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Microhabitat-specific early-larval survival of the maritime ringlet (*Coenonympha tullia nipisiquit*)

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Abstract

Maritime ringlet butterflies (*Coenonympha tullia nipisiquit* McDunnough) are rare, endangered salt marsh butterflies with larvae that survive periodic tidal submergence. Only six disjunct populations are known to exist. First-instar larvae were released and monitored in seven microhabitats within a salt marsh in Bathurst, New Brunswick, Canada. From resighting data, microhabitat-specific daily death rates were estimated with maximum likelihood. The survival of the larvae released in groups was compared by calculating minimum number of larvae known to be alive (MNKA). Death rates were low in microhabitats with the larval host plant, salt meadow cordgrass (*Spartina patens* (Aiton) Muhl.) and the major nectar source, sea lavender (*Limonium carolinianum* (Walter) Britton), a habitat with a moderate frequency of flooding. Because microhabitats have a large effect on the survival rate of young larvae, use of microhabitat profiles in salt marshes as habitat-quality indices is recommended in critical-habitat assessment and reintroduction efforts.

INTRODUCTION

Maritime ringlet butterflies (*Coenonympha tullia nipisiquit* McDunnough, Satyridae) are a rare subspecies of the widespread holarctic common ringlet butterflies (*Coenonympha tullia* Müller). Found only in salt marshes in maritime Canada, maritime ringlets are subjected to periodic tidal submergence in their pre-adult stages, and they are one of the two species of salt marsh butterfly in the region. The maritime ringlet has an extremely limited distribution and is listed as federally endangered in Canada. Until recently only three populations in New Brunswick and one in the Gaspé Peninsula, Quebec, were known to exist (Webster, 1994*a*, 1995). Two new populations have been established for several years after successful reintroduction efforts (R. P. Webster, pers. comm.). Historically, maritime ringlets may have had a wider distribution surrounding the Chaleur Bay, and the present distribution may be due to alteration of the salt marshes, through the building of dikes and ditches, grazing, exploitation for salt hay, and burning, all of which were once prevalent along the northern Atlantic coast (Roberts & Robertson, 1986; Adam, 1990). The general isolation of the salt marshes and the apparent philopatric nature of maritime ringlets prevent this subspecies from readily colonizing other salt marshes. Several *Coenonympha* species receive conservation attention in Europe partly because of their low vagility (Joy & Pullin, 1997; Lhonore & Lagarde, 1999; Cassel *et al*., 2001). With so few extant maritime ringlet populations in such a strongly delimited and vulnerable habitat type, there is considerable need to identify the critical microhabitat requirements of this butterfly.

The natural history of the maritime ringlet differs in several ways from that of the inornate ringlet, (*Coenonympha tullia inornata* Edwards), the sister North American subspecies that occurs in the adjacent uplands (Webster, 1994*a*, 1995). The occurrence of the maritime ringlet coincides with salt meadow cordgrass, *Spartina patens* (Aiton) Muhl. (Poaceae) and sea lavender, *Limonium carolinianum* (Walter) Britton (Plumbaginaceae). Salt meadow cordgrass grows in the high marsh zone within a salt marsh and is known to be the primary host plant of the larvae (Webster 1994*a*, 1995). Sea lavender is considered to be the primary nectar source for the adult maritime ringlets and a good indicator of maritime ringlet occurrence, although the adults can readily use other nectar sources such as sea goldenrod (*Solidago sempervirens* L., Asteraceae), sea milkwort (*Glaux maritima* L., Primulaceae) and Virginia rose (*Rosa virginiana* Mill., Rosaceae). The maritime ringlet is univoltine, and the adults fly from late July to mid-August, a month later than adults of the common ringlet (Wiernasz, 1989) from populations within a kilometre of the salt marshes. Larvae enter diapause during the second instar in late September, and they resume growth

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and development in late May of the following year (Webster, 1994*b*). The allozyme data in Wiernasz (1989) indicate that the maritime ringlet is genetically distinct from other univoltine populations of the common ringlet, and once the maritime ringlet's biology is better understood, it will probably be necessary to re-evaluate its taxonomic status. Regardless, the maritime ringlet is a remarkable evolutionary phenomenon that occupies a rare niche as a salt marsh butterfly: a natural heritage in need of protection.

Given the range of microhabitat types in a salt marsh (Miller & Egler, 1950; Long & Mason, 1983; Adam, 1990) and the vulnerability of butterfly larvae to predation (Dempster, 1983, 1984; Cornell & Hawkins, 1995), we expected that a great deal of insight into the population biology of this butterfly could be gained by following larval survivorship in their habitat. We therefore placed larvae on plants in different microhabitats and resighted them repeatedly throughout a 47 day period. This modified mark–release–recapture technique permitted us to estimate microhabitat-specific rates of larval survivorship, which is uncommon among immature invertebrate studies because of the difficulty of marking (White & Singer, 1987), high probability of mark loss, dispersal and low recapture rate. We estimated daily death rate using maximum likelihood (Lebreton *et al.*, 1992), and we compared survival across microhabitats with Akaike's Information Criterion (Akaike, 1973; Hilborn & Mangel, 1997) and contingency table tests.

MATERIALS AND METHODS

Study site

We conducted this study on the salt marsh at Daly Point Natural Reserve in Bathurst, New Brunswick, Canada (Fig. 1). A narrow sandbar and pebble beach separate most of the marsh from the tidal flat. The vegetation pattern of this marsh is similar to that of the northern New England salt marsh described by Jacobson & Jacobson (1987), with clear zonation of vegetation according to the height above sea level.

The low marsh habitat along tidal streams experiences daily tidal submergence (Nixon, 1982), and a dense monoculture of *Spartina alterniflora* Loisel dominates. Flooding of the high marsh habitat is less frequent, and *S. patens* and *Juncus gerardi* Loisel (Juncaceae) dominate, the latter in slightly higher sites. Permanent stands of the grass *Distichlis spicata* (L.) E. Greene (Poaceae) are found in the high marsh where drainage is poor. The eastern half of the marsh supports mixed vegetation dominated by forbs (see Miller & Egler, 1950; Jacobson & Jacobson, 1987; Warren & Niering, 1993; Theodose & Roths, 1999 for descriptions of such forbs). The vegetation in this part of our site was a mixture of *S. alterniflora*, *S. patens*, *Limonium carolinianum* (Walter) Britton, *Glaux maritima* L. (Primulaceae), *Plantago maritima* L. (Plantaginaceae) and *Triglochin maritima* L. (Juncaginaceae). The southwestern portion of the marsh is drier, and non-halophytic grasses such as *Festuca rubra* L. grow there among *S. patens* and *J. gerardi*. Above the tidal inundation level, the salt marsh plants are replaced by *R. virginiana* and other woody plants, or by freshwater marsh plants (e.g., *Typha* spp.), depending on the elevation and proximity to fresh water sources.

Webster (1994*a*) divided this marsh into 10 microhabitats according to the vegetation composition, the density of *S. patens* and *L. carolinianum*, the height of *S. patens*, and hydrology (Table 1, Fig. 1). We follow his classification in this study.

Release of the larval cohorts

To obtain eggs, we captured 25 female *C. tullia nipisiquit* from a larger population nearby at the Peters

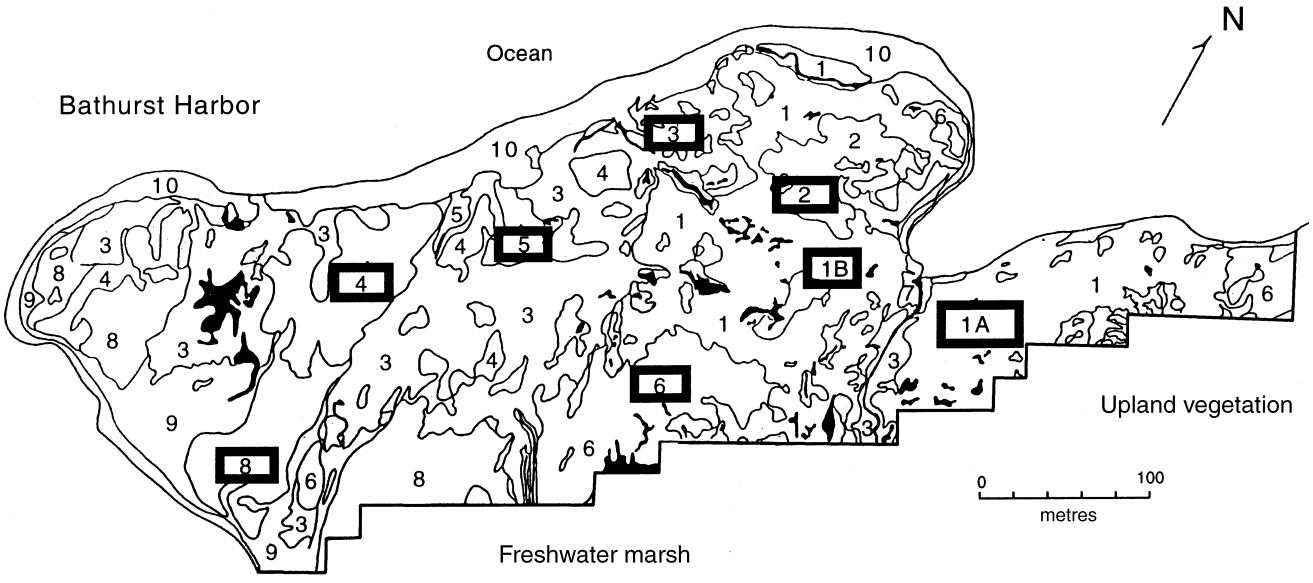

Fig. 1. Microhabitats in the salt marsh at Daly Point, New Brunswick. The larval release sites are indicated as rectangles. Map courtesy of R. P. Webster.

Table 1. The ten microhabitat types found in the salt marsh at Daly Point, Bathurst, New Brunswick, following Webster (1994*a*).

Microhabitat	Description
1	Mix of *Spatina patens*, *S. alterniflora*, *Glaux maritima*, *Plantago maritima* and *Limonium carolinianum* (50–150 plants/400 m^2), very wet.
2	*S. patens* (90–95% stem density, 15–20 cm tall), *S. alterniflora*, and *L. carolinianum* (50–150 plants/400 m^2).
3	*S. patens* (90–100% stem density, 30–40 cm tall), *Solidago sempervirens* and *L. carolinianum* (< 50 plants/400 m^2).
4	*S. patens* (90–95% stem density, 20-30 cm tall), *S. sempervirens* and *L. carolinianum* (100–200 plants/400 m^2).
5	*Distichlis spicata* dominant, very wet.
6	*Juncus gerardi* dominant (85–95% stem density), *Argentina egedii*, *P. maritima* and *S. sempervirens*.
7	*S. alterniflora* (90–100% stem density) and *L. carolinianum* (< 20 plants/400 m^2), wet.
8	*Festuca rubra* (80–90% stem density), *G. maritima*, *P. maritima*, *A. egedii*, *S. sempervirens* and *Ligusticum scothicum*, dry area.
9	*S. sempervirens* common to abundant, *Aster* sp., *L. scothicum*, *Cuscuta* sp., *J. gerardi* and others.
10	Beach, varied vegetation.

River in Beresford, New Brunswick, in early July 1999. Because it was an unusually warm year, the flight season of *C. tullia nipisiquit* was a few weeks earlier than usual. We placed up to seven females with a clump of *S. patens* in a 2 litre plastic container with the top of the lid replaced by net fabric, left in half shade. We collected eggs each day and kept them at room temperature until hatch.

We prepared release sites in Microhabitats 1–6 and 8 (Fig. 1). There was only one release site in each microhabitat except Microhabitat 1, which had two release sites on either side of the tidal stream. Microhabitats 7, 9 and 10 were excluded because they were physically unlikely to support *C. tullia nipisiquit* larvae or found to be underutilized by maritime ringlets from previous observations (Webster, 1994*a*). A release site was an island of vegetation 10 cm in diameter within a clearing made by clipping the surrounding vegetation. We avoided use of cages in larval releases in order to minimize potential caging effects that influence microclimate and predation. Without cages, the chances of larval escape are increased, but larvae were not likely to move from release points because *Coenonympha* spp. larvae, especially in the early instars, are sedentary as long as the food is abundant (A. H. Porter, pers. obs.). Joy & Pullin (1999) studied overwintering survival of a bog-dwelling population of *C. tullia* in England using a similar larval release scheme. We assumed movement of larvae into or out of the release sites was negligible. Release sites were searched before the release to make sure no larvae were present before the release of the cohorts. Each release point contained a single first-instar larva, and the clearing deterred the larva from wandering into the surrounding vegetation by walking across grass blades. Release sites were 50 cm apart, and the size of the clearing was increased where vegetation was tall. We also created multiple-release sites in each microhabitat type because it was necessary to save time and effort in creating release sites. A multiple-release site was a patch 30 cm in diameter and contained ten larvae. Single and multiple release sites in each microhabitat varied in number (Table 2) depending on the number of larvae available for release. Release sites in each microhabitat occupied about 112 m^2, except 1(b) which was smaller because it only contained ten single-release sites and four multiple-release sites (Table 2). All the larvae were in the first-instar stage, a cohort in a microhabitat was released on the same day, and all the cohorts were released within 2 weeks from late July to early August. After the release of the larvae, we returned every 3–4 days to the release sites to search for the larvae until early September. By then, the growth rate of *S. patens* as well as *C. t. nipisiquit* decreased.

Table 2. The number of single- and multiple-release sites in microhabitats. Only Microhabitat 1 had two groups of release sites in separate areas (see Fig. 1). Every multiple-release site contained ten larvae.

Microhabitat	Single-release sites	Multiple-release sites
1 (A)	50	0
1 (B)	10	4
2	40	6
3	40	3
4	31	6
5	40	6
6	38	6
8	12	4

Survivorship estimation from single-release sites

Our estimation model is modified from that of Lebreton *et al*. (1992). The data consist of records of sightings of larvae at various times after release into single-release sites (1 larva/site). We used these records to estimate simultaneously the finding rate f and the daily death rate d. The fact that a living larva may not be found even when present necessitates the calculation of f in order not to overestimate d. The parameters f and $1–d$ are equivalent to the capture rate p and survival rate ϕ in Lebreton *et al*. (1992). We assumed that both f and d are constant through the early larval period.

We used maximum likelihood (Edwards, 1992) to obtain the most likely values for f and d. Each possible value of f and d can be seen as an hypothesis. The likelihood of an hypothesis being supported given the data observed is proportional to the probability of observing the data given the hypothesis (Edwards, 1992), and the most likely hypothesis (i.e. values of f and d) yields the largest-likelihood value. The likelihood is often calculated in natural logarithm form for ease of computation. The basic likelihood model is

$$\ln L[d, f|\mathbf{O}] = \left[\sum_{j=1}^{S}\left\{\sum_{t=1}^{T}\left\{O_{tj}\ln\left[f(1-d)^t\right] + (1-O_{tj}) \times \ln\left[1-f(1-d)^t\right]\right\} + \left\{r\ln f + (\tau_j - r)\ln(1-f)\right\}\right\} + C\right]$$

where T is the ending time (the time of the last sighting), S is the total number of sites, $\mathbf{O}$ is a data matrix of O_{tj}, O_{tj} is the number observed at site j at time t, τ_j is the last time period in which the larva was seen alive at site j, r is the total number of times the larva was observed, and C is a proportionality factor that is constant for a given data set and can be ignored for our purposes. In this case, O_{tj} is either 1 (found) or 0 (not found).

To maximize the likelihood, we used a Metropolis–Hastings algorithm (Press *et al.*, 1992), which locates a global maximum regardless of local maxima by moving upward (towards a maximum) but allowing downward movement with a certain probability. The algorithm randomly varies a value of f or d and settles on joint maximum-likelihood estimates $\hat{f}$ and $\hat{d}$. The algorithm saves 10,000 parameter combinations within 2 likelihood units of the maximum to obtain support limits (Edwards, 1992), roughly equivalent to 95% confidence limits. We excluded the multiple release site data from the survivorship estimation because the uncertainty about the individual survival duration is confounded under the multiple-release scheme.

To compare the mortality rate across the microhabitats, we used Akaike's Information Criterion (Akaike, 1973; Hilborn & Mangel, 1997). This criterion is frequently used in conjunction with maximum likelihood to compare non-nested alternative models (Hilborn & Mangel, 1997). Specifically, we calculated the difference between the natural logarithm of maximum likelihood based on pooled observation data from Microhabitats $a + b$ and the sum of maximum likelihoods based on separate observation data from Microhabitats a and b,

$$\Delta \ln L = \ln L\left[d_{a+b}, f_{a+b}|\mathbf{O}_{a+b}\right] - (\ln L\left[d_a, f_a|\mathbf{O}_a\right] + \ln L\left[d_b, f_b|\mathbf{O}_b\right]).$$

$2\Delta\ln L$ follows a χ^2 distribution with degrees of freedom equal to the difference in the number of estimated parameters (in this example, the degrees of freedom is 2). AIC can also be applied to compare groups of microhabitats.

Comparison of larval survival among multiple-release sites

We calculated minimum number known alive (MNKA; Nichols & Pollock, 1983; Montgomery, 1987) of the larvae at the end of the observation period for each multiple-release site. We compared the percentage of surviving larvae among the microhabitats that had at least one surviving larva at the end of the observation period (microhabitats 1, 2, 4, 8) using a contingency table test.

RESULTS

Single-release sites

The daily death rate of the larvae in single-release sites was lowest in Microhabitats 1 ($\hat{d}$ = 0.0867) and 2 ($\hat{d}$ = 0.0986) (Table 3). Microhabitat 4 had a moderately low death rate ($\hat{d}$ = 0.1445). Death rates of $d > 0.15$ were found in Microhabitats 3 and 6. The finding rates were high ($\hat{f} > 0.6$) in Microhabitats 1, 2 and 4 (Table 3). The likely cause of the low finding rates in Microhabitats 3 and 6 is the height of vegetation. *Spartina patens* and *J. gerardi* in these microhabitats are taller than 30 cm, and *S. patens* grows over matted thick thatch from previous years. Searching for the larvae among the tall and dense vegetation had proven to be difficult. A maritime ringlet larva is 3 mm long after hatching, and the cohorts have grown to 6 mm by the end of the observation. A newly hatched larva is pale tan, and it turns cryptic bluish-green once it starts feeding on *S. patens*. The likelihood model yields estimates of survivorship that are independent of the finding rate (Lebreton *et al.*, 1992), so this does not bias our survivorship estimates. We excluded Micro-habitat 5 from further analysis because we found no larvae, and Microhabitat 8 because of the small initial cohort size.

Microhabitats 1 and 2 and Microhabitats 3, 4 and 5 were found to be highly significantly different with regard to $\hat{f}$ and $\hat{d}$ by Akaike's Information Criterion test ($2\Delta\ln L$ = 51.138, d.f. = 2, $P < 0.0001$). The plot of d against lnL (Fig. 2) clearly illustrates this result because the likelihood curves of those two groups do not overlap. Microhabitats 1 and 2 were not significantly different ($2\Delta\ln L$ = 1.514, d.f. = 2, P = 0.469). Microhabitat 4 was not significantly different from 6 ($2\Delta\ln L$ = 1.7018, d.f. = 2, P = 0.427), but it was significantly different from 1 ($2\Delta\ln L$ = 16.968, d.f. = 2, P = 0.0002) and 2 ($2\Delta\ln L$ = 8.654, d.f. = 2, P = 0.0132). Microhabitat 4 was only marginally different from Micro-habitat 3 ($2\Delta\ln L$ = 5.799, d.f. = 2, P = 0.0551).

Table 3. Estimated daily death rate ($\hat{d}$) and finding rate ($\hat{f}$) along with the two-unit support limits (SL) from single-release sites. The two-unit support limits can be considered similar to 95% confidence limits (Edwards, 1992).

Microhabitat	n	$\hat{d}$	two-unit SL	$\hat{f}$	two-unit SL
1	60	0.0867	(0.0760, 0.0986)	0.6905	(0.5080, 0.8392)
2	40	0.0986	(0.0838, 0.1148)	0.6826	(0.4714, 0.8446)
3	40	0.1903	(0.1511, 0.2431)	0.2492	(0.0154, 0.7272)
4	31	0.1445	(0.1169, 0.1794)	0.7489	(0.4037, 0.9540)
6	38	0.1504	(0.1221, 0.1861)	0.4281	(0.1278, 0.7778)

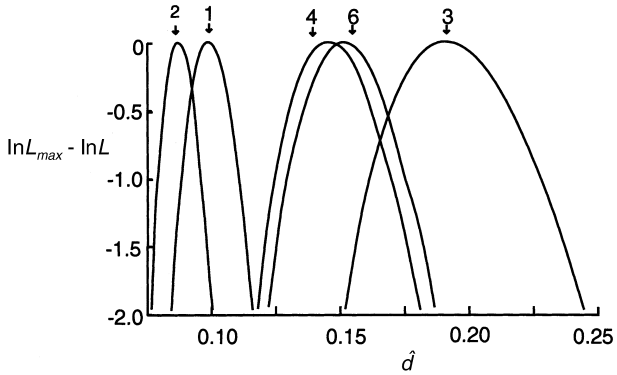

Fig. 2. The plot of daily death rate $\hat{d}$ vs standardized log likelihood values for the five microhabitats within two-unit support limits.

Multiple-release sites

At the end of the observation period, 12.5% of the larval cohort was alive in the multiple-release sites in Microhabitat 1, 15% in Microhabitat 2, 1.67% in Microhabitat 4, and 5% in Microhabitat 8 (Table 4). No larvae were found in Microhabitats 3, 5 and 6. Based on MNKA, the survival rates of larvae were significantly different among the microhabitats that had at least one surviving larva at the end of the observation period (χ^2 = 10.77, d.f.= 3, P = 0.013).

The number of surviving larvae in early September was too small to meaningfully estimate the survival rate over winter, but three larvae in Microhabitat 1 and one larva each in Microhabitats 2 and 4 were found alive in the following June, and the larva in Microhabitat 4 pupated.

DISCUSSION

The quality of microhabitats within a salt marsh differs considerably for the early-instar larvae. The single-release site mortality data suggest that Microhabitats 1 and 2 are likely to be the most suitable habitats for maritime ringlet larvae (Table 3). The results obtained from MNKA at multiple-release sites also show that the death rates among microhabitats were significantly different and lowest in Microhabitat 2 (Table 4). The quality of Microhabitat 4 seems to be fairly good for the young maritime ringlet larvae as well; although it had a significantly higher death rate than Microhabitats 1 or 2, larvae survived better in Microhabitat 4 than in Microhabitat 3, and a larva pupated in Microhabitat 4. Microhabitats 1, 2 and 4 contain the important host plant *S. patens* and the nectar source *L. carolinianum*, and these microhabitats coincide with the area in this marsh where newly emerged adults were frequently captured (Webster, 1994*a*). Although the exact processes that generated the vegetation pattern and its relationship to the survival of the maritime ringlets are still unclear, the abundance of *S. patens* and *L. carolinianum* seems to be a fair indicator of good early-instar larval habitat for the maritime ringlets.

We found Microhabitats 3, 5 and 6 to be unsuitable as maritime ringlet habitats. Although speculative, we present possible causes for the high mortality in those habitats.

The poor survival of larvae in Microhabitats 3 and 5 may be due to frequent tidal inundation. Prolonged tidal submergence appears to have adverse effects on the survival of larvae (M. Sei, unpublished data; Joy & Pullin, 1997), and the presence of fish and marine invertebrates (Pfeiffer & Wiegert, 1981; Daiber, 1982; Rozas & Zimmerman, 2000) during submergence may have increased predation. Vegetation structure (Dempster, 1984) and nearby landscape features (e.g. a sandbar) (Daiber, 1982; Long & Mason, 1983) may influence the size of the predator community, contributing to differential predation. Although we found that Microhabitat 3 was unfavourable, the same vegetation type in the southwestern part of the marsh, which experiences less frequent tidal inundation, had a high density of freshly emerged adults (Webster, 1994*a*).

The dominant vegetation in Microhabitat 6, *J. gerardi*, may not be eaten by the maritime ringlet. Even if the maritime ringlet can use *J. gerardi*, it seems likely to be a low-quality host, as it produces few new shoots in late summer, unlike *S. patens* (Bertness & Ellison, 1987). Because it is infrequently inundated, Microhabitat 6 may also support non-salt marsh specialist predators, which perhaps may result in predation pressure higher than other microhabitats.

We made two assumptions about early-instar larval movement in and out of the release sites. The first assumption was that this migration rate is so slow that there is no movement across the clearing. This first assumption seems to be met as we have often resighted larvae in exactly the same location within a site, or if they moved, the displacement was a few centimeters at most over 3 or 4 days (M. Sei, pers. obs.). Similarly, previous studies of overwinter survival among bog-dwelling *C. tullia* did not have problem with larval movement (Joy & Pullin, 1999). The second assumption is that the habitat quality does not affect their movement rate (i.e. they will not migrate to a high-quality habitat from a low-quality habitat). Our second assumption would be violated if the larvae moved out of study sites, and it would overestimate $\hat{d}$, but it would not affect our conclusion that the habitat quality among the microhabitats differs significantly as perceived by the larvae.

Table 4. The minimum number of larvae known to be alive (MNKA) in multiple-release sites at the end of the observation, and the percentage of the larvae that had survived. We released ten larvae into each multiple-release site.

Microhabitat	Number of multiple-release sites	MNKA	% survival
1	4	5	12.5
2	6	9	15.0
3	3	0	0
4	6	1	1.67
5	6	0	0
6	6	0	0
8	4	2	5.0

At worst, we can regard $\hat{d}$ as a qualitative indicator of habitat quality.

As one of a few salt marsh butterfly species, the maritime ringlet is an evolutionary phenomenon worth preserving. Gaining knowledge of the microhabitat-specific survival of the maritime ringlet is necessary as none of their habitats is permanently stable. In the short term, the salt marsh vegetation is often disturbed by winter ice scour (Richard, 1978; Roberts & Robertson, 1986) and tidal erosion of the marsh itself (Jacobson & Jacobson, 1987). Because salt marshes inhabited by the maritime ringlets often occur near or within city limits, the butterflies are at risk of habitat loss or habitat deterioration by urban and industrial sprawl and pollution (Roberts & Robertson, 1986; Adam, 1990). In the long term, the vegetation may also change as the salt marsh hydrology changes owing to a rise in sea level (Warren & Niering, 1993) or vegetation competition patterns are altered from increased soil nitrogen level (Valiela, Teal & Sass, 1975; Levine, Brewer & Bertness, 1998).

To conserve maritime ringlets successfully, we should recognize the importance and ephemerality of their microhabitats. Microhabitats differing subtly in hydrology and vegetation have profound effects on early-larval survivorship. As salt marshes and microhabitats within them are not static in time and space, the preservation of this subspecies may require relatively intensive management. Because of the ringlet's low vagility and the disjunct nature of the extant salt marshes, ringlets have a low probability of recolonizing an unoccupied but suitable salt marsh by themselves. Owing to this lack of metapopulation structure (Hanski & Simberloff, 1997), local extinction is an extremely serious threat to the maritime ringlet.

We need to provide aggressive stewardship to ensure the persistence of the maritime ringlet populations. In addition to the adult-population density monitoring now being done, periodic monitoring of their habitats to assess the extent of short *S. patens* stands with *L. carolinianum* favourable to the early-larval survival (i.e. Microhabitats 1, 2 and 4) will afford more security in their management. Although older larvae and adults may be less sensitive to microhabitat differences, *L. carolinianum* attracts adult maritime ringlets as a nectar source. The presence of nectar sources positively affects adult survival and reproduction in California populations of *C. tullia* (Weissman, 1972), and maritime ringlet females are known to nectar frequently as they age and deplete their fat reserves (Webster, 1994*a*). The extent of favourable microhabitat can be used to choose reintroduction sites and to assess habitat quality for extant populations. The former will protect the maritime ringlet further from extinction, and it is essential in realizing downlisting or delisting. The latter can be used to protect the extant populations. The decline in favourable microhabitat size predicts decline of the population, and the microhabitat change can be reversed if the cause is small in scale (e.g. vegetational change due to nitrogen loading) and the change is detected at an early stage.

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