

Factors Influencing Larval Survival of the Invasive Browntail Moth (*Lepidoptera: Lymantriidae*) in Relict North American Populations

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ABSTRACT Scant attention has been paid to invasive species whose range and abundance has decreased after an initial range expansion. One such species is the browntail moth *Euproctis chrysorrhoea* L., which was discovered in the eastern United States in 1897. Its range expanded until 1914; after 1915, however, its range contracted and now it persists in only two isolated coastal locations. Although a biological control agent has been implicated in this range collapse, cold inland winter temperatures may also help to restrict browntail moth populations. We surveyed coastal versus inland habitats in Maine and Massachusetts for browntail moth overwintering mortality and larval density per web. We also performed an experiment assessing these same variables in coastal versus inland habitats on different host plant species and at different initial larval densities. We also analyzed temperature records to assess whether winter temperatures correlated with changes in the invasive range. Overwintering mortality was lower in coastal populations for both the experimental populations and in the Maine field survey. Experimental populations in Cape Cod coastal areas also had lower rates of fall mortality and higher larval densities, suggesting that coastal areas are better year-round habitats than inland areas. There were no consistent differences between coastal and inland populations in their response to larval density or host plant, although overall survival in both areas was higher at low initial larval densities and affected by host identity. There was also no difference in two measures of the coldest winter temperatures during browntail moth's expansion and contraction. Our results show that climate affects browntail moth, but suggest that winter temperatures cannot explain both the rapid expansion and subsequent collapse of this pest.

KEY WORDS population collapse, overwintering mortality, invasive species, *Euproctis chrysorrhoea*, forest defoliator

Interest in the dynamics of species invasions has increased dramatically in recent years. Much of the research concerning these biological invasions addresses the ecology and control of non-native species that, if left unchecked, are capable of severe economic and ecological harm (Mack et al. 2000). Often overlooked, however, are those established invasive species whose populations inexplicably decline after initial success and rapid range expansion. Simberloff and Gibbons (2004) provided several case studies of this phenomenon and suggested that these near or total extirpations are likely caused by a combination of biotic (e.g., competition, predation) and abiotic (e.g., restricted spatial scale, climate) factors. Understanding the factors underlying the collapse of such species may help us manage other invasive species.

In the early 20th century, the browntail moth, *Euproctis chrysorrhoea* L. was considered one of the most

dangerous invasive species in eastern North America. First discovered in coastal Massachusetts in 1897 (Fernald and Kirkland 1903), it spread across the eastern United States and into southern Canada over the next two decades (Fig. 1) (Burgess 1923). A polyphagous herbivore that defoliated a wide range of tree species, browntail moth was considered an economic and environmental hazard equal to or exceeding that of the gypsy moth, *Lymantria dispar* L. (Burgess and Crossman 1929). In addition to defoliating trees, browntail moth also posed a risk to human health: their larvae possess urticating hairs that can cause allergic reactions ranging from skin rashes to death (Blair 1979). Initial control efforts for browntail moth focused on the mechanical removal of overwintering larvae and the introduction of several specialist and generalist parasitoids (Howard and Fiske 1911). These efforts met with little apparent success (Schaefer 1974); around 1915, however, browntail moth began to disappear from much of its formerly invaded range. Its distribution continued to shrink until, by the 1960s, they were restricted to relict populations in two coastal enclaves in Maine and Massachusetts (where they continue to persist).

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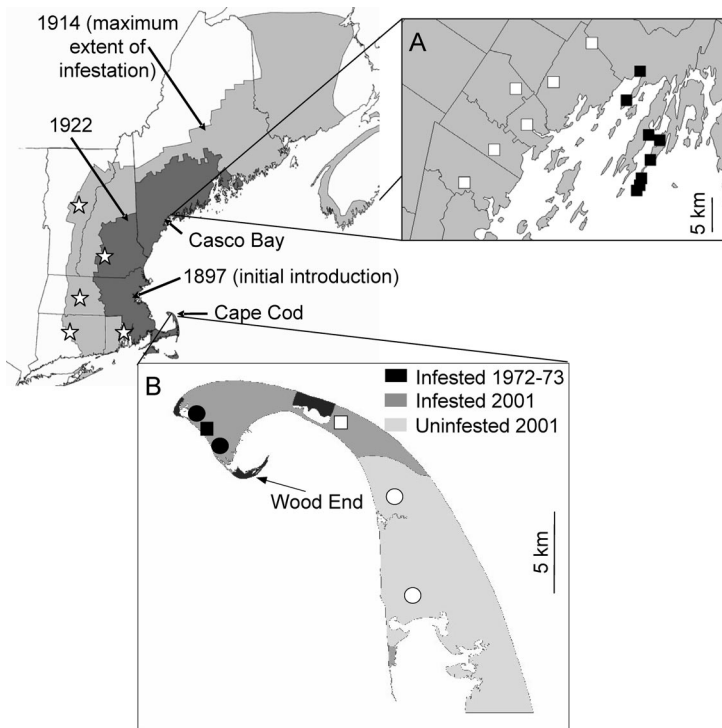


Fig. 1. Distribution map showing spread and retreat of browntail moth across New England (redrawn from Burgess 1923 and Elkinton et al. 2006). Stars indicate location of weather stations used in the historical analysis of winter temperatures (1897–1932). (A) The Casco Bay region of Maine showing inland (□) and coastal (■) field survey sites; (B) Cape Cod, MA, showing browntail moth inland and coastal sites for both the experiment (○ and ● for inland and coastal sites, respectively) and the Massachusetts field survey (□ and ■ squares for inland and coastal sites, respectively).

The puzzle of the browntail moth's rapid range expansion and subsequent contraction in eastern North America has been largely ignored by researchers. Schaefer (1974) carried out the only major work done on browntail moth in North America since the 1920s. He researched browntail moth population dynamics in both the Maine and Massachusetts enclaves and suggested that high overwintering mortality in colder inland areas might have contributed to the range contraction. He showed that browntail moth webs transported to interior locations in Maine experienced higher overwintering mortality than browntail moth webs remaining in coastal locations.

We have recently presented evidence that the decline of browntail moth in its invasive range was likely caused by the non-native tachinid parasitoid *Compsilura concinnata* Meigen, (Diptera: Tachinidae), a biological control agent introduced to North America in 1906 for suppression of both browntail moth and gypsy moth (Elkinton et al. 2006). Our reanalysis of data collected in the mid-1920s (Burgess and Crossman 1929) showed that *C. concinnata* parasitism was five times higher at inland versus coastal sites. This led us to experimentally test the hypothesis that increased parasitism by *C. concinnata* contributed to the disappearance of browntail moth from inland sites. We found that *C. concinnata* parasitism was absent in the coastal sand dune habitat on Cape Cod, MA, where

browntail moth is abundant, very high at inland sites where browntail moth is absent, and intermediate in the coastal scrub habitat where browntail moth occurs at low density (Elkinton et al. 2006). In combination with previous research (Burgess and Crossman 1929), our results implicate *C. concinnata* as an important factor in the collapse of browntail moth populations across its invaded range. It does not necessarily follow, however, that *C. concinnata* is the only factor behind the enigmatic decline of the browntail moth; a full explanation of this event requires understanding the role played by climate and other potentially influential factors.

We report the results of field surveys and experimental manipulations assessing whether climatic differences between inland and coastal sites, acting alone or in combination with other factors, might help explain the current restricted distribution of browntail moth in North America. We tested two hypotheses advanced by Schaefer (1974): (1) browntail moth mortality is higher in inland versus coastal habitats and (2) low winter temperatures may have contributed significantly to the contraction of the invasive range of the browntail moth. In parallel with field surveys conducted in both extant browntail moth populations (Maine and Massachusetts), we established experimental populations in coastal and inland habitats on Cape Cod, MA, and measured both the total larval

density per web and the percent fall and overwintering mortality. Because *C. concinnata* only parasitizes browntail moth larvae in the spring, overwintering and fall mortality are unaffected by this parasitoid. To assess whether browntail moth larval performance and survival in coastal (browntail moth historically and currently present) versus inland (browntail moth historically present but currently absent) habitats was affected by larval density and host plant identity, we replicated this experiment at two larval densities on three host plant species. Finally, we analyzed data on winter temperatures in five New England states from 1897 to 1932 to determine whether changes in winter temperatures correlate with the periods of observed browntail moth range expansion (1897–1914) and contraction (1915–1932).

Materials and Methods

Natural History of the System. Our research was performed on Cape Cod, MA, and near Casco Bay, ME, the last two regions that contain extant North American populations of the formerly widespread browntail moth (Fig. 1). The most frequently used host plant on Cape Cod by browntail moth is beach plum, *Prunus maritima* Marsh, and to a lesser extent black cherry, *Prunus serotina* Ehrh. (Schaefer 1974). It also uses black oak, *Quercus velutina* Lam., but defoliation of this species is rare (J.S.E., unpublished data). Its host plants in Casco Bay, where beach plum does not occur, include apple, *Malus domestica* Borkh., red oak *Quercus rubra* L., black cherry, and various species of hawthorn, *Crataegus* sp. In striking contrast to browntail moth populations on Cape Cod, browntail moth in Casco Bay frequently defoliates mature red oak trees.

The ecology and developmental stages of the browntail moth are described in detail elsewhere (Fernald and Kirkland 1903, Schaefer 1974); briefly, larvae hatch in late summer from egg masses laid by adult moths and then feed in communal groups. In the fall, early instars collectively congregate on the terminal branches of their host plant and spin a multi-layered web in which they overwinter. Larvae emerge from the web in the spring, feed, and complete three more instars before pupating; the adults emerge in July.

Experimental Manipulation—Cape Cod, MA. We performed a field experiment to assess whether browntail moth fall survival, larval density, and overwintering survival in coastal versus inland habitats on Cape Cod was influenced by larval host plant and initial larval density. Our fully factorial experiment crossed two habitat types (coastal, inland) with three host plant species (beach plum, black cherry, black oak) at two initial larval densities (one egg mass/branch, three egg masses/branch) for a total of 12 treatment combinations. We collected egg masses from beach plum in naturally occurring, high-density browntail moth populations at Wood End, MA, on 5–6 August 2002. It was necessary to collect them from this coastal location because they do not occur in suffi-

ciently high densities in inland locations. Egg masses were collected shortly before larval emergence. Beach plum twigs, each with one egg mass, were placed individually in 30-ml cups and kept shaded until deployment. We also reared 30 egg masses individually in the laboratory to estimate the number of larvae emerging per mass.

We deployed the egg masses on 7 August 2002 by placing them on Cape Cod at two coastal sites (≈ 100 m from the ocean edge) in areas where browntail moth is common and two inland sites (1–1.5 km from beach) where browntail moth has not occurred for many years (Elkinton et al. 2006; Fig. 1). We attached egg masses to six widely spaced branch tips on each of three individual plants of the most commonly used host plant species on Cape Cod (beach plum, black cherry, and black oak) using twist ties. Any naturally occurring egg masses or larvae were removed before placement of the experimental populations. Three branches on each tree received three egg masses per branch tip, and the other three received one egg mass per branch tip. We revisited each plant 1 wk later and replaced any nonhatching egg masses with a fresh egg mass.

Browntail moth larvae from the experimentally deployed egg masses fed until September 2002 and then spun communal webs in which they overwintered. We collected these webs on 9 April 2003, before browntail moth larvae had emerged from them. The webs were placed individually in plastic bags and returned to the laboratory to count the number of larvae emerging from each web. We dissected each web after larvae had stopped emerging from it and counted the number of dead and any remaining living larvae.

Field Survey—Cape Cod, MA. In parallel with the above experiment, we also collected naturally occurring webs from inland and coastal sites in Cape Cod in April 2003 before larval emergence (Fig. 1). One week before collecting the experimentally deployed webs, we searched beach plum, black cherry, and black oak for webs at inland and coastal sites where naturally occurring browntail moth populations were found. We selected ≈ 30 trees per host plant type in each of the habitats and randomly selected a single web from each tree; each web was placed in a plastic bag, returned to the laboratory, and subsequently treated as described above for the experimental populations.

Field Survey—Casco Bay, ME. Two days after conducting the field survey in Cape Cod, we performed a smaller parallel survey in Casco Bay, ME (Fig. 1). Because browntail host plants differ in the two areas, we selected the most commonly used hosts (apple, black cherry, and hawthorn) as we had done in Cape Cod. We visited eight coastal sites (< 0.5 km from coast) and six inland sites (2–6 km from coast); each site was > 1 km from each other. At each site, we sampled the first tree of the three host plant species found with browntail moth overwintering webs. We collected six webs from each tree and treated them as described above.

Analysis of Historical Climate Data. Because overwintering mortality in insects is often linked to ex-

tre low temperatures (Bale 1991, Chown and Terblanche 2007), we focused our analyses on two measures of extreme temperature for each year: the coldest minimum temperature of the winter and the number of days below -25°C . The latter temperature has been reported to cause 100% mortality to browntail moth larvae (Gilliatt 1921, Pantyukhov 1964, but see Sacharov 1930). We used historical records from the National Climatic Data Center (NOAA 2005a) to determine the coldest winter (December–February) temperatures at weather stations in five New England states (Connecticut, Rhode Island, Massachusetts, Vermont, and New Hampshire) during 1897–1914, the 18-yr “expansion” phase of browntail moth distribution, and 1915–1932, the following 18-yr “contraction” phase over which browntail moth distribution sharply decreased (Fig. 1). We selected one weather station in each of five states within but close to the boundary of the area infested by browntail moth in 1914 (see Fig. 1). Each station possessed a continuous record of winter temperatures from 1897 to 1932. These weather stations were located in Northfield, VT; Concord, NH; Amherst, MA; Hartford, CT; and Providence, RI. Yearly data for each state for this 36-yr period was converted to degrees Celsius. We also compared coldest winter temperatures and number of days below -25°C at weather stations near our experimental sites, Portland, ME, and Chatham, MA, from December 2002 through February 2003 with the 30-yr average coldest winter temperature for these sites (1974–2003).

Statistical Analysis of Experimental and Field Survey Data. We measured the number of browntail moth larvae per web entering the winter, percent fall mortality, and percent overwintering mortality. Fall mortality was calculated as $100 \times (1 - [\text{number of larvae per web entering the winter}/\text{estimated number of larvae emerging from the deployed egg masses}])$. Fall mortality was calculated for only the experimental populations because we did not know the initial number of egg masses per branch for field-collected webs. Overwintering mortality was calculated as $100 \times (1 - [\text{number of larvae emerging from each web}/\text{number of larvae per web entering the winter}])$.

For the experimental data, all response variables were calculated as the mean of all webs per tree in each host plant \times site \times egg mass density combination. There were six replicates (3 trees per host plant \times 2 sites) for each of the 12 treatment combinations for an initial total of 72 replicates; 5 replicates were destroyed over the course of the experiment, however, leaving us with a total of 67 replicates.

For the survey data, all response variables were calculated as the mean of all webs per tree in each host plant \times habitat combination. For the Cape Cod survey, there were 90 replicates (3 host plants \times 30 replicates per host plant) for each of the two habitat types for an initial total of 180 replicates; 3 replicates were destroyed, however, leaving us with a total of 177 replicates. The Casco Bay survey had 14 replicates: 9 black cherry trees (5 coastal, 4 inland), 3 apple trees (1 coastal, 2 inland), and 2 hawthorns (both coastal).

For the Cape Cod experimental data, we used general linear models (SAS Institute 2003) to test for the main effects of habitat type (coastal, inland), host plant (beach plum, black cherry, black oak), initial egg mass density (one egg mass, three egg masses), and all two-way interactions. Site was initially included as a blocking variable; when it proved to be insignificant, it was removed and the analyses rerun. Our response variables were percent fall mortality, larval density, and percent overwintering mortality.

For the Cape Cod survey data, we used general linear models (SAS Institute 2003) to test for the main effects of habitat type (coastal, inland) and host plant (beach plum, black cherry, black oak), and the habitat \times host interaction. Our response variables were larval density and percent overwintering mortality.

For the Casco Bay survey data, we used a general linear model (SAS Institute 2003) to test for the main effect of habitat type (coastal, inland). Because all host plant species were not present in both inland and coastal habitats, we were unable to analyze the main effect of host plant. Our response variables were larval density and percent overwintering mortality.

In all of the above analyses, data were square root transformed when appropriate to improve normality of residuals. We performed means separation tests, where appropriate, using Tukey’s honestly significant difference (HSD).

Statistical Analysis of Historical Climate Data. We used analysis of variance (ANOVA) to test for differences in the mean yearly values of the coldest daily minimum temperature of the winter and mean number of days per winter below the temperature threshold of -25°C between the expansion (1897–1914) and contraction (1915–1932) phases of the browntail moth invasion at each weather station in the five New England states.

Results

Larval Mortality in Experimental Populations Between Emergence and Web Formation. A total of 290 ± 24.6 (mean \pm SE, $n = 30$) larvae per egg mass emerged from the egg masses used to create the experimental populations; we used this figure as our estimate of initial larval density (Fig. 2). Fall mortality in coastal experimental populations was 20% lower than in inland areas ($F = 20.5$; $df = 1,57$; $P < 0.001$) and 17% lower in the low (one egg mass) versus high (three egg masses) density treatments ($F = 9.04$; $df = 1,57$; $P = 0.004$). Although there was no main effect of host plant identity ($F = 0.31$; $df = 2,57$; $P = 0.74$), there was a significant habitat \times host interaction ($F = 4.11$; $df = 2,57$; $P = 0.022$); larvae feeding on black cherry had lower mortality in coastal versus inland habitats (58 ± 4 and $87 \pm 5\%$; Tukey’s HSD with $\alpha = 0.05$). All other two-way interactions were not significant ($P > 0.05$).

Larval Density per Web. The number of browntail moth larvae per web on Cape Cod was higher in coastal versus inland sites (Fig. 3). This was true for both the experimentally created populations and

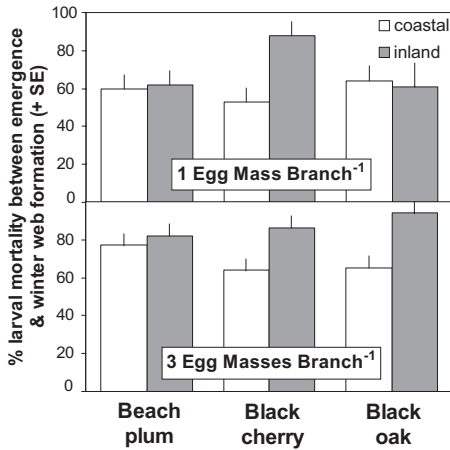


Fig. 2. Fall mortality (% of browntail moth larvae dying before entering the web) in low-density (one egg mass branch⁻¹, top) and high-density (three egg masses branch⁻¹, middle) experimental populations. The experiment was carried out in inland (>1 km from coast) versus coastal (<0.5 km from coast) habitats on three host species (beach plum, black cherry, and black oak).

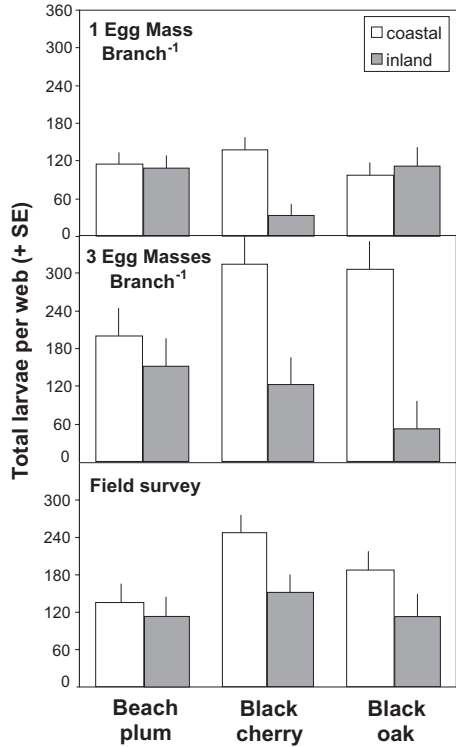


Fig. 3. Larval density per overwintering web in low-density (one browntail moth egg mass per branch, top) and high-density (three browntail moth egg masses per branch, middle) experimental populations and in a contemporaneous field survey (bottom) on Cape Cod, MA. In the experiment, larvae from both the one and three egg mass treatments formed a single communal web per branch. Both the experiment and field survey were carried out in inland (>1 km from coast) versus coastal (<0.5 km from coast) habitats and on three host plant species (beach plum, black cherry, and black oak).

those surveyed in the field (experimental populations: $F = 21.2$; $df = 1,57$; $P < 0.001$; Cape Cod field survey: $F = 4.97$; $df = 1,171$; $P = 0.027$). Coastal and inland habitats surveyed in Casco Bay did not differ in larval density ($F = 0.13$; $df = 1,12$; $P = 0.72$).

Host plant identity did not affect larval density in our experimental populations ($F = 0.20$; $df = 2,57$; $P = 0.82$). However, there was an effect of host plant identity in our Cape Cod field survey ($F = 3.21$; $df = 2,171$; $P = 0.043$). Black cherry webs had more larvae than did beach plum webs (200 ± 20 and 124 ± 20 larvae; Tukey's HSD with $\alpha = 0.05$). Black oaks had larval densities intermediate between those of the other two host plants (151 ± 24 larvae) and did not differ in larval density from either of the other two host plants.

Overwintering Mortality. Overwintering mortality was lower in coastal versus inland sites for both the experimentally created populations and the Casco Bay field survey ($F = 22.2$; $df = 1,57$; $P < 0.001$ and $F = 16.7$; $df = 1,12$; $P = 0.002$, respectively; Fig. 4). Coastal and inland overwintering mortality did not differ in the Cape Cod field survey ($F = 0.22$; $df = 2,171$; $P = 0.64$).

Host plant identity affected overwintering mortality in experimentally created populations and in the Cape Cod field survey ($F = 5.83$; $df = 2,57$; $P = 0.005$ and $F = 4.32$; $df = 2,171$; $P = 0.015$, respectively); in both cases, larvae feeding on black oaks had higher overwintering mortality rates than did larvae on black cherry or beach plum (Tukey's HSD with $\alpha = 0.05$). In the Cape Cod field survey, there was also a significant habitat \times host plant interaction ($F = 3.15$; $df = 2,171$; $P = 0.046$). In inland habitats, larvae feeding on black oak had a higher overwintering mortality than did larvae feeding on beach plum (Tukey's HSD with $\alpha = 0.05$).

The density of experimentally deployed egg masses affected overwintering mortality ($F = 6.59$; $df = 1,57$; $P = 0.013$). Overwintering mortality in the low-density treatment was 60% lower than in the high-density treatments (8 ± 3 and $20 \pm 2\%$, respectively). All of the two-way interactions were not significant (all $P > 0.05$).

Analysis of Historical Climate Data. The 1897–1914 expansion and 1915–1932 contraction phases of browntail moth distribution did not differ for the coldest minimum temperature of the winter for any of the five New England states ($P > 0.4$ in all cases; Fig. 5). In fact, mean values for the coldest minimum temperature of the winter were lower during the expansion phase than the contraction phase at all five weather stations. Similarly, there were more days below -25°C in the expansion phase than in the contraction phase at four of the five sites (Providence, RI, had no days below -25°C in either period). Again, however, there was no significant difference in yearly values between the expansion and contraction phases during each

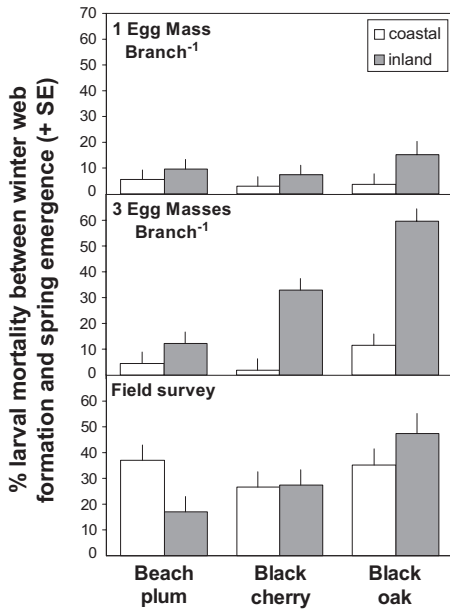


Fig. 4. Overwintering mortality, expressed as percent of browntail moth larvae dying per web, in low-density (one browntail moth egg mass per branch, top) and high-density (three browntail moth egg masses per branch, middle) experimental populations and in a contemporaneous field survey (bottom) on Cape Cod, MA. The experiment and field surveys were carried out in inland (>1 km from coast) versus coastal (<0.5 km from coast) habitats on three host species (beach plum, black cherry, and black oak).

phase at any of the five weather stations ($P > 0.4$ in all cases).

The coldest temperature of winter 2002–2003 in Portland, ME, was -27°C ; this was the fifth-coldest value in the past 30 yr. In contrast, the coldest day of winter 2002–2003 in Chatham MA, was -12°C , which was the 22nd-coldest value in the past 30 yr. Neither coastal site had winter temperatures anywhere near as cold as the more northerly interior sites such as Northfield, VT, where browntail moth existed during the 1897–1914 expansion phase. The minimum winter temperatures at these sites from 1974 to 2003 are not notably different from the values that occurred during the 1897–1914 expansion phase or the 1915–1933 contraction phase. For example, Portland, ME, experienced 26 d below -25°C from 1974 to 2003 compared with 11 d from 1897 to 1932.

Discussion

Our experimental results provide support for the hypothesis of Schaefer (1974) that larval overwintering mortality is lower in coastal versus inland habitats (Fig. 4). Although higher winter temperatures are likely responsible for this difference (see below), winter temperatures cannot explain why coastal and inland habitats on Cape Cod also differed in percent fall mortality and larval density (Figs. 2 and 3). Although the Casco Bay survey did not find a between-habitat

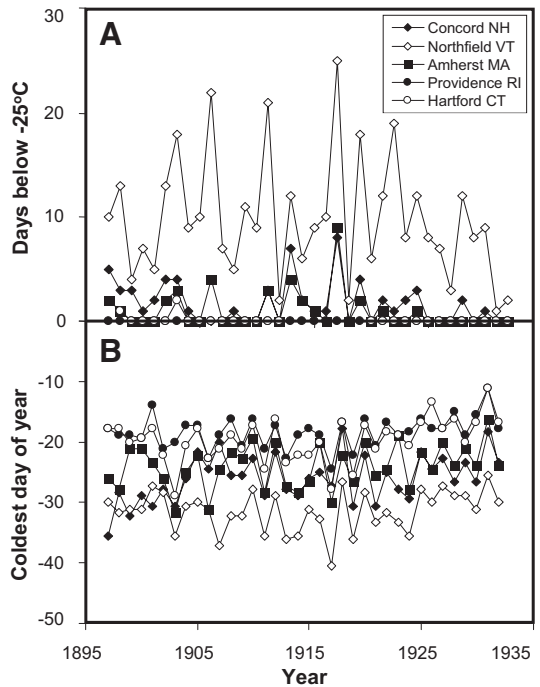


Fig. 5. (A) Number of days each winter (December–February) when temperatures fell below -25°C and (B) coldest temperature of the winter at weather stations located within the range occupied by browntail moth in five New England states during the expansion (1897–1914) and contraction (1915–1932) phases of the browntail moth invasion. Lines above the x-axis indicate the expansion (left double-headed arrow) and contraction (right double-headed arrow) phases. See Fig. 1 for weather station locations.

difference in larval density, its low degree of replication (14 versus 177 replicates for the Cape Cod survey) suggests that care be taken in interpreting the results from this site. The coastal- versus-inland differences we observed in pre- and postwinter mortality were unaffected by host plant species and initial larval density, and the results from the field surveys largely agreed with those of our experiment. Our findings are especially striking given that the inland sites were only 1–1.5 km from the coast, a distance that we did not anticipate would affect our results.

The most likely explanation for the lower overwintering mortality in coastal habitats is that coastal habitats experience less severe winter temperature regimens. Temperature data from the weather stations closest to our experimental plots and field survey locations on Cape Cod and Casco Bay support this idea. On Cape Cod, the mean and lowest minimum temperatures recorded ≈ 0.5 km from the ocean in Provincetown, MA, from December 2002 to March 2003 were -4.3 and -13°C ; a station in Chatham, MA, ≈ 1.5 km from the ocean recorded mean and lowest minimum temperatures of -5.2 and -20°C over the same period (NOAA 2005b). At the two weather stations closest to our sampling areas in Maine, the mean and lowest minimum temperatures recorded over this pe-

riod on Peaks Island, ME (≈ 0.1 km from the ocean) were -6.1 and -18°C (Weather Underground 2005); the station in Portland, ME, ≈ 1.6 km from the ocean recorded -9.3 and -27°C (NOAA 2005b).

The lower temperatures in Casco Bay corresponded to higher winter mortality there than on Cape Cod. Browntail moth mortality supposedly approaches 100% as winter minimum temperatures go below -25°C (Gilliatt 1921 and Pantyukhov 1964, as cited in Schaefer 1974), although there are reports that larvae can survive brief exposure to temperatures below -32°C (Sacharov 1930). Most inland browntail moth populations in the northeast would be regularly exposed to temperatures lower than the -25°C threshold (NOAA 2003), and $>50\%$ of overwintering browntail moth larvae die in inland habitats even during mild Maine winters (Maine Forest Service 2005). The coastal versus inland differences in overwintering mortality are thus likely caused by temperature. It is worth noting, however, that (1) during its range expansion, browntail moth survived and reproduced in extremely cold areas such as northern Vermont and inland Ontario; and (2) during its subsequent range collapse, browntail moth disappeared from portions of southern New England where winter temperatures exceed those found in Casco Bay.

In our analysis of the historical weather data at the five sites in the former range of browntail moth, the most obvious differences in temperatures were between sites reflecting the expected north-south gradient. For example, Northfield, VT, had 184 d below -25°C during the 1897–1914 expansion phase compared with 171 d below -25°C in the 1915–1932 contraction phase. In contrast, Hartford, CT, had 3 and 0 d, respectively, below -25°C in these two phases. The fact that expansion and contraction of the winter moth populations occurred simultaneously over this entire region despite vast between-site differences in winter temperatures is further evidence that winter temperature had little to do with expansion or contraction. Previous work indicating high rates of larval parasitism by the tachinid *C. concinnata* in inland populations (Elkinton et al. 2006) suggests that this agent was the primary cause of the disappearance of browntail moth from most of its former range in North America.

Year-round differences in climate between coastal and inland areas are the most likely explanation for the fact that prewinter mortality was lower in coastal habitats (Fig. 2) and that larval density per web in coastal habitats was more than twice that found in inland areas (Fig. 3). Larval density, the number of larvae per web entering the winter, assesses the suitability of prewinter conditions for the growth and survival of early-instar larvae. Our results thus suggest that coastal areas are more hospitable to browntail moth larvae in the fall as well as in the winter. One possible explanation for these findings is that the coastal climate is more favorable to browntail moth growth and development on a year-round basis; another one is that predation on early instars unrelated to *C. concinnata* is higher in inland habitats. Previous research documented lower vegetation diversity (both in terms of

species number and percent cover) in high browntail moth density sand dune habitats versus the browntail moth absent inland habitats (Elkinton et al. 2006); the low vegetation diversity in the sand dune habitat may support fewer predator and parasitoid species. Pentatomid bugs were sometimes observed feeding on early instars in our plots, and the hymenopteran parasitoid *Trichogramma minutum* Riley also parasitizes browntail moth eggs. Schaefer (1974) found *T. minutum* in 0.5% of surveyed egg masses, however, and we observed no *Trichogramma*-related parasitism at all. Although the braconid parasitoids *Apanteles laeticolor* Vier and *Meteorus versicolor* Wesm. also attack and emerge from early instar browntail moth, Schaefer (1974) recorded very low parasitism ($<2\%$) by them in his studies of browntail moth of Cape Cod and in Casco Bay, and we only rarely encountered cocoons of these species. Avian predators are a possibility as well: although we saw little evidence that birds had attacked any of our webs, Klarenberg et al. (1982) recorded that great tits, *Parus major* L., prey on browntail moth larvae in the Netherlands.

Our analysis of historical weather data does not support the suggestion that low winter temperatures “may also have contributed significantly to the reduction in (browntail moth) distribution” (p. 199–200 in Schaefer 1974). There were no significant differences between coldest temperatures of the year in the 1897–1914 expansion and 1915–1932 contraction phases of browntail moth invasion in any of the five New England states (Fig. 5) (NOAA 2005a). There were also no differences between these two time periods in the number of days in which the minimum temperature equaled or dropped below -25°C for any of the five weather stations from the southern, central, and northern portions of the range. Despite the fact that our research took place during the third-coldest winter (in terms of mean winter temperatures) in the past 30 yr (NOAA 2005b), browntail moth larvae successfully overwintered in inland habitats where, despite an abundance of host plants, they are currently absent. In addition, winter temperatures can explain neither why browntail moth expanded more quickly northward than in any other direction after its 1897 introduction, nor the post-1915 collapse of the southern and western portions of the browntail moth’s invaded range (Fig. 1). Finally, browntail moth in England is restricted to coastal habitats, although even minimum winter temperatures at inland sites there rarely dip below 0°C (MET 2005).

Taken as a whole, our results argue that climate was not a primary driver of the rapid rise and subsequent collapse of browntail moth in North America. Arguing against this, however, is the fact that we did find higher overwintering mortality in “inland” sites <6 km from the shoreline. If this relatively short distance is sufficient to significantly increase overwintering mortality, how did browntail moth previously survive at the northern range limits? Although Northfield, VT, for example, should be far too cold for overwintering survival to occur, it is contained within the circa-1914 range limits reported by Burgess (1923). Setting aside

the possibility of cartographic error, it is possible that the "populations" were identified by defoliation after dispersal events; if so, these areas may have contained transient rather than established populations. Alternatively, browntail larvae may have overwintered in local 'refuge' habitats whose microclimates were considerably warmer than the surrounding areas. Regardless of population dynamics at the range boundaries, however, it remains undisputed that browntail moth has previously occupied a much larger range than it does currently.

Larval host plant identity influenced overwintering survival, a fact that concurs with the findings of other researchers (Fig. 4) (Schaefer 1974, Mizuta 1978, Klarenberg et al. 1982). A recent study found that the pupal mass of larvae reared on black oak was significantly lower than that of larvae reared on beach plum (D.P., unpublished data). In our experiment, larvae on black oak had a substantially higher overwintering mortality than did larvae on other hosts (Fig. 4). This result held true only for inland sites, however, suggesting that abiotic stress magnifies the effect of host quality on overwintering survival. Schaefer (1974) found that browntail moth pupae vary in mass as a function of host plant and suggested that poor host quality decreases the ability of browntail moth larvae to withstand cold temperatures.

Browntail larval density per web on Cape Cod, MA, in both our experimental populations and field surveys (144 ± 19 and 158 ± 17 [SE] larvae/web, respectively) was lower than reported elsewhere. Elkinton et al. (2006) recorded 767 ± 92 larvae/web in Cape Cod, MA, whereas Schaefer (1974) reported means of 276 ± 8 larvae/web (this density estimate, however, excludes webs with >700 larvae, and he recorded at least one web with $>4,000$ individuals). In contrast, the number of browntail moth larvae we recorded entering webs in Casco Bay, ME, agreed almost exactly with data collected by Schaefer (1974): 211 ± 80 and 210 ± 8 larvae/web, respectively (J.E., unpublished data). The most likely explanation for the difference in Cape Cod populations is that both Schaefer (1974) and Elkinton et al. (2006) collected webs found in the high-density browntail moth populations in Wood End, MA, whereas both the experimental work and field surveys reported in this paper were carried out in coastal scrub areas where browntail moth densities are frequently 10-fold lower (Elkinton et al. 2006). At the high densities that occur at Wood End, each beach plum bush is infested with many webs, and as a result, a high proportion of webs contain larvae from two or more egg masses.

The density-dependent fall and overwintering mortality we observed in our experiment shows that increases in aggregation size through the coalescing of progeny from several egg masses does not increase survival (Figs. 2 and 4). This is despite the fact that (1) gregariousness and coloniality may offer protection from predators or parasitoids and (2) silk enclosures have been shown to confer considerable thermal advantage to species that use them (Fitzgerald and Underwood 2000). One explanation may be that high-

density aggregations offer protection from relatively rare but potentially catastrophic mortality events like desiccating winds or short, intense cold shocks. Many nematodes, for instance, aggregate into clumps in response to desiccating conditions, increasing their survival by reducing their overall surface area (Simons and Poinar 1973, Solomon et al. 1999). In the absence of such catastrophic conditions, high-density aggregations may have the opposite effect and increase per-capita mortality (through greater intraspecific resource competition) relative to low-density populations (Turchin 2003). It is also possible that larger webs are more easily found by searching predators and thus suffer disproportionately from such mortality (Klarenberg et al. 1982), although Elkinton et al. (2006) found no evidence of density-dependent parasitoid mortality among late-instar browntail moth under similar circumstances. Selection in such circumstances might nonetheless favor aggregation if rare but catastrophic mortality events devastate nonaggregating populations; such may be the case in this system. Because browntail moth populations form "overwintering" webs even when found in relatively warm climates like that of North Africa (Kirby 1897), however, it is also possible that there is no adaptive advantage to this behavior.

Perhaps a more likely explanation is that the multi-egg mass webs may be an inadvertent byproduct of the unusually high larval densities that exist on Wood End. All of the webs in our experimental populations were built surrounding the twig containing the egg mass from which the larvae emerged. This suggests that larvae do not travel far from their natal branch to form webs, even though feeding activity may extend 1–2 m along the branch. At the Wood End site where Elkinton et al. (2006) and Schaefer (1974) documented webs formed from multiple egg masses, we have collected >100 egg masses from a single beach plum bush. At such densities, many branch tips support two or more egg masses. Multiple egg mass webs may thus arise through larvae spinning a web on the branch tip where oviposition initially occurred rather than through active aggregation of larval groups.

Our research supports earlier suggestions (see Schaefer 1974) that higher overwintering mortality in inland habitats may have helped slow the spread of browntail moth and provides further evidence that climate affects browntail moth survival. However, our comparative analysis of winter temperatures during the expansion and contraction phases of the browntail moth invasion does not support the premise that the reversal of this invasion was primarily driven by climatic factors. Instead, the multi-decadal decline of browntail moth in its invasive range after its rapid expansion across throughout the east coast of North America is more likely caused by parasitism by *C. concinnata* (Elkinton et al. 2006). This conclusion is tempered, however, by our inability to explain how the two relict populations differ from other patches of outwardly identical coastal habitat that remains browntail moth-free. Future research should focus on the potential interaction(s) between biotic (parasi-

toid- and predator-induced mortality) and abiotic (temperature) factors in the early success and enigmatic decline of this noxious pest.

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