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EARLY-SPRING FLOODS DECREASE THE SURVIVAL OF HIBERNATING LARVAE OF A WETLAND-INHABITING POPULATION OF NEPTIS RIVULARIS (LEPIDOPTERA: NYMPHALIDAE)

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The effect of early-spring submergence on larvae of a wetland-inhabiting population of the butterfly *Neptis rivularis* (SCOPOLI, 1763) (Nymphalidae: Neptini) was investigated in laboratory. Wild-collected, late hibernation larvae originating from inundated marshes of the Třeboň Basin (Czech Republic) were exposed to two conditions possibly experienced during the floods, aerated (as under running water) and anoxic (as in still water). Submergence for up to three days did not affect larval survival; longer submergence caused substantial mortality, no larva survived the longest submergence tested (21 days). Since there were no differences between aerated and anoxic treatments, the mortality seemed to be due to a failure of osmotic balance. Very short submergence thus does not influence larval survival in field, but prolonged floods may substantially reduce population size. However, the extent of the floods varies in the years, there are some upland colonies of *N. rivularis* in the area, and the butterfly is a relatively good disperser. It is thus assumed that the species compensates for inundation-caused mortality by a re-colonisation of its sites.

Key words: butterfly, floodplain ecology, inundation, larval dormancy, population dynamics, survival, winter mortality

INTRODUCTION

Awareness of continuing degradation and decline of wetland habitats throughout the world have sparked interest in conservation-oriented studies of wetland biota, including invertebrates (BATZER & WISSINGER 1996). In this context, habitat requirements, population dynamics and other conservation-related issues of wetland Lepidoptera were studied (e.g. DEMPSTER 1995, FISHER *et al.* 1999, WETTSTEIN & SCHMID 1999, SPITZER *et al.* 1999, WEBB & PULLIN 2000). Several authors addressed direct questions related to management and/or restoration of habitats of threatened wetland species (e.g. PULLIN *et al.* 1995, DENNIS & EALES 1997), including the effects of periodic winter- and early spring floods on the survival of hibernating Lepidoptera larvae. Such floods, causing in some instances long-term submergence of entire habitats, are undoubtedly among the most prominent physical factors affecting population dynamics of wetland species. This might be especially important in case of insects, since their dormant developmental stages cannot avoid submergence by leaving the flooded space.

Impacts of winter or early spring submergence on butterfly larvae have so far been investigated in detail in case of two European species, *Coenonympha tullia* (HAWORTH, 1803) (Nymphalidae: Satyrinae) and *Lycaena dispar batavus* (OBERTHÜR, 1923) (Lycaenidae). The former butterfly showed substantial decrease of survival even after short submergence (JOY & PULLIN 1997, 1999), while the latter species withstands prolonged submergence (up to 28 days) without decline in survival, depending on timing of flood relative to that of diapause (WEBB & PULLIN 1998). In addition, survival of floods was affected by predation pressure (WEBB & PULLIN 1996) and varied in populations of different origin (NICHOLLS & PULLIN 2000). Clearly, flooding affects populations of the two wetland-inhabiting butterflies in entirely different ways and it is desirable to study the impact of this important ecological factor in a wider range of wetland species.

We studied in laboratory the effects of early-spring inundation on hibernating larvae of a wetland-inhabiting population of the butterfly *Neptis rivularis* (SCOPOLI, 1763) (Nymphalidae: Neptini). Two conditions possibly experienced by the larvae, which may differ in impact on their survival, were simulated. These were 1) aerated condition, likely to prevail in the beginning of flood and/or at waterside sites communicating with running water; and 2) anoxic condition, which may prevail in pools of still water in late days of floods. In addition, we present the map of distribution of *N. rivularis* in the area of interest, and discuss relation of the species' distribution to the extent of inundated areas.

MATERIAL AND METHODS

Neptis rivularis is widely distributed in the southern part of Palaearctic region, in a long belt that stretches from Japan to Central Europe. At the western margins of its distribution, it has restricted and often insular distribution, ascending upstream major rivers and reaching Upper Austria and Switzerland (LEPIDOPTEROLOGEN ARBEITSGRUPPE 1987). In the Czech Republic, it is restricted to the wetland habitats of the Třeboň Basin, Southern Bohemia, which is a flat and humid area of marshes, floodplain forests, peat bogs, fishponds and wet meadows. Owing to its restricted distribution in the country and its local dependency on wetland habitats, it is considered as vulnerable at national scale and enjoys legal protection (NOVÁK & SPITZER 1982, SPITZER 1992).

The butterfly is univoltine, on the wing from June until August. The larvae develop on several species of the *Spiraea* shrubs, in the Třeboň Basin – and the entire Czech Republic – only on *Spiraea salicifolia* (L.) (SPITZER 1958, HLÁSEK & HLÁSEK 1997). Adults generally stay in the close vicinity of the shrubs; rich *Spiraea* inflorescences seem to be their principal nectar source. All local colonies are thus restricted to habitats of the shrub, i.e. to wet meadows, margins of fishponds and water channels, riverbanks and sparse floodplain forests. Young larva overwinters in a hibernaculum (made out of partly eaten and silk-spun leaf of the foodplant) attached to a *Spiraea* twig by silken cord. The hibernacula are easily spotted on the shrubs in winter or early spring, when most of the other leaves already fell. HLÁSEK and HLÁSEK (1997) speculated that floods cause high mortality during hibernation, since *Spiraea* shrubs are especially abundant on sites affected by snowmelt floods (many of them are situated on the bottom of inundation embankments built for fishpond protection). At such localities, the water depth may reach several metres during flood culmination, and pools of still water often remain there for several weeks.

Submergence experiment

The hibernacula were collected at the Nová řeka Marsh, extensive periodically flooded sedge grassland along the Lužnice River (49°00'N, 14°53'E, alt. 430 m; Fig. 1). At this locality, extensive growths of *Spiraea salicifolia* host the largest of *N. rivularis* colonies in the Třeboň Basin. In February 2000, 180 hibernacula were collected and kept at outdoor-simulating conditions (constant 5°C) until mid-March, i.e. when spring floods usually inundate the locality.

Prior to the experiment, the hibernacula were randomly divided into 9 groups of 20 individuals, which were put into Petri dishes with lids replaced by loose mesh. The following treatments were applied: submergence to aerated water for periods of 3, 10 and 21 days ("aerated" treatment, 3 groups); submergence to anoxic water for the same periods ("anoxic" treatment, 3 groups), and 3 not-submerged controls. One of the control groups was brought into room temperature at the beginning of the experiment. The two remaining controls were kept at constant 5°C for another 21 days, i.e. for the duration of the longest submergence period, one of them on air and one under nitrogen atmosphere (Table 1). To avoid any damage to the diapausing larvae, we did not check their condition before commencing the experiment. Therefore, the actual number of larvae that were alive at the beginning of experiment might have been lower than the N = 20.

The Petri dishes with the "aerated" larvae were submerged, without removing the larvae from their hibernacula, to the bottom of a 3 liters jar filled with water aerated by an aquarium aerator to simulate conditions in a running river. The jar for the anoxic treatment was fully filled by water, from which air oxygen was reduced by boiling. Larvae of both aerated and anoxic treatments were submerged into their jars after the water had cooled down to 5°C. The "anoxic" jar was covered by pure nitrogen atmosphere, and sealed to prevent oxygen influx. Care was taken not to allow air bubbles to

Table 1. Numbers of surviving larvae and numbers of adult butterflies emerged, after submergence of hibernating larvae of *Neptis rivularis* at different submergence conditions

	No. surviving individuals			No. surviving individuals		
Surviving after	24 hours	10 days	adult ♂/♀	24 hours	10 days	adult ♂/♀
No submergence	Oxygen atmosphere			Nitrogen atmosphere		
Control 1 (0 days)	15	14	3/2			
Control 2 (21 days)	13	12	2/3	14	12	5/7
Submergence	Aerated water			Anoxic water		
3 days	17	12	3/4	13	12	6/3
10 days	4	4	2/1	7	7	–/4
21 days	0	0	–/–	0	0	–/–

remain in the Petri dishes. Constant low temperature (5°C) and a continuous darkness were maintained during the whole duration of the experiment.

After termination of respective submergence periods, the hibernacula were brought to room temperature, which activated the till-now dormant and motionless larvae. The hibernacula were carefully lifted from water and put individually to Petri dishes with tissue paper and a few fresh *Spiraea* leaves. After 24 hours, surviving larvae were counted. Larva was considered alive if it showed any movement. For subsequent days, we fed the larvae with fresh leaves of their foodplant and kept a high humidity in the dishes to avoid desiccation. As in WEBB and PULLIN (1998), we repeated the counting of surviving individuals in each group ten days after termination of submergence, to check a delayed post-submergence mortality. After the second check, we transferred the larvae individually into rearing cages, continued feeding them with fresh leaves and reared them up to maturity.

We were interested in the effects of time of submergence, and of the two different treatments, on larval survival. Since classical cross-tabulation testing would not allow reflecting possible higher-level interactions among the factors, the log-linear models (LLM) for multidimensional contingency tables (ZAR 1996) were applied for analyses. The LLMs express multi-way relationship among independent variables and their interactions in a linear fashion through logarithmic transformation. The analyses were done using the STATISTICA 5.1. package (STATSOFT 1995), using the programs' procedure of automatic model fitting, which first fits a model with no relationships between factors; then a model with all two-way interactions, and so on. After finding a model that fits the data, the program proceeds to eliminate all higher-level interactions that have no statistically significant effect on distribution of dependent variable (i.e., the counts of surviving larvae in individual groups). The resulting model is the one that includes the least number of interactions necessary to fit the observed situation. The default options for model selection were used: p(1) [minimum significance level on which the model sufficiently fits the data] > 0.1, p(2) [level of significance for individual terms to be included into the model] < 0.05, and Δ [the value added to each cell count to avoid zeros] = 0.5.

In reporting statistical significance of interactions between independent variables on fit of the models, two statistics are presented. Partial association χ^2 compares the fit of a model that includes all two-way interactions with the model that excludes the interaction of interest. Marginal association χ^2 compares the model that includes all main effects (i.e., all effects of lower order than the one of interest) with the model that includes the interaction between the factors of interest.

RESULTS

Distribution of N. rivularis

The butterfly inhabits patches of *S. salicifolia* at both inundated and upland sites in the Třeboň Basin (Fig. 1). The inundated sites generally adjoin major rivers, they often lie within flood regulation embankments. The upland sites are characteristic for sites with a higher level of ground water, i.e. on raised bogs and moorlands. This pattern is further complicated by planting of *S. salicifolia* as an ornamental plant: both hibernacula and adults of *N. rivularis* were found at planted hedgerows of *S. salicifolia* in the town Třeboň repeatedly for three consecutive years (1996–1998).

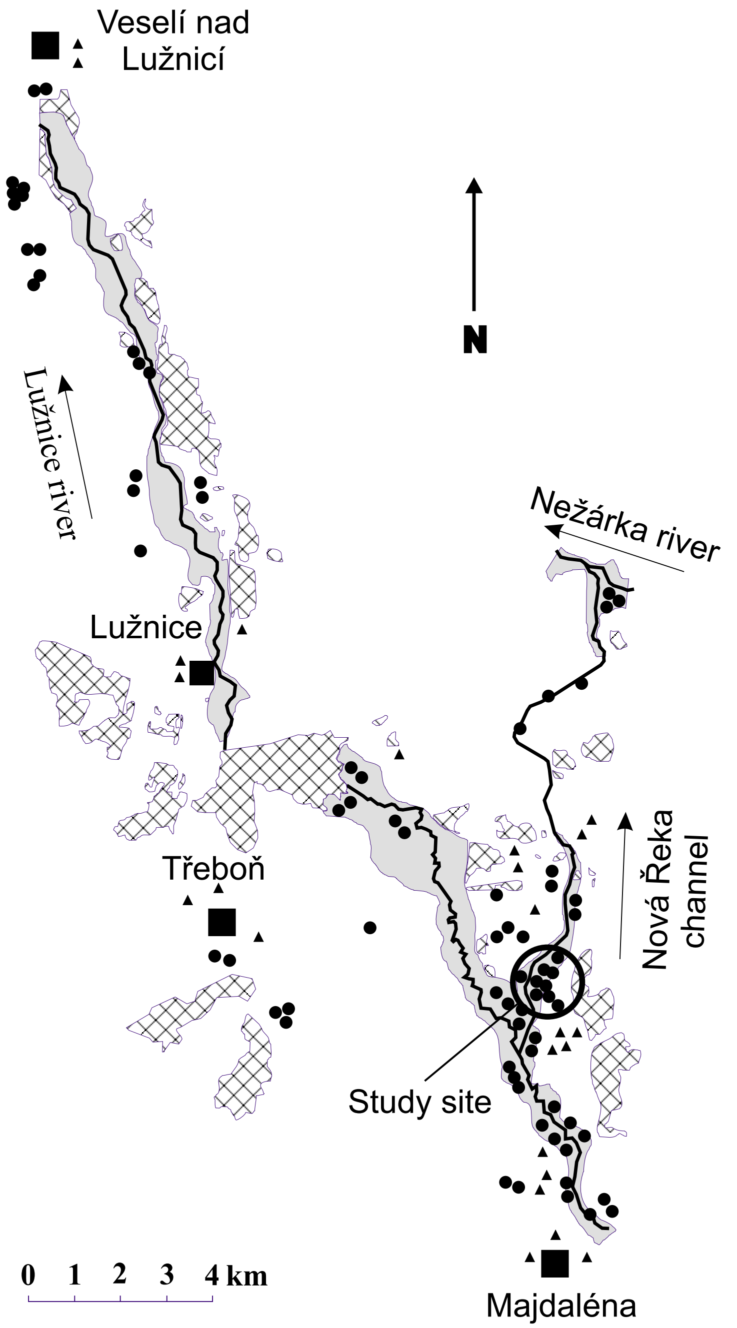

Fig. 1. Map of the central part of Třeboň Basin (along Lužnice river) with colonies of *Neptis rivularis* (●) and records of stray adults of the butterfly (▲), as encountered during 1996 season. The gray pattern indicate inundated areas, the light dashed area shows major fishponds

Virtually all growths of the shrub showed traces of presence of *N. rivularis*, such as the hibernacula, young larvae or empty pupal cases. Searching within the shrubs was extremely time-consuming due to their peculiar architecture; it was not feasible to quantify densities of pre-adult stages of *N. rivularis.* It was nevertheless clear that even several very small shrubs patches (ground cover ≈ 2 m^2, distance to the closest patches > 200 m, growing e.g. near drainage channels among cultivated fields) hosted larval hibernacula. It follows that we regard practically all patches of *S. salicifolia* in the area of interest as utilised by *N. rivularis*. This does not imply that there are well-defined adult colonies at all patches: in total, 24 stray butterflies were recorded over 500 meters away from the foodplant patches in 1996, suggesting relatively good dispersal ability of the species (Fig. 1).

Submergence experiment

In the three not-submerged controls (samples of 20 individuals), 71% (SD = 3.9%) of larvae showed signs of life when brought into room temperature (Table 1). Survival did not differ in the three controls (Pearson's chi square, $\chi^2 = 0.476$, d.f. = 2, $p = 0.79$) and did not decrease in any of the controls after 10 days following the treatment ($\chi^2 = 1.65$, d.f. = 2, $p = 0.98$). Thus, there was similar baseline mortality in the three controls and no delayed lethal effect after activation. Similar proportions of larvae survived 3 days of submergence (aerated: 85%, anoxic: 65%; aerated vs. anoxic: $\chi^2 = 2.13$, d.f. = 1, $p = 0.14$). The two groups did not differ in numbers of larvae surviving the first 10 days after activation ($\chi^2 = 0.23$, d.f. = 1, $p = 0.63$).

The number of surviving larvae sharply declined with prolonged submergence, and no larvae survived the longest submergence time; all larvae were dead and swollen after the 21-day treatment (Table 1). The LLM analysis which compared larval survival among the two treatments and 3 submergence periods revealed that the pattern was best described by the effect of time only (goodness of fit of the model: $\chi^2 = 1.28$, 6 d.f., $p = 0.97$). The effect of time on larval survival was highly significant (interaction survival:time, partial $\chi^2 = 28.02$, d.f. = 2, $p < 0.0001$; marginal $\chi^2 = 28.03$, d.f. = 2, $p < 0.0001$), whereas the anoxic and aerated treatments did not differ in their effects (partial $\chi^2 = 0.01$, d.f. = 1, $p = 0.94$; marginal $\chi^2 = 0.01$, d.f. = 1, $p = 0.94$).

Comparison of numbers of surviving larvae among the two treatments and the aerated and anoxic controls (21 days) confirmed that the submergence itself, rather than aerated or anoxic conditions, caused the larval mortality (goodness of fit of the model: $\chi^2 = 0.04$, d.f. = 4, $p = 0.99$). The difference in survival between the larvae submerged for 21 days and the non-submerged controls was, naturally, highly significant (partial $\chi^2 = 24.86$, d.f. = 1, $p < 0.0001$; marginal $\chi^2 = 24.87$, d.f. = 1, $p < 0.0001$). On the other hand, the anoxic vs. aerated conditions did not affect larval survival neither in association with time (partial $\chi^2 = 0.02$, d.f. = 1, $p = 0.89$; marginal $\chi^2 = 0.03$, d.f. = 1, $p = 0.87$), nor in relation to the submergence or non-submergence (partial $\chi^2 = 0.00$, d.f. = 1, $p = 0.99$; marginal $\chi^2 = 0.01$, d.f. = 1, $p = 0.94$).

In total, 45 adults were reared until adult stage. Adult sex ratio did not differ from 1:1 ($\chi^2 = 0.18$, d.f. = 1, $p = 0.67$). Proportions of successfully emerged individuals (of the larvae that were still alive 10 days after activation) did not differ between aerated and anoxic treatments ($\chi^2 = 0.55$, d.f. = 1, $p = 0.46$).

DISCUSSION

Hibernating larvae of *N. rivularis* survived submergence in laboratory for up to three days without detectable decline in survival. Longer submergence caused substantial mortality, and no larva survived the longest period tested, i.e. 21 days. In constant 5°C temperature, there was no difference in mortality between the groups submerged in aerated as opposed to anoxic water. Thus, very short inundation periods would probably not influence larval survival in the field, under either running or still water, but a prolonged flood may cause substantial reduction of population size.

The nature of the injury causing mortality in the larvae was not clearly determined in this study. However, we expect that the mortality was not caused by anoxia – an impossibility of respiration of aerial oxygen. This assumption is supported by two observations: mortality did not differ between aerated and anoxic submerged conditions, and it was not increased under nitrogen atmosphere (not submerged) in comparison to the untreated control and air control. The volume of the experimental jars was big enough to dilute possible waste metabolites, so that the larvae were not poisoned by them. The only plausible explanation we suggest is a failure of osmotic balance, in other words, uncontrolled intake of large amount of water into the body through the cuticle.

Our results confirm previous observation by HLÁSEK and HLÁSEK (1997), who viewed floods as a serious mortality factor. *N. rivularis* is considerably less tolerant to flooding than one of the other two European butterflies studied so far, the Large copper (*Lyacena dispar batavus*), which would survive without substantial increase in mortality for 28 days, and presumably for longer (WEBB & PULLIN 1998). On the other hand, it is more tolerant than the Large heath butterfly *Coenonympha tullia*, which – unlike *N. rivularis* – showed significant increase in mortality after submergence as short as three days. However, the latter species responds to flooding by an active escape reaction, which is unlikely in larvae of *N. rivularis* encased in their hibernacula. Also, at least some individuals of *C. tullia* may survive for as long as 28 days of submergence (JOY & PULLIN 1997), but no such case was detected in *N. rivularis*. Finally, we did not find – unlike of *C. tullia* but similarly to *L. dispar batavus* – an evidence for a delayed mortality at activating conditions of previously submerged larvae, suggesting that larvae that survive a flood may normally reach their maturity. *N. rivularis* is thus, with respect to winter flooding, intermediary between the two other species.

The differences in survival among the three wetland-inhabiting species correspond relatively well with character of their habitats. In the lowland fens of Britain and Netherlands, prolonged winter floods are a rule and the populations of *L. dispar batavus* that occupy such sites are likely to be adapted to them. On the other hand, winter floods are not regular phenomena at British habitats of *C. tullia,* i.e. upland moors: in the studies of JOY and PULLIN (1997, 1999), flooding of moorland sites was human-induced as a restoration practice. Colonies of *N. rivularis* in the Třeboň Basin are found at sites with the both inundation regimes, and some of the colonies are never flooded. Moreover, the species is found at many habitat types throughout its wide Palearctic range, including forest-steppes, and feeds on several species of *Spiraea*, some of which are not restricted to wetlands (cf. NICULESCU 1965, MURZIN 2000). Therefore, some populations of *N. rivularis* may normally not experience inundations. Since it was shown that populations of wetland butterflies of different geographical origin may be differently adapted to flooding (NICHOLS & PULLIN 2000), we expect that populations of *N. rivularis* from non-wetland habitats would less tolerate water submergence.

It should be noted that the larval mortality observed in our experiment does only weakly reflect the real situation in the field. Since the foodplant of *N. rivularis* may reach considerable height (up to 3 metres) at some localities, a natural anti-flooding defence for the larvae would be to hibernate in the upper parts of *Spiraea* shoots. On the other hand, hibernating too high on *Spiraea* branches would expose the larvae to increased predation by insectivorous birds. HLÁSEK and HLÁSEK (1997) mentioned feeding specialisation of overwintering local blue tits on *N. rivularis* hibernacula. While collecting our experimental material (February 2000), we noted that about 50% of hibernacula were attacked by birds and the content was eaten out. The ability of birds to orientate themselves according to the leaf damage caused by lepidopteran larvae is well known (e.g. HEINRICH & COLLINS 1983, MURAKAMI 1999) and is expectable in *N. rivularis*, which offers easily accessible and detectable morsels for foraging birds. Predation pressure might even increase during floods, when only non-submerged food is available for birds. During a major flood in April 1996 we observed flocks of warblers foraging on the tops of *Spiraea* branches, which were in these days only a few centimeters topping water surface. These circumstantial evidences suggest that larvae of *N. rivularis* hibernating at flooded sites have to seek a balance between two risks, predation and prolonged submergence. If we take into account that the floods vary among years in duration and intensity, it would follow that the larvae hibernating in intermediate heights should have the highest survival when averaged among years. This hypothesis should be testable by manipulative field experiments.

At the floodplain sites of the Třeboň Basin, the early spring floods do not occur every year, and both extend and duration of flooding varies among sites and years. Adult butterflies have relatively long flight period (SPITZER 1958) and, judged from the records of stray individuals, considerable dispersal ability. These facts, and relatively close "clustering" of *N. rivularis* habitats, should assure that major hostplant sites are easily recolonised if a major flood transitionally destroys some local colonies. Our results point to possibly large diversity of anti-flooding adaptations of wetland inhabiting butterflies, ranging from inundation tolerance in sedentary, closed populations of *Lycaena dispar batavus*, to a low tolerance, but considerable dispersal and recolonisation ability in *Neptis rivularis*.

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