

Coastal dunes as important strongholds for the survival of the rare Niobe fritillary (*Argynnis niobe*)

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Abstract We studied the oviposition and larval habitat preferences of the Niobe fritillary (*Argynnis niobe*) in the dunes of the east Frisian Island Langeoog (German North Sea). By ascertaining habitat quality we are able to assess the minimum habitat size for populations of *A. niobe* in dune islands. The preferred oviposition and larval habitats were best characterised by a combination of (1) host-plant abundance, (2) host-plant quality and (3) vegetation structure. The oviposition and larval habitats of *A. niobe* were characterised by low-growing vegetation with bare ground and a warm microclimate. In contrast to the also common *V. tricolor* ssp. *curtisii*, the leaves of the host plant *V. canina* showed a lower C/N ratio, suggesting that differences in plant quality may account for host-plant use. *A. niobe* seems to depend on very large areas of potential larval habitat, thus explaining its ongoing decline in the increasingly fragmented Central European landscape. Our data indicate that grass encroachment is a major threat for *A. niobe* in coastal dunes due to its negative impact on microclimate and violet germination. Mosaic top-soil removal and low-intensity grazing should be suitable tools to promote rejuvenation of *V. canina*.

Keywords Butterflies · Conservation · Habitat quality · Host plants · Minimum habitat size · Vegetation structure

Introduction

Most butterfly species react very sensitively to the alteration of their habitats (Thomas 1991). Consequently, besides the extent of habitat area and isolation of populations, habitat quality is the major factor for the persistence of butterfly populations (e.g. Thomas et al. 2001; Anthes et al. 2003b; WallisDeVries 2004; Eichel and Fartmann 2008). In their resource-based definition of habitat, Dennis et al. (2006) describe two groups of resources required by butterflies, consumables (host plants and adult food) and utilities. Utilities define conditions under which butterfly populations exist and persist. Examples are physical sites for distinct activities (e.g. pupation, mate location), enemy-free spaces, and suitable conditions for development and activities such as appropriate local climates and microclimates.

Habitat quality of butterflies is mainly driven by the requirements of the immature stages (Fartmann 2004; Fartmann and Hermann 2006). The female's choice is responsible for a successful development of eggs and larvae. Ideally it chooses a site for oviposition with sufficient host plants in high quality and an adequate microclimate where the egg is protected against predators and parasitoids (Porter 1992; García-Barros and Fartmann 2009).

Host plant abundance is an important factor to maintain viable butterfly populations (Anthes et al. 2003a, b, 2008; Konvička et al. 2003; Eichel and Fartmann 2008). Additionally, at the time of hatching, these host plants should also be qualitatively optimal to support larval growth. Thus, the butterfly life-cycle has to be adapted to host-plant phenology (Munguira et al. 2009). The quality of available host plants, however, can vary because nutrient contents in plants change during the growing season. Young plant tissue contains the highest amounts of nitrogen, whereas the amounts of nitrogen and water decline with time (Bernays

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and Chapman 1994; Munguira et al. 2009). Microclimate plays a major role in determining habitat quality (Anthes et al. 2003a, b; Fartmann 2006a, WallisDeVries and van Swaay 2006) and is strongly influenced by vegetation structure (e.g. Stoutjesdijk and Barkman 1992).

Butterfly species living in warm and dry microhabitats of early successional stages have undergone a dramatic decline (Thomas 1991; Beneš et al. 2002; Fartmann 2004, 2006b). Intensifying agriculture, abandonment of low-intensity land use and afforestation led to habitat loss, fragmentation and decreasing habitat quality, especially for butterfly species colonising cultural landscapes (van Swaay et al. 2006). In contrast with inland areas, natural disturbances still play an important role in coastal ecosystems, including dune systems.

Although, habitat area is well known as one of the main factors determining survival of butterflies, reliable data on minimum areas for long-term survival of butterfly populations are rare. The few studies presenting minimum area data often do not consider the spatial arrangement of patches within habitat networks nor the quality of single habitat patches. Despite increasing habitat loss and decreasing habitat quality, habitat networks can still support strong populations for a long time. Yet, in the long run these are usually insufficient and will become extinct. Such ‘declining’ populations often lead to an underestimation of minimum habitat size for long-term persistence (Bulman et al. 2007).

The Niobe fritillary (*Argynnis niobe*) has suffered a dramatic decline in central Europe during last decades (Fric and Konvička 2002; Bos et al. 2006) and is now endangered in Germany (Pretscher 1998). However, knowledge about the ecology (Ebert and Rennwald 1991; Fartmann and Hermann 2006) and the reasons for the ongoing decline remains poor.

We studied *A. niobe* in a coastal dune ecosystem of the German North Sea, where the species is still common. We aimed to determine the key factors of habitat quality in *A. niobe*. Our study focussed on a microhabitat analysis considering vegetation structure at occupied and random oviposition and larvae sites, respectively. Additionally, inter-specific host-plant quality was tested to explain the preference for one of the two potential host plant species common in the study area. Through ascertaining habitat quality we are able to assess the minimum habitat size for populations of *A. niobe* in dune islands.

Materials and methods

Study species

A. niobe is a univoltine *Viola*-feeding butterfly species, with the adult flight period occurring in most regions

between June and August. Following hibernation in the egg stage (Bink 1992), larvae hatch in spring and develop between mid-April and the end of June. The development of the pupa takes about 14 days (Bink 1992).

So far, little has been known about the habitat characteristics of *A. niobe*. Observations of egg-laying females and larvae are rare (e.g. Hafner 2005). In central Europe, *A. niobe* occurs from the coast to the sub-alpine region (SBN 1987). Formerly, the Niobe fritillary was widespread throughout central Europe but it has declined severely during past decades (e.g. Fric and Konvička 2002; Bos et al. 2006). In Germany, the East Frisian Islands are the last remaining strongholds of *A. niobe* besides the Bavarian Alps and the southern parts of the Black Forest (Fig. 1).

Study area

We studied *A. niobe* on the East Frisian Island of Langeoog in the North Sea (Lower Saxony, Germany; Fig. 1). The island is about 10.9 km long and has an area of about 20.4 km² (Petersen and Pott 2005). Langeoog is influenced by an Atlantic climate with a mean annual temperature of 8.7°C and a mean precipitation of 737 mm (DWD 2007). The East Frisian Islands are sandy barrier islands and are influenced by tides. They developed in a tidal range between 2.0 and 3.5 m (Streif 1990). Structural components of the island are beaches, dunes, wet and dry dune slacks as well as salt marshes and tidelands.

The study sites were situated in grey-dune vegetation (*Koelerion albescentis* and *Ammophilion arenariae*, cf. Rennwald 2002) with *V. canina* and *V. tricolor* ssp. *curtisii* as potential host plants. All sites belong to the national park “Niedersächsisches Wattenmeer”.

Methods

Oviposition and larval microhabitat

From April to June 2006 we systematically searched for larvae of *Argynnis niobe* in grey-dune vegetation adjacent to the potential host plants *V. canina* and *V. tricolor* ssp. *curtisii*. From the beginning of July till August we focussed on observing oviposition and searched for eggs on and around the host plants (‘focussed search’).

To characterise egg-laying and larval habitats of *A. niobe* we measured the following parameters: slope aspect (°) and inclination (°) were recorded using a compass with inclinometer. Additionally, potential sunshine duration (in hours) was measured using a horizontoscope after Tonne (1954) during the peak of caterpillar development in May and egg deposition in July (May and July have the same values for sunshine durations). For the characterisation of the microhabitats the following

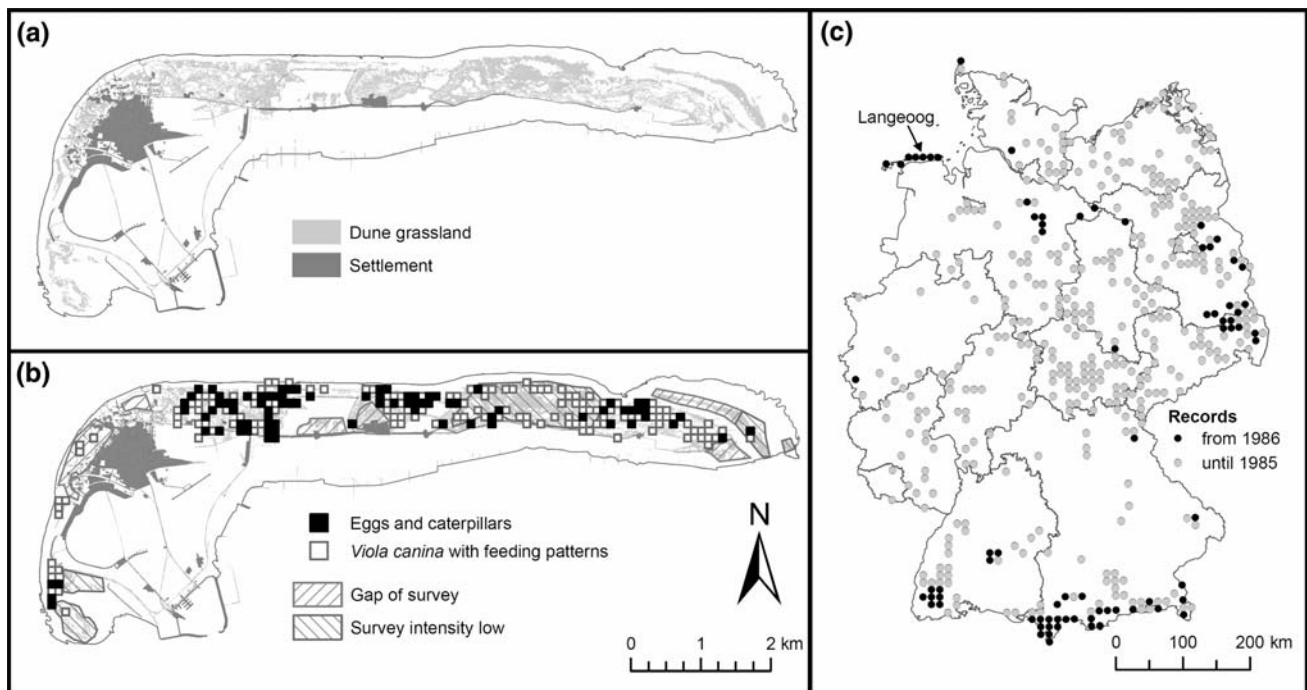


Fig. 1 **a** Study area Langeoog with grey-dune vegetation as potential larval habitat of *Argynnis niobe*. **b** Distribution of eggs and larvae of *A. niobe* on Langeoog based on a 100 × 100 m grid. **c** Distribution of *A. niobe* in Germany. Sources: Aquazoo-Löbbecke Museum (2007), Bayerisches Landesamt für Umwelt (2007), Brockmann (1989), Ebert and Rennwald (1991), Föhst and Broszkus (1992), Kraus (1993),

Lederer and Künnert (1963), Lobenstein (2003), NLWKN (2006), Reinhardt (1983, 2005), Stamm (1981) and H. Andretzke, S. Buchholz, S. Caspari, J. Gelbrecht, S. Hafner, H. G. Joger, J. Kleinekuhle, D. Koelman, D. Kolligs, A. C. Lange, D. Lück, P. Mansfeld, B. Nannen, R. Ohle, R. Reinhardt, F. Röbbelen, A. Schmidt, P. Schmidt, M. Sommerfeld, R. Trusch (in litt)

parameters were recorded in a radius of 50 cm around the egg or larva: medium turf height (cm), cover (%) of shrubs, herbs, mosses, lichens, litter, bare ground, *V. canina* and *V. tricolor* ssp. *curtisii*. Furthermore, horizontal vegetation cover (%) from 5 to 30 cm height (in layers of 5 cm intervals), oviposition height (cm), distance to the next host plant (cm) and diameter of the host plant (cm) were recorded.

In order to detect habitat preferences we recorded the available habitat structures (mentioned parameters above and same area) in the surroundings of individual host plant. Sites were chosen by walking 10 m in a random direction from the egg or caterpillar observation. Because we found no evidence that *V. tricolor* ssp. *curtisii* (e.g. feeding larvae, oviposition on the plant) is being used as a host plant in our study region, all estimations or measurements were taken at the closest *V. canina* individual. At oviposition sites the following parameters were additionally measured: oviposition substrate and exposure of the egg.

Vegetation types at egg-laying and larvae sites were recorded after Petersen and Lammerts (2005). In order to compare food quality of *V. canina* and *V. tricolor* ssp. *curtisii*, leaf samples of both species were collected and air-dried between 25th of May and 11th of June. After the field season the leaf samples were dried at 60°C and

ground. Finally, the C/N ratio of the leaves was measured using an elemental analyzer (EuroVektor Instruments).

Minimum habitat size

To estimate the minimum habitat size for a population we compared the area of potential larval habitats for islands occupied by *A. niobe* and un-occupied islands in the southern North Sea from Texel (NL) to the Skalingen peninsula (DK) ($N = 23$ islands). As our study showed (see “Discussion”) the total area of grey-dune grassland [according to Petersen and Lammerts (2005)] per Island can serve as a good proxy for the potential larval habitat. The area of grey-dune vegetation of each East Frisian Islands was calculated from digital habitat maps (source: Nationalpark Niedersächsisches Wattenmeer 2007). Values for other islands were taken from Petersen and Lammerts (2005).

Statistical analysis

Used and unused plant and microsite parameters were compared using Mann–Whitney U test (MWU) for continuous variables and with χ^2 tests for categorical variables. The box plots include the median and the 10, 25, 75 and the

90% percentiles. Stepwise-forward logistic regression was applied to assess those parameters possessing the highest explanatory power for oviposition-site and larval-habitat electivity. All statistical tests were performed with SPSS 11.5.1. Median values are given unless otherwise stated. Differences in sample size between analyses originate from missing values for some variables.

Results

Oviposition and larval microhabitat

In total, we found 299 clutches with 303 eggs (107 microsities) and 89 larvae (66 microsities) of *A. niobe*. Eggs were mainly laid singly, only in four cases as couples. Up to 22 eggs were found per microsite. Most of the clutches (151, 51.5%) were deposited on mosses, mainly *Dicranum scoparium* and *Hypnum lacunosum*. Furthermore, clutches occurred on *V. canina* (67, 22.4%) and litter (63, 21.1%). Other substrates were rarely used. With 228 clutches (76.3%) the vast majority were protected against direct solar irradiation (e.g. by shading through grass tussocks of *Ammophila arenaria*, *Corynephorus canescens* or *Koeleria arenaria*). Only 22 (7.4%) of the egg clutches were not shaded. The remaining 49 (16.4%) clutches could not be classified into the two categories mentioned above. Females of *A. niobe* deposited their egg clutches close to the ground up to a height of 6 cm (median = 2.5 cm).

Except for one caterpillar that was found under *V. tricolor* (but *V. canina* was also present at this site), all specimens were detected adjacent to *V. canina*. Larvae of *A. niobe* were observed feeding during daylight on *V. canina* (18 × on leaf, 3 × on flower, 1 × on leaf and flower), but never on *V. tricolor*.

Egg clutches and larvae were predominantly situated close to the host plant *V. canina* (Fig. 2). Whereas all larvae were detected within a radius of 15 cm around the host plant, this was only partly true for the egg clutches found by focussed search (MWU, $U = 7,431.5$, $P < 0.01$) and even more so for the egg clutches found by observing ovipositing females (MWU, $U = 1,073.5$, $P < 0.001$). The maximum distance between an egg and the host plant *V. canina* was 53 and 430 cm, respectively (focussed search and ovipositing females, respectively). In general, egg clutches which were found by observing an egg-laying female were further away from the host plant than clutches found by focussed search (MWU, $U = 4,072.0$, $P < 0.001$), indicating a bias in the former.

Most egg clutches and larvae were found in sites with short turf and open vegetation (Table 1). For both egg clutches and larvae the occupied sites had significantly lower turf heights than the random sites. The vegetation

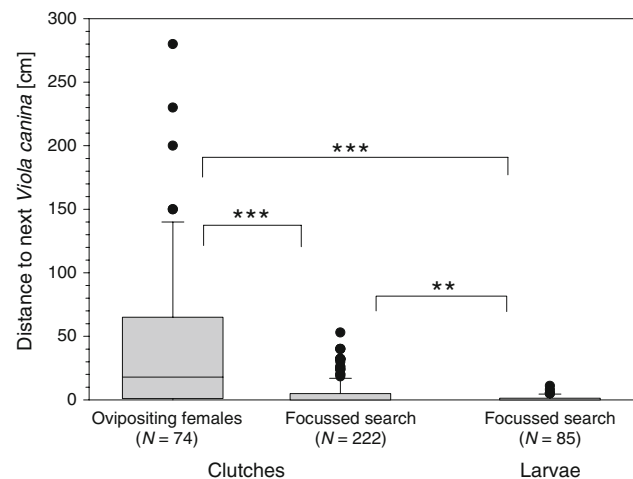


Fig. 2 Distance of egg clutches (ovipositing females and focussed search) and larvae of *Argynnis niobe* from the host plant *Viola canina* (MWU; ** $P < 0.01$, *** $P < 0.001$). The following outlier is not pictured: ovipositing females: 430 cm

layer mainly consisted of mosses, whereas the cover of herbs was relatively low (Table 1). A certain amount of litter was usually present. Higher amounts of bare soil rarely appeared. Shrub and lichen cover were low. Yet, for larvae as well as for eggs none of the parameters differed between occupied and random host plants.

Egg clutches and larvae were mainly found on flat or slightly inclined sites (median_{egg clutches} = 5°, median_{larvae} = 3°; Fig. 3). Aspects of occupied and random sites did not differ significantly for both egg clutches and larvae (Table 2). Sites occupied by egg clutches or larvae were well exposed to the sun. Potential daily sunshine duration was significantly higher for larvae than for oviposition sites (median_{larvae} = 14.0 h, median_{eggs} = 13.5 h; Fig. 4).

About 95% of the egg clutches and larvae were found in grey-dune plant communities (Table 3). Egg-laying and larval habitats were mainly situated in *Festuco-Galietum* (oviposition sites: 34.6%; larvae sites: 51.5%) and *Violo-Coryneporetum* (23.4; 16.7%). Furthermore, *A. niobe* reproduced in *Elymo-Ammophiletum festucetosum* (19.6; 13.6%) and in open stages of *Carex arenaria* stands (12.1; 10.6%). Mature white dunes (*Elymo-Ammophiletum festucetosum*; 5.6; 4.5%) contributed marginally.

Host-plant abundance and quality

V. canina occurred on all microsities with *A. niobe* eggs or larvae. *V. tricolor* in contrast was only present on 6 of the oviposition sites (6%) and 27 of the larvae sites (41%). The occupied sites (oviposition and larvae) were characterised by a significantly higher cover of *V. canina* (each time median = 5%) than random sites (each time median = 2.5%, Table 1). *V. tricolor* cover was in general lower and did not differ between occupied and random sites.

Table 1 Mean (range of) turf height, cover of vegetation layers and potential host plants in a circle of 50 cm at oviposition and larvae sites of *Argynnis niobe*

	Oviposition sites			Larvae sites		
	Occupied (<i>N</i> = 107)	Random (<i>N</i> = 71)	Statistics (<i>U</i>)	Occupied (<i>N</i> = 66)	Random (<i>N</i> = 43)	Statistics (<i>U</i>)
Turf height (cm)	15 (5–50)	20 (7.5–60)	2,712.5**	11 (4–30)	15 (4–40)	840.5 ***
Cover (%)						
Shrub layer	0 (0–35)	0 (0–30)	3,715.0 ^{NS}	0 (0–25)	0 (0–40)	1,377.5 ^{NS}
Herb layer	20 (5–60)	25 (5–80)	3,613.5 ^{NS}	35 (10–75)	35 (10–70)	1,396.0 ^{NS}
Litter	20 (5–80)	20 (2.5–80)	3,724.5 ^{NS}	15 (0–70)	20 (0–75)	1,155.0 ^{NS}
Moss	50 (0–90)	60 (10–85)	3,547.0 ^{NS}	62.5 (5–90)	60 (10–95)	1,200.5 ^{NS}
Lichen	1 (0–70)	0 (0–60)	3,197.5 ^{NS}	0 (0–40)	0 (0–30)	1,307.5 ^{NS}
Bare ground	2.5 (0–35)	0 (0–30)	3,217.5 ^{NS}	0 (0–60)	0 (0–60)	1,386.5 ^{NS}
<i>Viola canina</i>	5 (0–40)	2.5 (0.5–15)	2,548.0 ***	5 (0–45)	2.5 (0.25–15)	989.0 **
<i>Viola tricolor</i>	0 (0–2.5)	0 (0–2.5)	3,519.0 ^{NS}	0 (0–5)	0 (0–2.5)	1,110.5 ^{NS}

In each case occupied sites are compared with random sites

** *P* < 0.01, *** *P* < 0.001

NS not significant

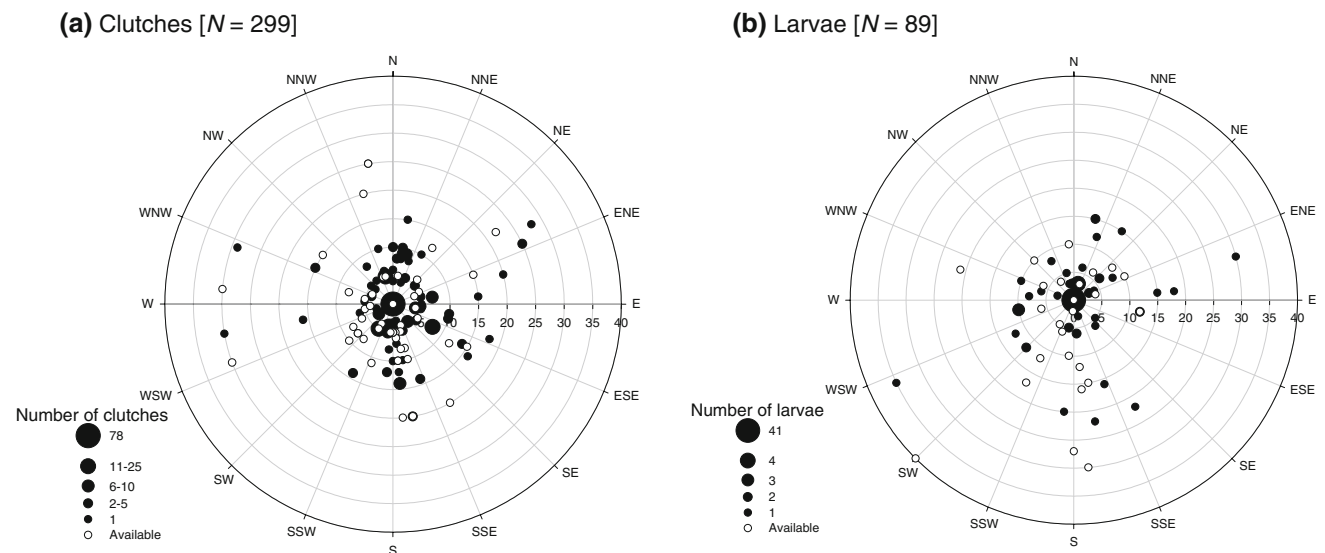


Fig. 3 Aspect and slope at occupied and random sites of egg clutches and larvae of *Argynnis niobe*. Due to a better clarity data for random sites with no aspect and slope are pictured as one [24 × on oviposition sites (*N* = 71) and 18 × on larvae sites (*N* = 43)]

The analysis of the C/N ratio showed significant differences between *V. canina* and *V. tricolor*. The leaves of *V. canina* had a lower and less variable C/N ratio (median = 14) than the leaves of *V. tricolor* (median = 19; Fig. 5).

Preference analysis

Both, the oviposition pattern and the larvae distribution of *A. niobe* were best explained by (1) host-plant abundance and (2) vegetation structure parameters (Table 4a, b; see odds ratio [Exp(B)]): The likelihood of a site being

accepted for oviposition increased with cover of *V. canina* and vegetation density in 10 cm height, but decreased with turf height. Larvae were most likely to be found on sites with high cover of *V. canina* and low turf height (Table 4b).

Minimum habitat size

Presence of *A. niobe* on North Sea islands was restricted to islands with at least 100 ha of connected grey-dune vegetation (Fig. 6). Thus, most populations occur on the West Frisian and East Frisian Islands. The largest size of connected

Table 2 Aspects of occupied and random oviposition and larvae sites of *Argynnis niobe*

Aspect	Oviposition sites		Larvae sites	
	Occupied	Random	Occupied	Random
N	6	3	3	1
E	10	4	4	2
S	9	6	5	9
W	4	4	4	2
Flat	78	53	50	29
Total	107	70	66	43

Slopes of less than 10° to the horizontal were classified as flat (Warren 1993)

Oviposition sites: $\chi^2 = 1.263$, $df = 4$, $P = 0.868$

Larvae sites: $\chi^2 = 4.401$, $df = 4$, $P = 0.354$

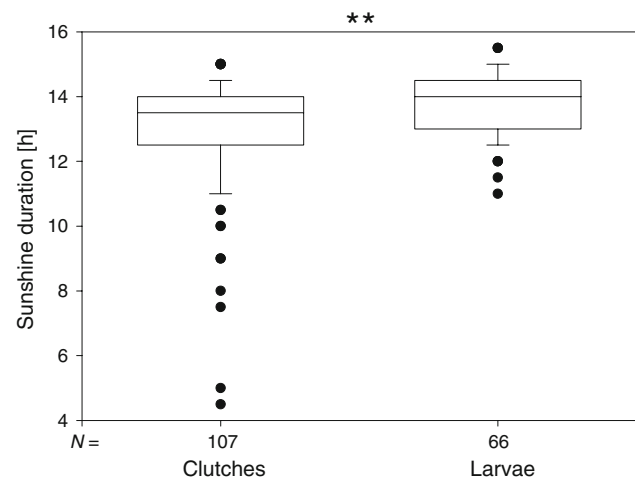


Fig. 4 Maximum daily direct insolation duration in May (growth of larvae) and July (peak flight time of females) at oviposition and larvae sites of *Argynnis niobe* (MWU, $U = 2,632.5$, $**P < 0.01$)

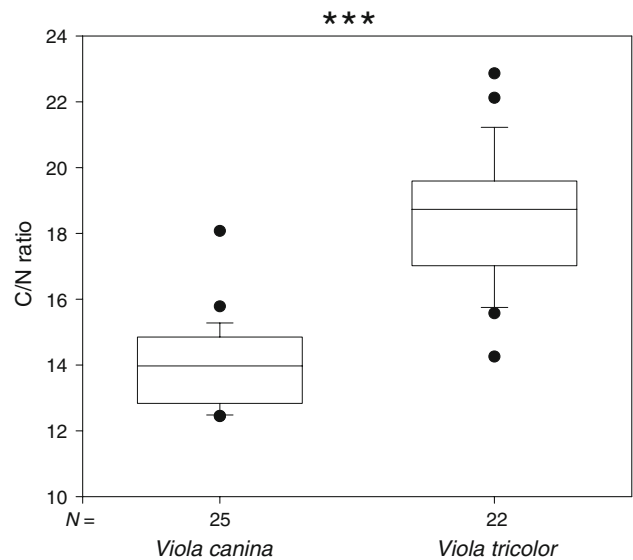


Fig. 5 C/N ratio of the leaves of *Viola canina* and *V. tricolor* ssp. *curtisii* (MWU, $U = 17.0$, $*** P < 0.001$)

grey-dune vegetation on an island without records of *A. niobe* was 81 ha (Minsener Oog, D).

Discussion

Habitat quality

The oviposition and larval habitat requirements of *A. niobe* were best explained by a combination of (1) host-plant abundance, (2) host-plant quality and (3) vegetation structure. In terms of host-plant abundance, sites with a high cover of *V. canina* were preferred both for oviposition and by larvae. Sufficient food is essential for the survival of

Table 3 Absolute and relative frequencies of plant communities at oviposition and larvae sites of *Argynnis niobe*

Plant community	Larvae sites				Oviposition sites			
	Sites		Larvae		Sites		Egg clutches	
	N	Share (%)	N	Share (%)	N	Share (%)	N	Share (%)
White dune	3	4.5	4	4.5	6	5.6	8	2.7
<i>Elymo-Ammophiletum festucetosum</i>	3	4.5	4	4.5	6	5.6	8	2.7
Grey dune	63	95.5	85	95.5	101	94.4	291	97.3
<i>Festuco-Galietum</i>	34	51.5	48	53.9	37	34.6	107	35.8
<i>Elymo-Ammophiletum festucetosum</i>	9	13.6	9	10.1	21	19.6	43	14.4
<i>Violo-Coryneporetum</i>	11	16.7	15	16.9	25	23.4	92	30.8
<i>Carex arenaria</i> dominant	7	10.6	9	10.1	13	12.1	35	11.7
Not specified	2	3.0	4	4.5	5	4.7	14	4.7
Total	66		89		107		299	

Larvae sites (sites vs. larvae): $\chi^2 = 1.542$, $df = 5$, $P = 0.908$

Oviposition sites (sites vs. egg clutches): $\chi^2 = 15.789$, $df = 5$, $P < 0.01$

Table 4 Stepwise-forward logistic regression on predictor variables at random sites and sites occupied by *Argynnis niobe*

Independent parameter	Parameter (B)	SE	Wald	P	Exp(B)
Oviposition sites^a					
Constant	0.800	0.414	3.734	NS	2.226
Turf height (cm)	−0.105	0.025	17.696	***	0.901
Horizontal cover (%) of vegetation in 10 cm height	0.031	0.011	8.094	**	1.031
Cover (%) of <i>Viola canina</i> in a circle with 50 cm	0.234	0.060	15.192	***	1.264
Model $\chi^2 = 44.96$, $R^2 = 0.305$, $df = 3$, $P < 0.001$, correctly classified: 73.3%					
Larvae sites^b					
Constant	1.733	0.632	7.519	**	5.655
Turf height (cm)	−0.137	0.040	11.535	**	0.872
Cover (%) of <i>Viola canina</i> in a circle with 50 cm	0.121	0.059	4.217	*	1.129
Model $\chi^2 = 19.39$, $R^2 = 0.221$, $df = 2$, $P < 0.001$, correctly classified: 71.6%					

Oviposition sites (N = 107) and random sites (N = 71), Larvae sites (N = 66) and random sites (N = 43)

* P < 0.05, ** P < 0.01, *** P < 0.001

NS not significant

^a Variables entered into the regression that were not significant: Cover (%) of herb layer, mosses, litter and bare soil in a circle within 50 cm

^b Variables entered into the regression that were not significant: Cover (%) of herb layer, mosses, litter and bare soil in a circle within 50 cm; horizontal cover of vegetation in 5 cm height

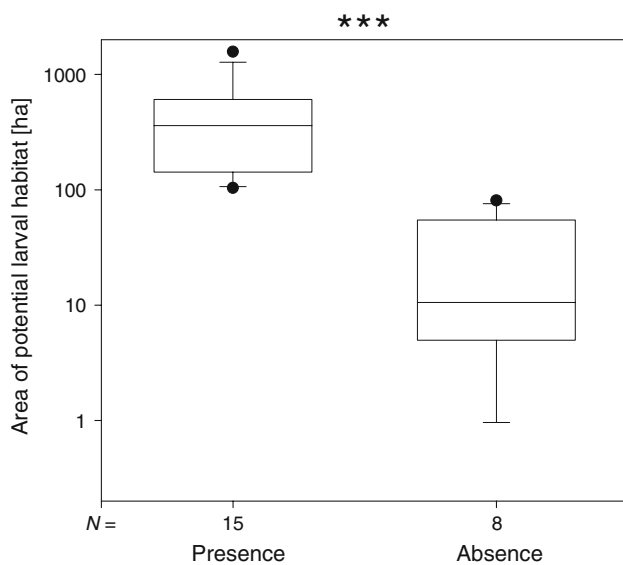


Fig. 6 Area of potential larval habitats (grey-dune vegetation) of *Argynnis niobe* on islands in the North Sea between Texel (NL) and the peninsula Skallingen (DK). Islands with populations of *A. niobe* were compared with islands without records (MWU, $U = 0.0$, *** $P < 0.001$). Sources: **a** area of potential larval habitats: East Frisian Islands: Calculation from vegetation maps of Nationalpark Niedersächsisches Wattenmeer (2007), other islands: Petersen and Lammerts (2005). **b** Records of *Argynnis niobe* in Denmark: M. Stoltze (personal communication); in Germany: (NLWKN (2006); H. Andretzke, J. Kleinekuhle, B. Nannen, R. Ohle, M. Sommerfeld); in the Netherlands: Bos et al. (2006)

butterfly larvae. In particular in species with gregarious larvae like *Euphydryas aurinia* (Anthes et al. 2003a, b; Konvička et al. 2003) or *Melitaea aurelia* (Eichel and Fartmann 2008), preferences for large plants or high

densities of host plants have previously often been observed. *A. niobe* is not a true gregarious species, but as our results show, in microhabitats with very favourable conditions up to 22 eggs can be found and thus shortage because of inter-specific food competition seems likely in some cases. Larvae of *A. niobe* were mainly found hidden under *V. canina*. Tall *V. canina* individuals can function as a rich food supply as well as an important hiding place in the open low-growing vegetation, where the larvae are protected against predators and adverse environmental conditions (cf. Möllenbeck et al. 2008).

During the time of caterpillar development the leaves of *V. canina* should be a more suitable food resource than those of *V. tricolor* due to a lower and less variable C/N ratio. A preference for plants with high nitrogen contents (narrow C/N ratio) was already detected for several butterfly species (e.g. Pullin 1986; Bourn and Thomas 1993). A higher nutrient content of the plant material accelerates the development of the larval instars (Bink 1986; Pullin 1986; Jordano and Gomariz 1994) and can also positively affect egg production of the females (cf. Bink 1986). Negative effects of high nitrogen contents have rarely been observed, although Fischer and Fiedler (2000) showed that an elevated nitrogen content in fertilised host plants (*Rumex acetosa*) resulted in high larval mortality in *Lycaena tityrus*.

Young leaves of *V. tricolor* appear earlier in spring compared to leaves of *V. canina*. In April shoots of *V. canina* were hard to find and very small, whereas shoots of *V. tricolor* were already common. As young plant material is known to contain the highest amounts of nitrogen and water (Bernays and Chapman 1994; Munguira et al. 2009), the observed differences in C/N ratio of the

two species might be explained by plant phenology. On the East Frisian Islands the life cycle of *A. niobe* seemed to be well synchronised with the phenology of *V. canina* (cf. Weidemann 1995). Within the grey dunes the vegetation structure is similar on the growing sites of *V. canina* and *V. tricolor* and *V. tricolor* is still common (personal observation). Therefore, a preference for *V. canina* because of different microclimatic conditions and host-plant availability is unlikely.

A. niobe showed a significant preference for low-growing vegetation for eggs and larvae. In the larval habitat herb-layer cover was low to moderate. In high and dense vegetation a cool and moist microclimate is prevailing, whereas sites with short turf and open vegetation can heat up better and therefore have a warmer and drier microclimate. On sandy soils the temperature difference between soil surface and air can exceed more than 20°C (Stoutjesdijk and Barkman 1992). Our measurements showed that the vegetation in the larval habitats of *A. niobe* can heat up to over 50°C during a summer day.

Warm microclimate as a consequence of vegetation structure must be considered as a key factor for the successful completion of Niobe fritillary's life-cycle. The colouration of the larvae may be cryptic, but it is also perfect for elevating body temperature by basking. *A. niobe* larvae were found basking several times. Porter (1982) observed for another fritillary species (*Euphydryas aurinia*) that basking larvae are able to accelerate their digestion in cool weather. Consequently, they can develop faster. Basking behaviour (at cool air temperatures) is also typical for most other fritillary species, also for species with brown caterpillars [e.g. *Argynnis adippe* (Warren 1995), *Issoria lathonia* (M. F. WallisDeVries personal communication and own observation)].

Desiccation is a threat for butterfly eggs (Porter 1992). The overwintering eggs of *A. niobe* may have a high risk of desiccation due to their long life-span and the high temperatures in the larval habitat. Whereas the oviposition sites in general were sun-exposed, the majority of the eggs were protected against direct solar irradiation, especially at noon. Most eggs were laid either in the moss layer under the host plant or north of grass clumps. Eggs being deposited on the stems or the bottom site of the leaves of *V. canina* are shielded against direct sun light as well. Therefore *A. niobe* seemed to lay the majority of eggs on microsites with a more less variable microclimate than in the surroundings. Kopper et al. (2000) made comparable observations on the North American fritillary species *Speyeria idalia*.

According to Wiklund (1984), species overwintering in the egg stage like *A. niobe* avoid depositing their eggs on their perennial host plants. They are supposed to choose solid substrates remaining at the same place until the larvae

hatch in the next year. In fact, the majority of eggs were laid on mosses and litter. Only a few eggs were found on *V. canina*. Considering the fact that eggs on *V. canina* are easier to detect, the real proportion of eggs deposited on *V. canina* may also be lower than our data suggest.

As a rule the females of *A. niobe* deposit their eggs close to *V. canina*. The presence of the host plant plays a major role for the egg-laying decision. However, some eggs were laid up to a few metres away. Thus, newly hatched larvae have to localise and reach their host plant. Larvae of some species like *Battus philenor* and *Pieris rapae* are only able to detect their host plants at close proximity (cf. Rausher 1979; Cain et al. 1985). It seems likely that the larvae of *A. niobe* are also capable to detect their host plant from a distance of at least a few decimetres away. This may be supported by the fact that typical egg-depositing places of other fritillary species like *A. paphia* are away from the host plant (Ebert and Rennwald 1991).

Minimum viable population

Usually only a fraction of all potential host plants in a flight area are used for oviposition or feeding and is suitable for a successful development of the larvae. Often the proportion of potential host plants that grow under favourable structural and microclimatic conditions is small (Fartmann 2006a; Anthes et al. 2008; Möllenbeck et al. 2008). According to our results, the environmental conditions at occupied and random host plants were very similar (exceptions: turf height and cover of *Viola canina*). In the grey-dune vegetation of Langeoog and most islands of the southern North Sea *Viola canina* is common (D: Haeupler and Schönfelder 1989; NL: van der Meijden et al. 1989). Thus the size of connected grey-dune vegetation should be a good proxy for the size of potential larval habitat.

Our knowledge on how big a habitat should be for long-term survival of a butterfly population is still poor. Warren (1992) assumed for British populations of the related fritillary species *Argynnis aglaja* and *A. adippe* that they require an area of 2–5 and 5–10 ha of highly suitable habitat, respectively. According to (Bink 1992) *Argynnis niobe* needs an area of 64 ha for maintaining a viable population. An *A. niobe* habitat network consisting of six connected calcareous grassland patches in the northern Swabian Alb (southwestern Germany) had a total size of 148 ha [5–53 ha per patch] (G. Hermann personal communication). With more than 100 ha of potential larval habitat in our study *A. niobe* seems to depend on extraordinarily large areas, possibly explaining the increasing rarity of the species in Central Europe. Bulman et al. (2007) found similar minimum habitat-network sizes for the equally declining *Euphydryas aurinia* ranging from 80 to 142 ha. But, if conditions are very favourable *A. niobe* is

able to persist in smaller networks. In western Germany, a network of heavy-metal grassland consisting of five connected patches with a total area of 5–10 ha has been known to harbour a stable metapopulation for many years. Thus the sites continue to support a persistent population because of a very slow rate of vegetation change. The sites are characterised by a sparse turf cover and very high densities of *Viola calaminaria*, the regional host plant (D. Lück personal communication).

There are several parameters that can influence minimum habitat size of viable populations. Habitat quality and spatial arrangement of habitat patches play a major role (Bulman et al. 2007). Minimum habitat size for long-term survival should decrease with increasing habitat quality and connectivity of patches. The East Frisian and the West Frisian Islands provide vast areas of well-connected grey-dune vegetation as potential larval habitats for *A. niobe*. However, *V. canina* has a clumped distribution in the grey-dune vegetation, such that long distances can appear between *V. canina* patches. Due to the overall low density of host plants in the grey dunes, average habitat quality on Langeoog must be characterised as low. The distribution pattern of *V. canina* can be explained by its diplochorous dispersal strategy. Seeds are catapulted in the direct vicinity of the plant (Oberdorfer 2001). Additionally, seeds are distributed by ants, which is typical for *Viola* seeds (Beattie and Lyons 1975). *V. canina* often germinates on ant nests (own observation).

All central European grassland violets are restricted to nutrient-poor habitats (Ellenberg et al. 2001) and nowadays nutrient-poor grasslands are rare in German inland areas, especially those providing large and well-connected patches on a landscape scale. The last two remaining strongholds of *A. niobe* on the mainland are restricted to extensive areas of nutrient-poor and *Viola*-rich grasslands. In the southern spurs of the Black Forest vast cattle-grazed commons with dry acidic grasslands (mainly *Festuco-Genistetum*) serve as a larval habitat and still contain stable populations of *A. niobe* (Hafner 2005). The wide distribution of *A. niobe* in the Bavarian Alps should also be explained by well-connected and traditionally used nutrient-poor grasslands, but this requires further study.

Conservation

A. niobe reproduces in all plant communities of the grey dunes where *V. canina* is present. On Langeoog, the most important plant communities are *Festuco-Galietum* and *Violo-Corynephorum*. *Ammophiletum festucetosum*, dominated by *Ammophia arenaria*, is colonised on older white dunes and on grey dunes. Open *Carex arenaria* vegetation serves as larval habitat for *A. niobe* as well. Grass encroachment, however, e.g. by *Carex arenaria* or

Deschampsia flexuosa, needs to be regarded as one major threat for *A. niobe* in coastal dune ecosystems. In recent years *Carex arenaria* dominated vegetation is spreading in grey-dune vegetation (Petersen and Lammerts 2005; Petersen and Pott 2005). Atmospheric nitrogen deposition contributes to grass encroachment (Kooijman et al. 1998; Petersen and Lammerts 2005). In dense *Carex arenaria* vegetation a cooler microclimate has to be expected compared to open dune grassland. Thus, dense *Carex arenaria* vegetation is not suitable for the development of *A. niobe* eggs and larvae. Additionally, the host plant *V. canina* may be suppressed in dense *Carex arenaria* vegetation. Furthermore, due to the increasing nitrogen deposition and global warming the growing season starts earlier and bare ground or litter soon becomes overgrown by fresh plant biomass leading to microclimatic cooling (WallisDeVries and Van Swaay 2006).

The influence of herbivores on dune succession has to be taken into account since grazing of rabbits may inhibit grass encroachment in dune vegetation (ten Harkel and van der Meulen 1995; Maes et al. 2006). Extensive grazing by cattle and horses has been shown to benefit grassland butterflies in coastal dunes in the Netherlands (Wallis-DeVries and Raemakers 2001). On Langeoog only a small area of grey dune vegetation is grazed by cattle. Rabbits are absent and the impact of hares and roe deer can be assumed to be marginal, because densities are typically low and neither species is a typical grazer.

Until now larval habitats of *A. niobe* on many of the West and East Frisian Islands were secured by natural disturbances. In the course of natural dune succession new larval habitats emerge. With progressive dune succession, however, these habitats get lost. Dune grasslands act as a primary habitat in contrast to other habitats on the mainland (except high altitude areas of the Alps). The coastal dunes of the Frisian Islands are furthermore influenced by wild herbivores like rabbits. In the national park “Niedersächsisches Wattenmeer” only minor parts of the grey dunes act as pastures for cattle. To ensure long-term survival under increasing eutrophication and grass encroachment, management will be necessary in the dune habitats, too. Mosaic top-soil removal to facilitate violet germination seems to be one possibility. Low-intensity grazing by cattle and horses (WallisDeVries and Raemakers 2001) should also directly promote rejuvenation of *Viola canina* through creating gaps for germination. Furthermore, grazing may affect violet germination indirectly through increasing ant densities (Randle et al. 2005). Ants disperse the *Viola* seeds effectively and protect them from herbivores around their nest and thus promote establishment.

We have shown here that open low-growing grey-dune vegetation resulting in a warm microclimate and high densities of *V. canina* determine larval habitat quality of

A. niobe on the East Frisian Islands. However, little is known about the larval habitats on mainland populations. In order to take appropriate measures for the conservation of Niobe fritillary further studies have to be carried out, especially in mainland habitats.

A major reason for the dramatic decline of *A. niobe* in central Europe over the last decades is probably the loss of potential larval habitat. On the mainland *A. niobe* should be seen as an element of the traditional cultural landscape depending on anthro-po-zoogenic disturbances. Traditional forms of land use maintain habitats for *A. niobe*; abandonment of land use would probably lead to an extinction of *A. niobe* (cf. Hafner 2005). If habitat quality in mainland populations is similar to that in the dunes, minimum habitat area for long-term survival should be higher in the mainland because patches are mostly not as well connected as on the islands.

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