ehrlich and Murphy, 1987; Harrison et al., 1988; Weiss et al., 1988; Harrison, 1991) and in simulations (Griebeler and Gottschalk, 2000b; Frouz and Kindlmann, 2001).

4.3. Future areas of study

In contrast to the model developed by Hochberg et al. (1994) and Clarke et al. (1998) for *M. rebeli*, we assumed that the number of host ant colonies is constant. We neither model dynamics between host ant colonies nor ant-dynamics within the nests nor the dynamics of the parasitoid. Especially, the interaction between the butterfly and the host ant colonies is neglected. It is already known that a butterfly is able to cause the dissolution of individual nests (Hochberg et al., 1992). The strong interspecific competition of the host ant with other *Myrmica* ants (Levings and Traniello, 1981) is also not taken into consideration. Furthermore, we assumed in our simulations that the probability of survival in the nests of the secondary host ant *M. scabrinodis* is equal to the

probability of survival in the nests of the primary host *M. sabuleti*. However, Hochberg et al. (1994) stated that all these processes are difficult to study in the field and this fact explains our simplifications. Finally, environmental stochasticity that may have large impacts on populations is excluded from our model and is expected to lead to increasing requirements in habitat size and quality. All these simplifications of the model were essential since suitable data about *Myrmica* ants and environmental stochasticity were not available.

Nevertheless, our investigation suggests that important insights into the vulnerability of *M. arion* populations could be gained by modelling populations. To apply the model in conservation planning, it is necessary to quantify correctly the key parameters of population dynamics at the respective sites. As our model predicts, the assessment of *Myrmica* nest densities is most important for the survival of *M. arion*. Underestimation or overestimation of the abundance of the host ants relative to non-host ants that may be caused by improper sampling in the field, leads to a severe misestimation of the extinction risk of a natural population (Figs. 4 and 5). An assessment of risk derived from field observations by Thomas (1990) was corroborated in our simulation study. Maintenance or re-establishment of grazing or mowing was successfully tested as a suitable conservation measure for declining *M. arion* populations. Grazing or mowing guarantee low vegetation height of swards that causes an increase in host ant abundance due to the resulting more favourable microclimatic conditions for the warmth-loving host ant species of the Large Blue Butterfly (Thomas, 1990; Thomas et al., 1998).

Acknowledgements

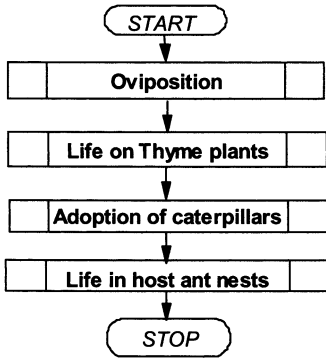
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Appendix A

The following five flowcharts provide a complete definition of the population model developed for *M. arion*. Charts are based on the life cycle of the butterfly that is presented in Fig. 2. Values of model parameters are summarised in Table 2. We assume a function ‘Random’ that yields a uniformly distributed random number in [0,1].

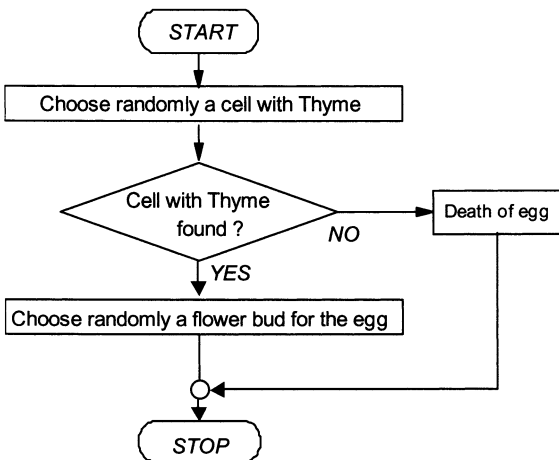
Simulation (life cycle)

(is repeated in each generation for each individual)



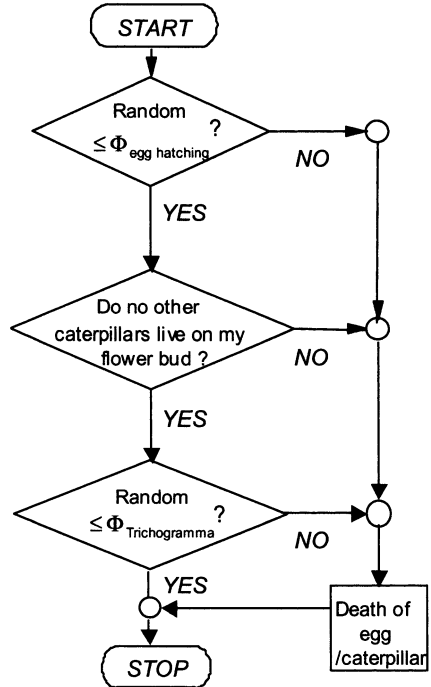
Oviposition

(is repeated λ -times for each butterfly)



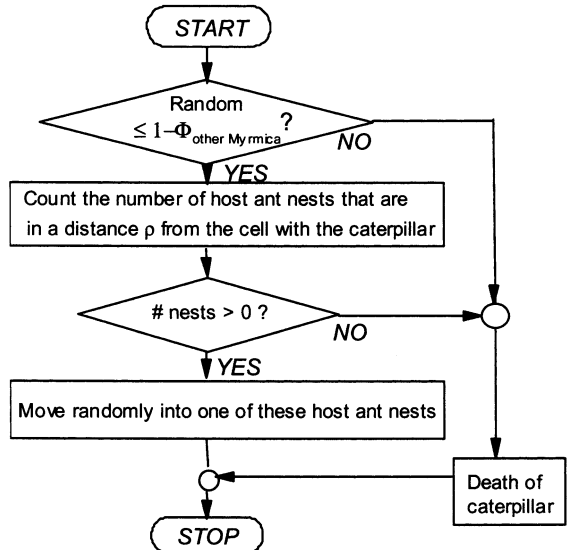
Life on Thyme plants

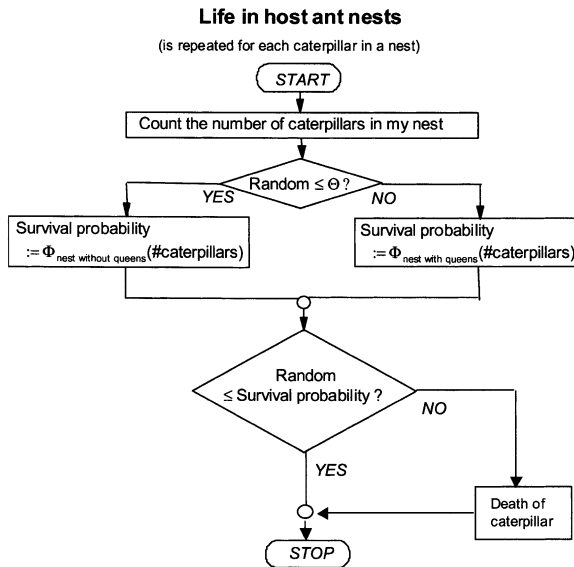
(is repeated for each egg)



Adoption of caterpillars

(is repeated for each caterpillar)





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