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IMPLICATING AN INTRODUCED GENERALIST PARASITOID IN THE INVASIVE BROWNTAIL MOTH'S ENIGMATIC DEMISE

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Abstract. Recent attention has focused on the harmful effects of introduced biological control agents on nontarget species. The parasitoid *Compsilura concinnata* is a notable example of such biological control gone wrong. Introduced in 1906 primarily for control of gypsy moth, *Lymantria dispar*, this tachinid fly now attacks more than 180 species of native Lepidoptera in North America. While it did not prevent outbreaks or spread of gypsy moth, we present reanalyzed historical data and experimental findings suggesting that parasitism by *C. concinnata* is the cause of the enigmatic near-extirpation of another of North America's most successful invaders, the browntail moth (*Euproctis chrysorrhoea*). From a range of ~160 000 km² a century ago, browntail moth (BTM) populations currently exist only in two spatially restricted coastal enclaves, where they have persisted for decades. We experimentally established BTM populations within this area and found that they were largely free of mortality caused by *C. concinnata*. Experimental populations of BTM at inland sites outside of the currently occupied coastal enclaves were decimated by *C. concinnata*, a result consistent with our reanalysis of historical data on *C. concinnata* parasitism of the browntail moth. The role of *C. concinnata* in the disappearance of browntail moth outside these enclaves has not been reported before. Despite the beneficial role played by *C. concinnata* in reversing the browntail moth invasion, we do not advocate introduction of generalist biological control agents. Our findings illustrate that the impact of such organisms can be both unpredictable and far-reaching.

Key words: biological control; browntail moth; *Compsilura concinnata*; *Euproctis chrysorrhoea*; forest defoliator; forest insect; invasive species; nontarget impacts; parasitoids; population dynamics.

INTRODUCTION

Classical biological control typically involves searching the native range of an invasive species for predators, parasitoids, or pathogens that can be introduced to attack the invader in its new habitat. The method has long been considered an environmentally benign approach to controlling invasive pests. In recent years, however, several studies have shown that some biological control agents have deleterious effects on native nontarget species (Simberloff and Stiling 1996, Follet and Duan 2000, Strong and Pemberton 2000a, b). Perhaps the epitome of ill-conceived introductions of parasitoids for classical biological control of insects is that of the generalist tachinid parasitoid, *Compsilura concinnata*. Introduced into eastern North America in 1906 primarily to combat burgeoning populations of gypsy moth, this parasitoid rapidly established but did not prevent outbreaks or spread of gypsy moths (Elkinton and Liebhold 1990, Williams et al. 1992). Within a few decades of its introduction, however, *C.*

concinnata became the dominant parasitoid of many native forest Lepidoptera in the northeastern United States (Webber and Schaffner 1926, Schaffner and Griswold 1934). It is now known to attack more than 180 species of native Lepidoptera and sawflies (Symphyta) (Arnaud 1978), and has been implicated in the decline of several giant silk moths (Saturniidae) (Boettner et al. 2000, Kellogg et al. 2003).

Compsilura concinnata is often cited as a prime example of a biological control agent that should never have been introduced (Simberloff and Stiling 1996, Strong and Pemberton 2000a, b), and various authors have advocated a major revision of policies governing the introduction of biological control agents (Miller and Aplet 1993, Simberloff and Stiling 1996, Follet and Duan 2000, Strong and Pemberton 2000a, b). The revised policies would include enhanced host-range testing of candidates for introduction and the rejection of generalist natural enemies such as *C. concinnata*. Although proponents of biological control argue that such generalist species would never be introduced today, examples exist of recent introductions of generalist species such as *Pimpla disparis*, an ichneumonid parasitoid first released in the 1970s and introduced repeatedly in subsequent years to control gypsy moth

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(Schaefer et al. 1989), including quite recently (Anonymous 2006).

In North America, a handful of apparently successful invasive species have inexplicably declined to very low numbers or eventually have become extinct (Simberloff and Gibbons 2004). One such species is the browntail moth, *Euproctis chrysorrhoea* (Lepidoptera: Lymantriidae). Accidentally introduced to North America and first discovered near Boston, Massachusetts, USA, in 1897 (Fernald and Kirkland 1903), the browntail moth (hereafter BTM) spread rapidly, reaching high population densities across a large region of northeastern North America (Fig. 1) (Burgess 1923). In addition to the widespread defoliation of many tree species, the larvae possess urticating hairs that cause a severe skin rash in humans (Blair 1979) and even caused the death of a few early researchers (Schaefer 1974). Early researchers considered it a greater invasive threat than the gypsy moth, and launched an ambitious, but apparently futile, control effort based primarily on mechanical removal of overwintering larval colonies (Fernald and Kirkland 1903). After 1914, however, BTM populations began an enigmatic decline (Burgess 1923) and eventually disappeared from most of their introduced range in North America. BTM is currently restricted to coastal enclaves at the tip of Cape Cod, Massachusetts, and the islands and peninsulas of Casco Bay in Maine, where high densities have persisted for decades (Fig. 1) (Schaefer 1974).

The decline of BTM followed the 1906–1910 introduction and establishment of several European parasitoids in North America for the control of both gypsy moth and BTM (Howard and Fiske 1911). These included three species of tachinid flies (Diptera): *Townsendiellomyia nidicola* and *Carcelia laxifrons*, both BTM specialists, and *C. concinnata*, an extremely polyphagous generalist species. As the threat posed by BTM receded, interest in this invasive species waned. Since the 1920s, with one notable exception (see Schaefer 1974), no research has been conducted on the population ecology of BTM in North America. Schaefer (1974) found relatively low parasitism of BTM (8–23%) by these tachinids in the sand dune habitats of Cape Cod and near Casco Bay. As a result, he concluded that natural enemies were not responsible for the decline of BTM in North America.

In contrast to Schaefer's (1974) findings, research in the 1920s by Burgess and Crossman (1929) showed that these tachinids, especially *C. concinnata*, caused substantial mortality of BTM, although with high between-site variability. When we partitioned the Burgess and Crossman data by collection localities into coastal and inland sites, a previously unrecognized pattern was evident. Combined parasitism by all three tachinid species in inland habitats was about twice as high as that in the coastal sites (Table 1), and parasitism by *C. concinnata* was five times as high inland. The overall levels of parasitism by tachinids at coastal sites (~20%) reported by Burgess and Crossman were comparable to

what Schaefer (1974) reported for Cape Cod and Casco Bay in 1972–1973.

Examination of historical BTM distribution on Cape Cod (Fig. 1, inset), as recorded by Schaefer (1974), reveals another puzzling pattern. The populations were restricted to sand dune habitats at the tips of peninsulas, even though beach plum, *Prunus maritima*, the favored host of BTM on Cape Cod (Schaefer 1974), grows in the sand dunes and in the scrub vegetation along the entire coast of Cape Cod, as well as in openings in the forested habitat inland. These sand dune habitats are sparsely vegetated, in contrast to the high plant diversity inland and in areas of coastal scrub. *Compsilura concinnata* is multivoltine (four generations per year) and requires alternate lepidopteran hosts in late summer and fall after completing a generation on early-season hosts such as gypsy moth or BTM (Culver 1919). Although early-instar BTM are present in this habitat in late August and September, neither we nor Schaefer (1974) have ever reared *C. concinnata* from early-instar BTM in late summer or from larvae reared from overwintering webs. We suspect that BTM larvae at this stage are too small for *C. concinnata* to attack. Our research previously showed that *C. concinnata* aggregates into experimental populations of gypsy moth from surrounding forest (Gould et al. 1990). At the tips of peninsulas on Cape Cod, there are no forests nearby. As a result, we suspected that the sand dune habitats where BTM occurs at high density might constitute enemy-free space (Jeffries and Lawton 1985), without tachinids that might cause high mortality at inland sites with more diverse vegetation.

Our preliminary observations confirmed Schaefer's (1974) finding that high densities of BTM were found mainly in the sand dune habitats of Cape Cod. Based on the evidence, we hypothesized that the current pattern of BTM distribution could be explained by higher tachinid parasitism in inland vs. sand dune habitats, and that areas currently infested with BTM have lower plant diversity than uninfested areas.

To test the hypothesis that the current distribution of BTM on Cape Cod is due to reduced parasitism from *C. concinnata*, we established replicate experimental BTM populations in inland habitats from which BTM had been extirpated, as well as in sand dune habitats within the coastal enclave where relict BTM populations persist. We also established experimental populations in BTM-infested areas of coastal scrub immediately adjacent to BTM-infested sand dune habitat, as well as uninfested areas of coastal scrub farther from this sand dune habitat (Fig. 1, inset). We assessed whether areas infested with BTM differ in terms of plant diversity and percent cover of vegetation by simultaneously conducting vegetation surveys in the habitats surrounding our experimentally created populations.

METHODS

Browntail moth life history

BTM larvae hatch in August, feed communally in late summer, and then overwinter as second or third instars

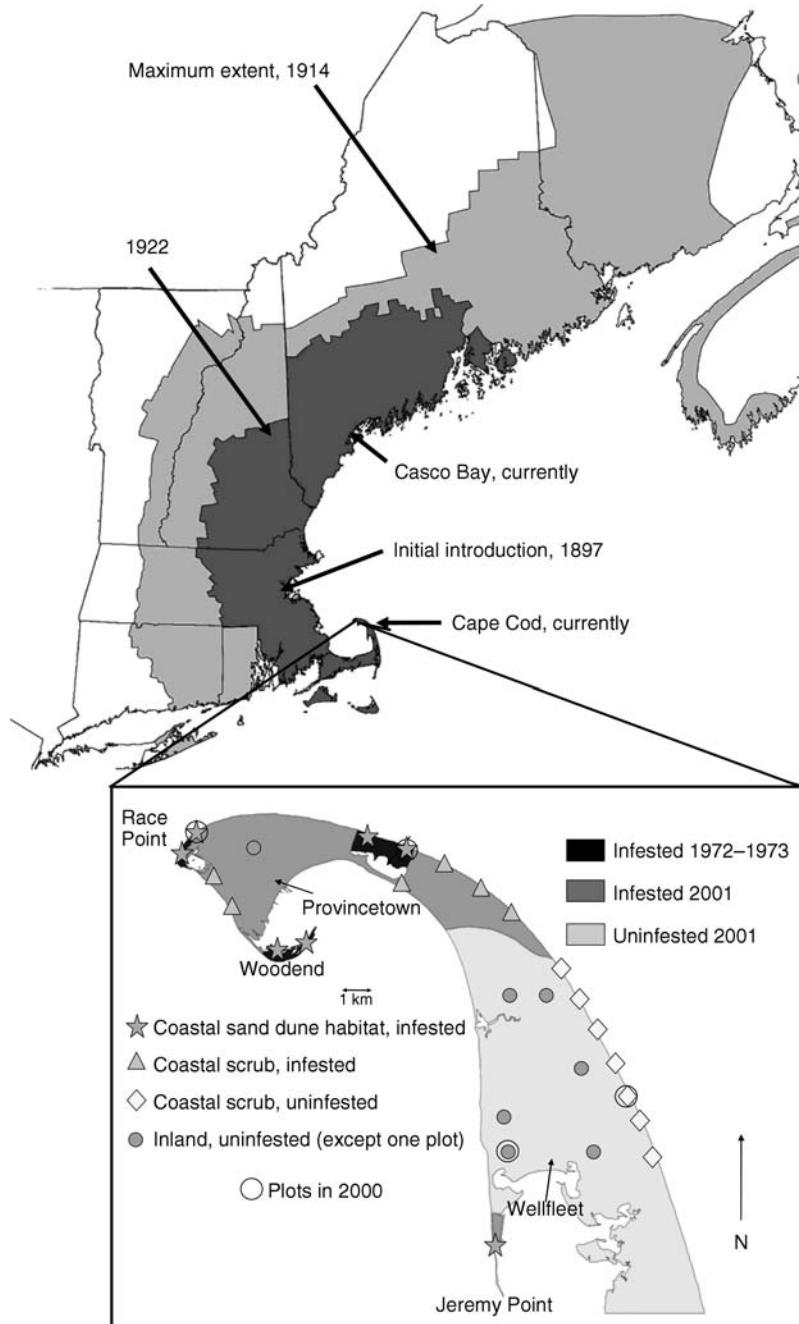


FIG. 1. Distribution map showing spread of BTM across New England to a maximum extent in 1914 (light shading) and its subsequent retreat to coastal enclaves. Dark shading indicates BTM distribution in 1922 (redrawn from Burgess [1923]). Inset: Outer Cape Cod showing plot locations of experimentally created BTM populations in the region generally infested (intermediate gray) or uninfested (light gray) with BTM in 2000 and 2001. Areas marked with the darkest shading show BTM distribution recorded in 1972–1973 by Schaefer (1974). These areas are sand dune habitats, which still contain the highest densities of BTM. Symbols indicate locations of experimental BTM populations in different habitat types.

inside communal “winter webs” that they spin on the tips of infested branches. In early spring, larvae emerge and resume feeding, completing their development and pupating in late June (Fernald and Kirkland 1903).

Establishing the experimental BTM populations and determination of mortality agents

The experiment was conducted on Cape Cod, Massachusetts, within the historically invaded range of

TABLE 1. Percentage of parasitism by tachinid parasitoids of browntail moth in coastal and inland New England habitats in 1923 (modified from Burgess and Crossman [1929]).

Location	<i>Compsi- lura concin- nata</i>	<i>Carcelia laxifrons</i>	<i>Townsendi- elliomyia nidicola</i>	Total tachinids
Coastal habitat				
Brewster, MA	3	7	27	37
Bourne, MA	5	22	29	56
Hampton, NH	1	5	6	12
Kingston, MA	0	0	13	13
Newbury, MA	53	3	1	57
Rowley, MA	28	2	8	38
Salisbury, MA	2	1	3	6
Sandwich, MA	0	0	18	18
Scituate, MA	1	0	19	20
York, ME	0	3	1	4
Mean, coastal	9.3	4.3	12.5†	26.1
Inland habitat				
Andover, MA	63	0	2	65
Burlington, MA	77	0	10	87
Dedham, MA	16	0	19	35
E. Kingston, NH	45	0	9	54
Sherborn, MA	66	2	1	69
Stratham, NH	13	0	0	13
Weston, MA	20	0	0	20
Mean, inland	42.9	0.3	5.9	49

Notes: Coastal towns border the Atlantic Ocean. Inland towns are all ≥ 10 km from the Atlantic Ocean. The means for both coastal and inland habitats are indicated by boldface type. Two-letter abbreviations are used for states in all cases: MA, Massachusetts; NH, New Hampshire; ME, Maine.

† We believe that the apparent higher parasitism by *T. nidicola* in coastal vs. inland towns is an artifact of how Burgess and Crossman (1929) estimated parasitism. See Appendix A for a full discussion.

BTM and one of the two areas where this species still persists. We utilized areas both within and outside of the current distribution of BTM (Fig. 1, inset). Four different habitat types were selected for the experiment: (1) coastal sand dune where BTM still occurs, often at high density; (2) coastal scrub habitat, which occurs immediately adjacent to the coastal sand dune habitat and has low to moderate BTM density; (3) uninfested coastal scrub habitat farther south from the infested area; and (4) uninfested inland habitat at least 1 km from the coast (Fig. 1, inset).

Prior to web deployment on beach plum, *Prunus maritima*, the favored host of BTM on Cape Cod (Schaefer 1974), at the infested sites, we counted and removed naturally occurring winter webs on beach plum and other vegetation within 4 m of beach plums on which we deployed BTM. We collected overwintering webs prior to larval emergence from Wood End, Massachusetts (Fig. 1, inset) in early spring of 2000 and 2001 by clipping winter-web-infested branch tips from beach plum. In both years we deployed webs in late March by attaching the clipped branch tips containing the webs to the target beach plum bushes with twist ties.

Experimental design: year 1

In 2000 we designed an experiment to test simultaneously for differences in mortality between habitats and for density dependence. We used two uninfested sites (one inland and one coastal with diverse vegetation) and two infested sites (both coastal sand dune habitat). At each site we selected 14 beach plums spaced at least 10 m apart along a single transect. On each beach plum we deployed 2.5, 5, 10, 20, 40, or 80 winter webs (~ 1900 , 3800, 7500, 15 000, 30 000, or 60 000 BTM larvae) with two replicates for each web density that were assigned to the bushes at random. These numbers are realistic and span the range of BTM densities we have observed on infested beach plum bushes on Cape Cod.

Experimental design: year 2

In 2001, we focused exclusively on documenting habitat effects. We used six sites within each of the four habitat categories and deployed a constant density of 20 winter webs ($\sim 15 000$ larvae) on four beach plums at each site. To get a precise estimate of the number of larvae released in 2001, we randomly selected 30 webs from the main collection site (Wood End) in early spring and held them individually inside plastic bags at room temperature in the laboratory. The larvae were counted as they emerged. A mean of (\pm SE) 767 ± 92 larvae emerged from each winter web.

In the fall or winter of both years following release at each site in the uninfested region, we searched for, counted, and removed all winter webs within a 50-m circular plot centered on the bushes on which we had deployed webs the previous spring. We did this in order to detect and remove any BTM offspring from these populations and to prevent any accidental reintroductions of BTM in areas where they did not then occur. We did not survey sites in the infested region because we had no way of determining whether the webs were naturally occurring or were the progeny of our deployed populations.

Collection and rearing of BTM larvae from the plots

In 2000, following larval emergence, we collected 50 larvae at two-week intervals from each bush within the plots. In 2001, we collected 50 larvae from each plot at two-week intervals. Larvae were returned to the laboratory and each one was placed on artificial diet in a 59-mL plastic cup. The artificial diet was based on the eastern tent caterpillar (*Malacosoma americanum*) diet from Bioserv (Frenchtown, New Jersey, USA) incorporating 25% dried and powdered foliage of black cherry, *Prunus serotina*. Larvae were reared on this diet until death or successful completion of development and adult emergence. In 2001 we made an additional collection of BTM pupae. These pupae were held individually in 59-mL cups until the emergence of BTM adults or parasitoids was complete.

Estimation of mortality

We tabulated the fraction of BTM larvae (both years) and pupae (2001 only) that died and determined the cause of death by identifying the species of parasitoids emerging from the larvae or by dissecting cadavers of larvae. We used a Wild M5A (Amphotech, Limited, Beverly, Massachusetts, USA) light microscope (60×–500×) to identify parasitoid adults (or pupae in the case of *Carcelia laxifrons*), which was done using the keys of Sellers (1943), Simons et al. (1974), and Wood (1987). Identification of tachinids was confirmed by Norm Woodley of the National Museum of Natural History–USDA Systematic Entomology Laboratory. We used the distinctive pupal stage to identify *C. laxifrons*, because the adults do not emerge until the following spring, but we confirmed this identification with adults that we reared from pupae held over the winter.

We used an American Optical One-Fifty (100×–1000×) microscope (AO Reichert, Buffalo, New York, USA) to identify any larvae that died from either of two diseases known to attack BTM: *EcNPV*, a nuclear polyhedrosis virus disease (Cory et al. 2000), and *Entomophaga aulicae*, a fungal pathogen (Hajek et al. 1991). Larval cadavers that yielded no emerged parasitoids, had none present following dissection, or contained no identifiable disease agents were classified as unknown mortality. We calculated the total larval mortality due to each agent through the use of standard mathematical techniques (Varley et al. 1973, Royama 1981, Bellows et al. 1992, Elkinton et al. 1992) that correct for the obscuring effects of multiple mortality agents acting simultaneously (see Appendix A).

Statistical analysis

We used general linear models Proc GLM in the SAS/STAT User's Guide 9.1 (2003) to test for effects of density and habitat type on mortality from parasitoids. To test for habitat effects we combined the data from both years, treating each plot as a replicate (28 plots total). Our GLM had habitat and year as main effects along with habitat * year interactions. The dependent variable in these analyses was cumulative mortality (c) from each cause of death (see Appendix A) transformed using arcsine (c)^{1/2}. We used Tukey's honestly significant differences test (hsd) (SAS/STAT 2003) to separate significant differences in parasitism between habitat types. To analyze the year 2000 data for density effects, we treated collections from each bush as a replicate; the GLM was density per bush nested within habitats, where we pooled the two plots from the sand dune habitat into a single habitat category. We also used GLM to determine if there was a significant difference in parasitism (transformed to arcsine square root) between inland and coastal sites in the Burgess and Crossman (1929) data (Table 1). We used the same statistical procedures (PROC GLM and Tukey's hsd test [SAS/STAT 2003]) to test for significant differences between habitats in the number of plant species and in the

percent cover derived from the vegetation sampling data described below.

Vegetation sampling

In 2001, we quantified diversity of vegetation in each of the four habitats in order to assess whether sand dune habitats had lower diversity and density of vegetation than the coast scrub and inland habitats. From the center of each of the 24 BTM release plots, we extended a 50-m transect line perpendicular to the coastline in an inland direction. We randomly selected five 1-m segments along each transect where we identified and counted all individual plants above or below each line segment and estimated the percentage of the segment covered or intersected by the canopy of each plant. Summing the total number of plant species counted on all five segments and averaging the percentage of each segment covered yielded an estimate of the number of plant species and the percent cover for each site.

RESULTS

Analysis of historical data

Differences in parasitism rates between inland and coastal towns evident in Table 1 were significant for *C. concinnata* ($F_{1,15} = 12.98$, $P = 0.003$), *C. laxifrons* ($F_{1,15} = 5.22$, $P = 0.037$), and *Townsendiellomyia nidicola* ($F_{1,15} = 12.98$, $P = 0.003$) and were marginally significant for total parasitism ($F_{1,15} = 4.18$, $P = 0.059$). The lower parasitism level for *T. nidicola* in inland towns is probably due to high levels of parasitism by *C. concinnata* and *C. laxifrons*, parasitoids that emerge prior to *T. nidicola* and would likely kill any BTM larvae also parasitized with *T. nidicola* (see Appendix A for a more detailed explanation of this issue).

Winter web density in areas with experimentally created populations

We observed the highest densities of BTM at the same locations (Fig. 1), as did Schaefer (1974) three decades ago. Before releasing BTM in the plots in 2001, we recorded and removed 69.2 ± 19.6 winter webs per sample area (mean ± 1 SE) in the sand dune habitat, 3.3 ± 1.3 winter webs in the adjacent BTM-infested coastal scrub, and no winter webs in either the uninfested coastal scrub or inland habitats (Fig. 1, inset).

BTM survival in experimentally created populations

Survival of BTM larvae in uninfested regions was extremely low, with progeny found only at only three of 14 sites. Conspicuous reductions in density of the experimental populations in the uninfested areas corresponded with peak tachinid emergence from the sampled BTM larvae. In the fall and winter following release of BTM in 2000, we found and removed one web at the inland site and seven webs at the coastal site. Following release in 2001, we found one web at one inland site and none at any of the others. We found no webs at any of

the six coastal uninfested sites. These numbers compare with the 310 and 80 webs we had deployed at each site in 2000 and 2001, respectively. We made no such counts at sites in the BTM-infested region, because we could not discriminate between the progeny of our experimental populations and those of the abundant naturally occurring populations.

Tachinid parasitoids *C. concinnata* and *C. laxifrons* accounted for most of the parasitism of BTM larvae (Fig. 2). In the 2000 density manipulation experiment, there was no effect of winter web density on parasitism by *C. concinnata* ($F_{3,32} = 0.20$, $P = 0.89$), *C. laxifrons* ($F_{3,32} = 2.21$, $P = 0.11$), or on unknown mortality ($F_{3,32} = 0.64$, $P = 0.60$) (see Appendix B).

BTM parasitism by *C. concinnata* and *C. laxifrons* differed significantly between habitat types when analyzed by year (*C. concinnata*: 2000, $F_{2,32} = 103$, $P < 0.001$; 2001, $F_{2,20} = 8.89$, $P < 0.001$) (*C. laxifrons*: 2000, $F_{2,34} = 12.56$, $P < 0.001$; 2001, $F_{2,20} = 17.65$, $P < 0.001$) and in the combined-year analysis (*C. concinnata*: $F_{3,23} = 103$, $P < 0.001$; *C. laxifrons*: $F_{3,23} = 16.63$, $P < 0.001$). In the sand dune habitat, BTM experienced lower mortality than in the other three sites (Tukey's hsd test, $P < 0.05$) from both tachinids together and from *C. concinnata* alone (Fig. 2). *Compsilura concinnata* was almost entirely absent from the sand dune habitat (Fig. 2A), but that species was the dominant source of mortality at inland sites (Fig. 2B). Mortality in coastal scrub sites was dominated by *C. laxifrons* in areas with and without natural BTM populations (Fig. 2C, D). Mortality from this species and from both tachinids together did not differ between BTM-infested and uninfested coastal scrub sites (Tukey's hsd test, $P > 0.05$). We recorded an average of $13.5\% \pm 1.7\%$ parasitism from *T. nidicola* (see Table 1), a BTM specialist tachinid parasitoid, at all sites. Because this species oviposits in neonate BTM larvae in late summer, parasitism had already occurred prior to our collection and deployment of the winter webs. Thus, we were unable to measure any habitat differences in parasitism by this species. We observed no mortality from either *EcNPV* or from *Entomophaga aulicae* among the cadavers dissected from our collections.

Pupal parasitism in 2001 was much lower than larval parasitism (Fig. 2) and was dominated by two hymenopteran parasitoids. The exotic ichneumonid *Pimpla disparis* caused the highest level of pupal parasitism (2.4–7.6%). There were no significant differences in parasitism between habitats for this species ($F_{3,10} = 1.23$, $P = 0.35$). The only other pupal parasitoid, the native ichneumonid *Itopectis conquisitor*, caused between 0.1% and 0.8% pupal mortality and did not differ between habitats ($F_{3,10} = 0.44$, $P = 0.73$).

Results of vegetation survey

The BTM-infested coastal scrub close to the sand dune habitat (Fig. 1, inset) and the uninfested coastal scrub farther away differed in neither the number of

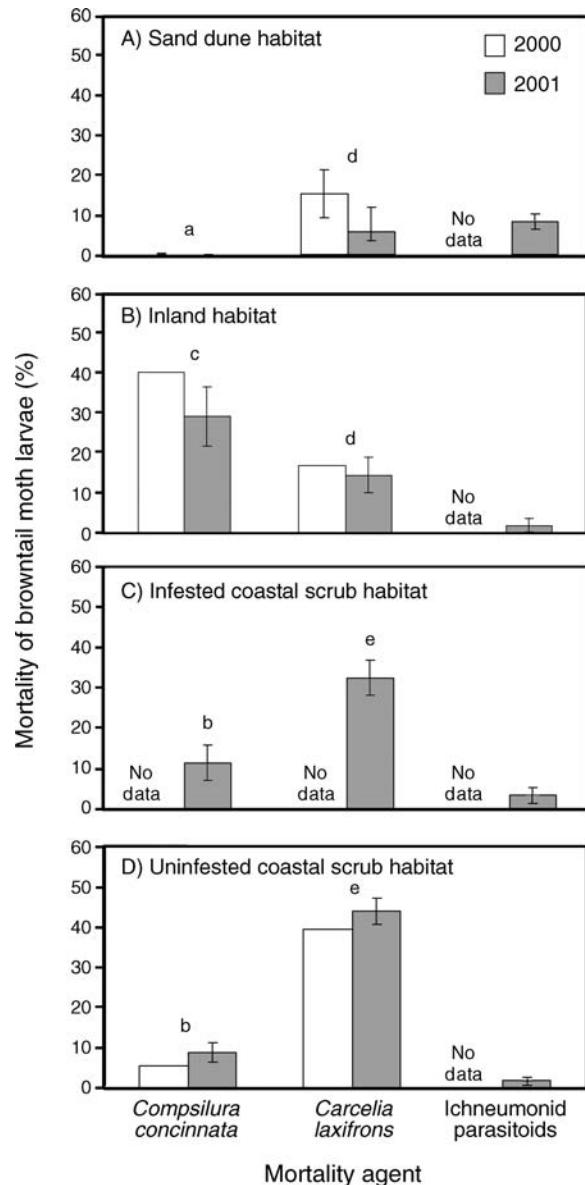


FIG. 2. Cumulative percentages of parasitism by two tachinid parasitoids of BTM larvae (*C. concinnata* and *C. laxifrons*) and by ichneumonid parasitoids of BTM pupae collected from beach plum in experimentally created populations on Cape Cod in different habitats (see Fig. 1, inset). The four habitat categories were: (A) sparsely vegetated coastal sand dune infested with BTM; (B) diversely vegetated inland habitat >1 km from the coast without BTM; (C) coastal scrub habitat with diverse vegetation, infested with BTM; and (D) coastal scrub habitat without BTM. In 2000, we had two plots in the infested sand dune habitat and one each in the uninfested coastal and inland habitats. The same lowercase letters above the bars indicate means within each species not significantly different by the Tukey's hsd test ($\alpha = 0.05$) in the analysis that combined data from both years. "No data" means there were no plots in that category in that year: in 2000 there were no plots in the infested coastal scrub habitat and we made no pupal collections, so we have no data on hymenopteran parasitoids from that year.

plant species ($F_{1,11} = 1.39$, $P = 0.26$) nor the percent cover of vegetation ($F_{1,11} = 0.37$, $P = 0.55$). We thus treated the BTM infested and uninfested coastal scrub habitat as a single habitat category in subsequent comparisons with the sand dune and inland habitat. In the resulting three habitat types there were significant differences in the mean number of plant species ($F_{3,22} = 5.73$, $P = 0.010$) and in our estimates of percentage vegetation cover ($F_{3,22} = 14.86$, $P < 0.001$) (see Appendix C). The sand dune habitat had significantly fewer plant species (6.2 ± 1.1 species) compared with 12.5 ± 0.8 species in the coastal scrub and 10.8 ± 2.4 species in inland habitats, which were not statistically different from one another (Tukey's hsd test, $P > 0.05$). Similarly, mean vegetation cover was $19.8\% \pm 3.5\%$ in the sand dune habitat, which was significantly lower than the $38.9\% \pm 2.3\%$ cover in the coastal scrub habitat and the $39.9\% \pm 4.1\%$ cover in the inland habitat.

DISCUSSION

Our results support the hypothesis that high-density BTM populations persist in dune habitats with sparse vegetation because mortality from tachinids is markedly reduced in this environment. The generalist parasitoid *C. concinnata* caused substantial mortality only at inland sites, a finding consistent with our hypothesis and our reanalysis of historical data (Table 1). *Compsilura concinnata* is multivoltine and summer cohorts require alternate lepidopteran hosts after completing a generation on early-season hosts such as gypsy moth or BTM (Culver 1919). The results of our vegetation survey indicate that sand dune habitats are significantly lower in plant density and have significantly lower species diversity than the other two habitat types. The lower density and relative lack of diversity of plant species in sand dune habitats may cause a reduction in alternate hosts for *C. concinnata*, thus reducing its population density substantially. As a result, the sand dune habitats where BTM occurs at high density may constitute enemy-free space (Jeffries and Lawton 1985) from tachinids that cause high mortality inland and in diversely vegetated coastal sites. Studies of BTM in Great Britain found similarly that BTM occurs mainly in coastal habitats with low vegetational diversity, except in outbreak years when populations spread across most of southeast Britain (Sterling and Speight 1989). There are of course other possible explanations for the absence of *C. concinnata* in the sand dune habitat, including absence of adequate nectar resources for adult flies and the harshness of the physical environment (e.g., exposure to salt spray).

Our experimental results show that parasitism by *C. concinnata* reaches high levels 1–2 km from the coast. This finding may explain the high levels of parasitism occurring in two out of 10 coastal towns in the historical data set (Table 1). We defined coastal towns as those bordering the Atlantic ocean. However, towns in Massachusetts are typically 7–10 km across, and we do

not know where in the towns Burgess and Crossman made their BTM collections. It is certainly possible that BTM from the two coastal towns with high parasitism rates were collected at sites several kilometers from the coast.

The univoltine *C. laxifrons* occurred at all sites and was the dominant species in coastal scrub sites with diverse vegetation. This species is thought to specialize on BTM (Schaefer 1974, Arnaud 1978), so its ability to locate our experimental populations far from naturally occurring infestations indicates extraordinarily good dispersal and host-finding capabilities. Our finding that *C. laxifrons* did not cause high parasitism in the sand dune habitat (Fig. 2A) implies that it did not generally disperse into the sand dunes from the nearby infested coastal scrub (Fig. 2C). This lends credence to an alternative hypothesis that *C. laxifrons* may persist in the absence of BTM by utilizing an as yet unidentified alternate host in the uninfested areas.

The occurrence of BTM populations in some forested and coastal scrub habitats on Cape Cod in close proximity to the infested sand dune habitat near Provincetown (Fig. 1, inset) is likely due to a source–sink dynamic (Pulliam 1988). According to this view, outflow of moths from the high-density sand dune populations colonize these nearby forested and coastal scrub areas, sustaining populations that could not persist farther from a source population due to high parasitism. This explanation is supported by the occurrence of higher densities of BTM (69.2 ± 19.6 winter webs per sample area) recorded in sand dune habitat compared with the 3.3 ± 1.3 winter webs per sample area in the coastal scrub. Source–sink dynamics have been posed to explain the persistence of outbreak populations of the western tussock moth, *Orgyia vetusta*, in the coastal scrub habitat of California (Harrison 1997). In that system, it is the dispersal of tachinids from patches of high host density that prevents populations of the poorly dispersing tussock moth from expanding.

The lack of density-dependent BTM mortality from *C. concinnata* in the 2000 experiment seems inconsistent with the results of previous research that experimentally manipulated gypsy moth population density and found strong spatially density-dependent mortality from *C. concinnata* (Gould et al. 1990). However, our study and that of Gould et al. differ in terms of spatial scale. Gould et al. (1990) created hectare-sized populations of gypsy moths by releasing up to 1.4×10^6 gypsy moth eggs/ha. Our experiments manipulated BTM densities on individual bushes, although the overall BTM densities (up to 60 000 BTM per bush, where each bush occupied ~ 4 m²) were higher than achieved by Gould et al. In either case, it is not clear what the presence or absence of spatial density-dependent parasitism implies regarding the ability of *C. concinnata* to exhibit temporal density-dependent parasitism or to stabilize gypsy moth or BTM populations.

Several species of native giant silk moths (Saturniidae) have become rare in or have been extirpated from northeastern North America (Tuskes et al. 1996, Boettner et al. 2000). Recent research strongly implicates *C. concinnata* in the decline of at least some of these species (Boettner et al. 2000, Kellogg et al. 2003). Our results suggest that *C. concinnata* has had another major and previously unknown beneficial impact, stopping the invasion of a noxious pest, the BTM. In fact, it is the affinity of *C. concinnata* for so many species of native Lepidoptera in northeastern deciduous forests that might have allowed it to persist at densities high enough to extirpate BTM from much of its range.

In many cases, the introduction of generalist natural enemies has caused damage to and even extinction of native fauna (Strong and Pemberton 2000a, b). With *C. concinnata*, we have evidence of powerful effects on both nontarget native species and on an economically important invasive species. It is noteworthy that another introduced generalist, *Pimpla disparis*, has become a significant source of BTM pupal mortality. As far as we know, this is the first record of *P. disparis* as a parasitoid of BTM. We do not know whether this new parasitoid will alter numbers or dynamics of BTM, although the maximum value of 8% (Fig. 2) that we recorded in any habitat is probably too low to have much influence. Despite the well-documented threat to native biodiversity from introductions of generalist natural enemies, releases of *P. disparis* continued unabated until very recently (Anonymous 2006).

We and others have advocated that proposals to introduce natural enemies be subject to a stringent review process that would weigh the potential risks and benefits (Arnaud 1978, Miller and Aplet 1993, Simberloff and Stiling 1996, Boettner et al. 2000, Follet and Duan 2000, Strong and Pemberton 2000a, b). Despite the apparent success at controlling BTM by the introduction of *C. concinnata*, we still are strong proponents of biological control efforts that focus on carefully selected specialist species rather than generalist natural enemies, because the impact of the latter on nontarget hosts is almost always both unpredictable and irreversible. Nonetheless, in some cases, such as the one described here, generalist natural enemies may effectively regulate invasive pest species (Symondson et al. 2002).

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APPENDIX A

A description of the calculation of mortality and a table showing percentage parasitism based on the observed percentage that died and on the estimated marginal attack rate by tachinid parasitoids of browntail moth in coastal and inland New England habitats, 1923 (*Ecological Archives* E087-161-A1).

APPENDIX B

A figure showing larval mortality from *C. concinnata*, *C. laxifrons*, and unknown causes plotted vs. the number of winter webs deployed per bush in 2000 (*Ecological Archives* E087-161-A2).

APPENDIX C

A summary of line transect vegetation survey of three habitat types with and without browntail moth (*Ecological Archives* E087-161-A3).