Ecology of Case-Bearing Moths (Lepidoptera: Coleophoridae) in a New England Salt Marsh

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ABSTRACT   The natural history, oviposition, feeding behavior, and parasitism of *Coleophora caespititiella* Zeller and *C. cratipennella* Clemens in a Rhode Island salt marsh are described. *C. cratipennella* is univoltine and feeds only on the rush *Juncus gerardi* Loisel. *C. caespititiella* is bivoltine; the spring generation larvae feed on *J. gerardi* and the fall generation larvae feed on the annual *Salicornia europaea* L. This is the first report of bivoltinism in this genus and the first report of a single *Coleophora* species feeding on plants in these two plant families. In *J. gerardi* monocultures, oviposition frequency increased with increasing flowering culm density and flower density per culm. In *S. europaea* monocultures, oviposition frequency initially increased with plant density, but moths appear to be satiated by high-density *S. europaea* stands. Overall, larvae infested 22% of the *J. gerardi* seed capsules and reduced seed set in these infested capsules by 60%. *C. caespititiella* larvae consumed from 4 to 25% of the seeds of *S. europaea*. Larvae were rarely seen to move from the flowering culm or plant where they were first encountered. Eighteen percent of *C. cratipennella* larvae and 10% of first-generation *C. caespititiella* larvae were parasitized by an unidentified ichneumonid wasp. Because these moths feed on two plant species with known asymmetric competitive interactions and consume more seeds of the dominant competitor (*J. gerardi*), the moths may mediate the competitive interactions between *J. gerardi* and *S. europaea*.

KEY WORDS   Insecta, *Coleophora* spp., feeding behavior, salt marshes

CASE-BEARING MOTHS in the genus *Coleophora* Hübner (Lepidoptera: Coleophoridae) occur worldwide in a wide range of temperate habitats (e.g., Wood 1892, Heinrich 1923, Waters 1927, McDunnough 1942, Pastrana 1963, Randall 1982b, Baldizzone 1983). These minute moths are commonly univoltine (Heinrich 1923) and monophagous (Jermy 1984), although within this genus many distantly related plant species are used as larval hosts (Heinrich 1923). Several *Coleophora* species are of economic importance, either as agents of biological control (Goeden & Ricker 1979) or as pests of economically important plants (Bryant & Raske 1975; Raske & Bryant 1977a,b; Pearson 1980). In contrast to the large body of information available for economically important species, relatively little is known of the biology of other Coleophoridae (Jordan 1958, 1962; Randall 1982a,b, 1986). For Coleophoridae lacking in economic importance in the United States, basic facts of the natural history of these moths are unknown.

Here, I describe the natural history, larval distribution, feeding behavior, and frequency of larval parasitism of two species of *Coleophora*, *C. caespititiella* Zeller and *C. cratipennella* Clemens (taxonomy follows Heinrich 1923) in a Rhode Island salt marsh. Specifically, I document the distribution of these moths and their respective host plants, quantify their effects on the seed production of their host plants, examine experimentally the

effects of variation in vegetation pattern on oviposition and feeding behavior, and examine the frequency and seasonality of attack on these moths by a parasitic wasp.

Materials and Methods

Study Site. These studies were conducted at Rumstick Cove, a protected embayment of Smith Cove in Barrington, Bristol County, Rhode Island. Like other New England salt marshes, the vegetation is of low diversity, and the dominant perennial plants occur in distinct zones delineated by the tides (Bertness & Ellison 1987). Below mean high water (MHW), the "lower marsh" is a virtual monoculture of the cordgrass *Spartina alterniflora* Loisel (Gramineae). Above MHW, the "upper marsh" is a mosaic of *Spartina patens* Muhl. (Gramineae) and *Distichlis spicata* (L.) Greene (Gramineae) (+1.2 to +1.4 m mean tidal height). These species are replaced above 1.4 m mean tidal height by the rush *Juncus gerardi* (the "*Juncus* zone"). Throughout the upper marsh, the annual succulent *Salicornia europaea* is found commonly in recently disturbed areas (Bertness & Ellison 1987, Ellison 1987). The flowering and fruiting phenology of these species is described in detail by Bertness et al. (1987). *Juncus* begins flowering in late April and its seeds dehisce in late July. The grasses flower and set seed in midsummer. *Salicornia* does not

commence flowering until late August, and seeds are dispersed in October (Bertness et al. 1987, Ellison 1987).

Like the marsh plant community, the marsh insect community is relatively simple (Smalley 1960, Cameron 1972, Rey 1981, Vince & Valiela 1981, Valiela et al. 1985). The most common phytophagous insects are the case-bearing moths, *Coleophora caespititiella* and *C. cratipennella*, the katydid *Conocephalus spartinae* (Fox) (Orthoptera: Tettigonidae) (Smalley 1960, Bertness et al. 1987), the beetle *Erynephala maritima* (LeConte) Blake (Coleoptera: Chrysomelidae) (Valiela et al. 1985, Ellison 1987), and the leafhopper, *Prokelisia marginata* (Van Duzee) Van Duzee (Hemiptera: Delphacidae) (Denno 1978). A third case-bearing moth, *Coleophora fagicosticella* Chambers is rare at Rumstick Cove, I encountered only five individuals of this species in 2 yr of sampling.

Moth Distribution. To determine the spatial and temporal distribution of the moth larvae, I surveyed seven permanent 30-m transects parallel to the water at 5-m intervals from MHW to highest high water (HHW). Every meter along each transect, I counted the total number of cases of each moth species in a 100-cm² quadrat and recorded the plant species on which cases were found. Transects were sampled monthly from May through September 1985.

Effect of Moths on *Juncus* and *Salicornia* Seed Production. To quantify effects of moths on *Juncus* seed production, infructescences were collected and examined for seed set and loss attributable to moths. Every 50 cm along two 20-m transects in the *Juncus*, all *Juncus* infructescences in a quadrat (10 by 10 cm) were collected in mid-July 1985. Total number of capsules and the number of capsules undamaged, attacked by moths, attacked by other herbivores (e.g., katydids), or aborted were counted for each infructescence. Capsules attacked by moths have a discrete hole where the larva attaches its case and enters the capsule, whereas those attacked by katydids have irregular tears or are shredded. Aborted capsules are small and shrivelled and show no signs of insect damage. After scoring infructescences, I counted the number of intact seeds in a randomly chosen subset of capsules from each of the four categories ($n = 100$ capsules/category).

I similarly examined *Salicornia* growing throughout the marsh in late September. Twenty-five individuals each from five moderate-density ($\approx 100/m^2$) *Salicornia* monocultures were collected. I counted the number of seeds eaten by moth larvae and the number of infructescences with aborted ovules.

Effects of Vegetation Pattern on Moth Oviposition and Feeding Behavior. The distributions of *Juncus* and *Salicornia* in the upper marsh are very different. *Juncus* occurs as a virtual monoculture above MHW, interrupted only by the disturbance-generated patches where *Salicornia* refuges (Elli-

son 1987). Moths looking for oviposition sites in early spring are searching a "sea" of *Juncus* for *Juncus* flowers (a relatively "fine-grained" environment sensu Levins [1968]), and may be influenced by local density of flowers in their search for good oviposition sites. Subsequent larval feeding behavior may similarly be affected by local seed or infructescence density.

In contrast, the second generation of moths searches for *Salicornia* in randomly-distributed (Bertness & Ellison 1987) isolated patches throughout the *Juncus* zone (a relatively 'coarse-grained' environment sensu Levins [1968]). Second-generation moth oviposition and larval distribution, therefore, is more likely to depend on *Salicornia* density within patches (i.e., resource concentration sensu Root [1973]).

In early May 1985, before emergence of the spring adult moths, 90 quadrats (10 by 10 cm, separated by 3 cm) were marked off in an area (5 by 2 m) of *Juncus* monoculture. Each quadrat was randomly assigned to one of nine treatments of a two-way factorial design. The treatments consisted of manipulating the number of flowering culms (1, 5, or control) and the number of flowers per culm (1, 5, or Control). Flowering culms and flowers were removed with small scissors when necessary to achieve the assigned frequency. The number of flowering culms in a control quadrat was 30 ± 2.3 ($\bar{x} \pm SD$), and the average number of flowers per control culm was 17 ± 4.6. All larval cases encountered in these quadrats were marked, and the number of second instars (when the case is first constructed) was used as an indicator of oviposition frequency. The cases are easily seen and censused and can be numbered with a fine rapidograph pen. Every week until just before capsule dehiscence, I located all larval cases and marked them with a unique number. In subsequent weeks, I relocated previously marked larvae and measured the (linear) distance moved. At the end of the experiment (25 July 1985), all culms in the quadrats were collected, and capsules were scored for predation, abortion, and seed number.

Two levels of variation in *Salicornia* availability were examined: patch size and plant density within patches. In late August 1984, I created 44 square patches in the *Juncus* zone. Twenty-four of the patches were 50 by 50cm, and twenty were 25 by 25 cm. Patches were created by spraying each marked patch with a general, non-persistent herbicide (Round-Up, Monsanto Company, St. Louis, Mo.). In early November 1984, patches were densely sown with *Salicornia* seeds. In May 1985, I randomly thinned the large patches to 1, 40, or 250 plants (8 replicates of each) and the small patches to 10 or 63 plants (10 replicates of each). These densities were chosen so that the density per square meter of quadrats with more than one plant would be either 160 or 1,000. Oviposition frequency was estimated as described above. Within all patches of more than one plant, 10 nonedge plants were

Table 1. Distribution of C. caespititiella and C. cratipennella across the marsh during summer 1985

Species and mo	Transect[a]			
	4	5	6	7
C. caespititiella				
May	6.5 (4.41)	6.5 (4.41)	0	12.9 (9.93)
June	19.4 (13.24)	29.0 (9.34)	16.1 (10.30)	2.9 (1.09)
July	29.0 (14.57)	43.2 (15.70)	54.8 (15.70)	93.5 (18.77)
Aug.	0	0	0	0
Sept.	38.7 (15.59)	22.6 (7.51)	64.5 (21.18)	429.0 (51.65)
C. cratipennella				
May	3.2 (3.17)	0	0	6.5 (4.41)
June	0	3.2 (3.17)	0	6.5 (4.41)
July	6.5 (4.41)	0	3.2 (3.17)	29.0 (10.39)
Aug.	0	0	0	0
Sept.	0	0	0	0

[a] For each transect, values are $\bar{x} \cdot 10^2$ ($\pm$SE) of larvae per 100-cm^2 quadrat (n = 30 quadrats per transect). No moth larvae were found in transects 1–3, so data only for transects 4–7 (in the *Juncus* zone) are presented.

randomly selected and tagged in June 1985. The solitary individuals in the low-density, large quadrats and the tagged plants in the other quadrats were censused throughout the summer for moth larvae. I followed the movement pattern of larvae on these solitary and marked plants as described above. In late September, these plants were scored for seed production.

Frequency of Parasitism on Moth Larvae. Several first-generation larvae (feeding on *Juncus*) brought into the laboratory in 1984 for rearing yielded small (8 mm long) parasitic wasps (Hymenoptera: Ichneumonidae) rather than the expected adult moths. Wasps were observed in the field ovipositing in the dorsal end of third and fourth instars in late June and early July (Fig. 1). To estimate frequency of wasp parasitism, on 15 July 1985 I enclosed 50 fourth-instar *C. caespititiella* and 50 *C. cratipennella* in fine mesh bags. Bags were examined weekly through 19 August 1985 for emergence of wasps or of adult *C. caespititiella*. Wasps were never observed or recovered from similarly caged second-generation larvae feeding on *S. europaea*.

Statistical Analyses. All data were analyzed using SPSS/PC+ version 2.0 (Norusis 1988) on an IBM-AT computer. Data were transformed when necessary to meet the assumptions of analysis of variance (ANOVA) and t tests (Sokal & Rohlf 1981). For frequency data, the nonparametric G test was employed (Sokal & Rohlf 1981).

Results

Natural History of C. caespititiella and C. cratipennella. Adults of both *Coleophora* species emerge from overwintered pupae from early May through early June and oviposit on *Juncus* buds and flowers (Fig. 1). After hatching, the larvae of these two species feed on *Juncus* seeds in June and July (Fig. 1). Captive rearings and field observations showed that first instars do not move from

their initial seed capsule and feed only on the seeds of that capsule. Second instars then construct the silk and debris cases characteristic of the Coleophoridae and move from capsule to capsule carrying the case. As the larva grows (through four instars), the case is lengthened at the proximal end. The two species are easily distinguished by their cases: *C. caespititiella* produces a white case (mean length at fourth instar, 5.5 $\pm$ 0.91 mm [$\bar{x}$ $\pm$ SD]), and *C. cratipennella* a brown one (mean length at fourth instar, 7.9 $\pm$ 0.95mm) (t = 8.41, df = 58, P < 0.001). To feed, a late instar leaves the case attached to the outside of the plant and moves into the capsule. Based on larval movement records (see below) and captive rearings, larvae can complete development on as few as five *Juncus* capsules.

Both species pupate in the soil within their cases in late July. *C. cratipennella* then enters diapause and overwinters as a pupa, but a second generation of *C. caespititiella* adults emerges in late August and oviposits in *Salicornia* flowers. These larvae feed on the developing seeds and pupate in early October. Fall larvae can complete development on 4–6 *Salicornia* seeds (in mass, one *Salicornia* seed is about equal to one *Juncus* capsule ($\approx$60 seeds). Spring larvae of both species are parasitized by an unidentified ichneumonid wasp (Fig. 1), but I have not observed these parasites attacking the second generation of larvae. Voucher specimens of these moths and the parasitoid have been deposited at Cornell University, Ithaca, N.Y. (lot no. 1197).

Moth Distribution and Abundance. Moth larvae were found only above +1.4 m mean tidal height (in the *Juncus* zone; Table 1), although *Salicornia* occurs at lower elevations (Ellison 1987). Larvae of both species were present on *Juncus* infructescences through the end of July and increased in frequency from late spring through early summer. *C. caespititiella* was more abundant than *C. cratipennella* in all transects at each census (Table 1). Larvae pupated in mid-July 1985, and second-generation larvae of *C. caespititiella* were not seen
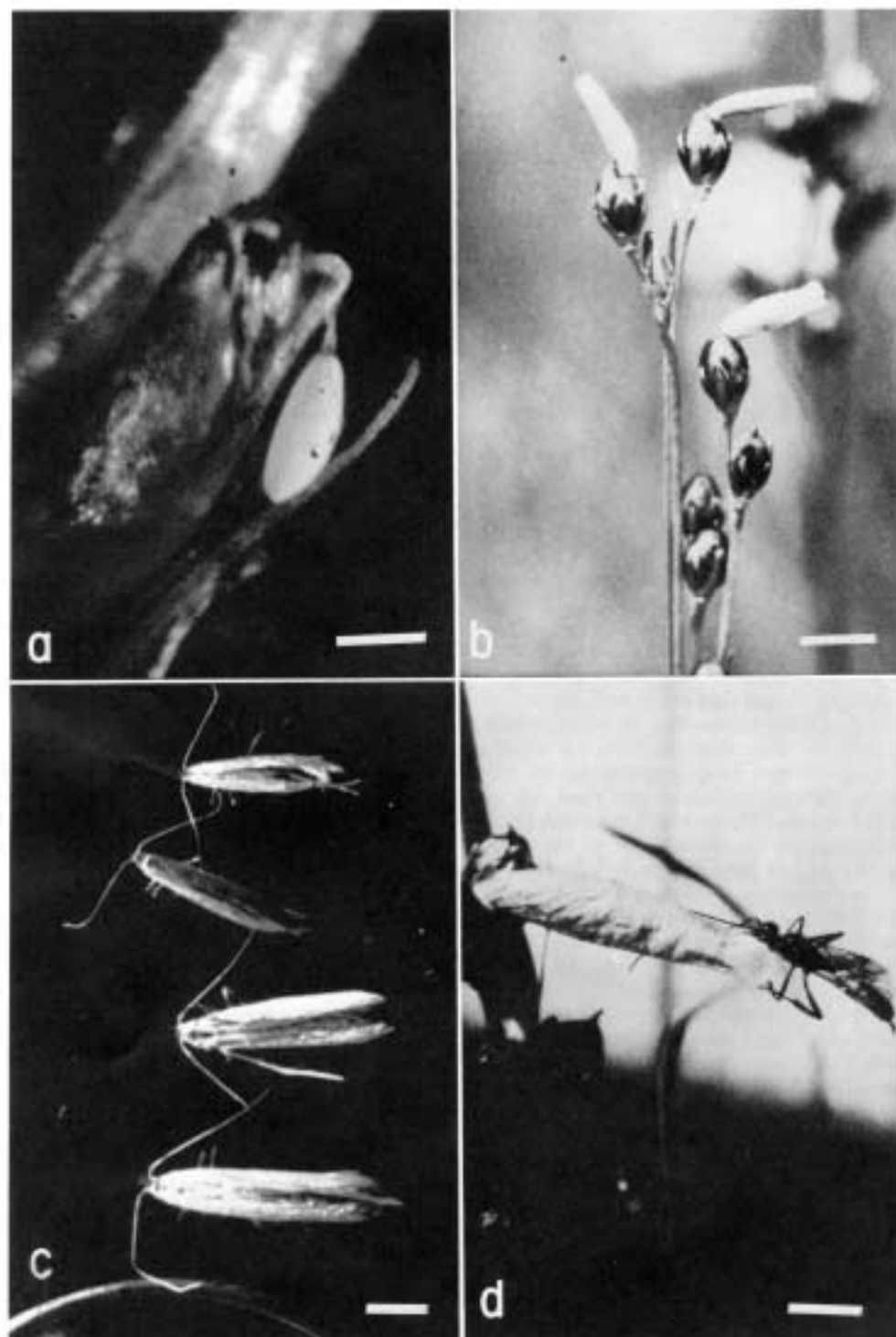
Fig. 1. Life stages of *Coleophora*. (a) *Coleophora* egg on flower bud of *J. gerardi*; scale, 1 mm (photo taken 30 May 1985). (b) Fourth-instar *C. cratipennella* on *J. gerardi* capsules; scale, 5 mm (photo taken 3 July 1985). (c) Adult *C. cratipennella* (bottom two) and *C. caespititiella* (top two) reared from pupae collected April 1985; scale, 2 mm. (d) Wasp ovipositing in *C. cratipennella* case; scale bar, 2 mm (photo taken 15 July 1985).

Table 2. Effects of changes in *Juncus* reproductive culm number and flower density on moth oviposition[a]

No. culms/ 100 cm²	No. capsules per culm		
	1	5	Control
C. caespititiella			
1	0	1	1
5	1	6	4
Control[b]	3	9	20
C. cratipennella			
1	0	2	1
5	0	5	3
Control	3	12	13

[a] Values given are the total number of second instars in each species recorded per treatment type. See text for statistics.

[b] A single *C. fagicosticella* was found in one of the control quadrats with five capsules per culm.

Table 3. Effects of changes in *J. gerardi* reproductive culm number and capsule density per culm on reproductive success[a]

No. culms/ 100 cm²	Capsules affected	No. capsules per culm		
		1	5	Control
1	Undamaged	44 (4)	35 (17)	42 (69)
	Aborted	11 (1)	6 (3)	13 (21)
	Moth	0 (0)	10 (5)	6 (10)
	Katydid	44 (4)	49 (24)	38 (62)
	Both	0 (0)	0 (0)	1 (1)
5	Undamaged	48 (21)	44 (99)	48 (262)
	Aborted	20 (9)	9 (21)	6 (32)
	Moth	16 (7)	10 (22)	8 (45)
	Katydid	11 (5)	35 (79)	37 (203)
	Both	5 (2)	1 (3)	1 (2)
Control	Undamaged	52 (14)	58 (81)	52 (222)
	Aborted	0 (0)	2 (3)	4 (15)
	Moth	22 (6)	14 (19)	10 (43)
	Katydid	26 (7)	25 (35)	33 (138)
	Both	0 (0)	1 (1)	1 (5)

[a] Values given are percentage (number) of capsules affected (undamaged, aborted, attacked by moths, katydids, or by both moths and katydids) per number of capsules per culm per number of culms per quadrat. See text for statistics.

until late August. The latter larvae occurred only on developing *Salicornia* infructescences; *Juncus* had senesced 2 mo previously.

Effect of Moths on Seed Production. Moth larvae significantly affected *Juncus* seed production. Undamaged capsules had 58.1 ± 2.34 seeds/capsule. Moths reduced seed production by 60% (19.5 ± 2.76 seeds/capsule among capsules attacked by moths, $t = 10.668$, df $= 98$, $P < 0.001$). Moths reduced *Salicornia* seed production by close to 25%. Undamaged plants produced 740 ± 137.8 seeds/plant, whereas plants attacked by moths produced 555 ± 93.4 seeds/plant ($t = 5.567$, df $= 48$, $P < 0.001$).

Effect of Vegetation Pattern on Moths. When *Juncus* inflorescence and flower density were modified, oviposition frequency was significantly affected by treatment. Oviposition frequency of both species increased with increasing culm density and increasing number of capsules per culm ($X^2 = 16.8$, df $= 4$, $P < 0.001$, G test) (Table 2). For a given density of moths, this result would be expected if adults seek oviposition sites in areas of high resource (flowering culm or capsule or both) concentration.

Forty-five percent of the capsules were either damaged by herbivores or aborted (Table 3). With an increase in the number of flowering culms per quadrat, the percentage of undamaged capsules and those with moth larvae increased, whereas the percentage attacked by katydids declined ($F = 11.587$; df $= 2$, 1613; $P < 0.001$) (Table 3). However, the number of capsules per culm did not affect final capsule condition (undamaged, aborted, or eaten: $F = 0.485$; df $= 2$, 1613; $P = 0.616$).

No differences in movement patterns were observed between the two moth species, so I discuss the larval movement pattern results pooled over the two species. In total, I tagged and followed the movement of 84 larvae in quadrats where flower and inflorescence density were manipulated. Eleven cases were not recovered at subsequent censuses, and 122 movement records were logged. The ma-

jority of tagged larvae in this manipulated area did not move over the course of the experiment. However, one larva was recovered 1 m away from its starting location (Table 3). Fifteen of the larval cases were shredded by an unknown predator.

I examined the data to see whether capsule or infructescence density had any effect on movement pattern. The movement patterns in each combination of infructescence densities (1, 5, or natural density control) and capsule per infructescence (1, 5, or natural control) were analyzed for significant differences among four movement categories: no movement, movement within infructescences, movement between infructescences in the same quadrat, and movement out of the quadrat. In two of the nine treatments moth larvae were more likely to stay in place (five infructescences, control capsule density: $X^2 = 12.393$, df $= 4$, $P < 0.005$, G test; control infructescence density, control capsule density: $X^2 = 12.997$, df $= 4$, $P < 0.005$, G test). In the remaining seven treatment combinations, there were no significant differences among larval movement categories (Table 4).

More *Salicornia* seeds per plant were available for moths in low-density patches than in high-density patches, although more total seeds were available in high-density patches than in low- density ones (Table 5). However, neither patch size nor total number of seeds per patch affected the percentage of seeds per plant consumed by moth larvae (Table 5). Within the large patches, the percentage of *Salicornia* seeds per plant consumed by moths decreased significantly at high density (Table 5).

In large *S. europaea* patches, oviposition frequency increased with increasing plant density ($F = 4.156$; df $= 2$, 165; $P = 0.017$) (Table 6). However,

Table 4. Frequency of distances moved by moth larvae in monocultures of *J. gerardi* where capsule and infructescence density were manipulated[a]

Distance moved, mm	Frequency
0	72
1–5	5
5–10	7
10–50	9
50–100	10
100–150	18
>500	1

[a] Data are pooled over both species and all treatments. See text for statistics by treatment.

although the number of second instars increased dramatically from low to intermediate density in the large quadrats (Table 6), the number of larvae declined slightly at the highest density (yet remained well above the number of larvae in the low density quadrats). In small *Salicornia* patches, there was no difference in oviposition frequency between density treatments ($F = 0.0345$; df = 1, 191; $P = 0.85$). This result, together with the slight decline in number of larvae observed at high plant density in large quadrats, may indicate satiation of moths looking for oviposition sites.

Marked *C. caespititiella* larval cases ($n = 200$) were never seen to move on any *Salicornia* plant in this experiment. Dissection of 20 randomly selected plants indicated that a single larva would leave the case and consume all the seeds in nearby infructescences. Because one larva can complete its development on 4–6 *Salicornia* seeds, movement to other infructescences rarely would be seen.

Table 5. Effects of *S. europaea* patch size on seed production and seed predation by *C. caespititiella*

Area, m[2a]	Density, no./m[2b]	No. seeds		Total no. seeds per patch (estimated)[c]	% Consumed[d]
0.0625	160	224.3	(15.45)a	2,243	8.2 (0.75)a
	1,000	93.8	(6.09)b	5,909	7.9 (1.66)a
0.25	4	3,359.3	(1,746.98)a	3,359	10.4 (5.26)a
	160	390.9	(29.75)b	9,773	9.5 (1.13)a
	1,000	60.0	(2.24)b	15,000	4.9 (1.14)b

Values given are $\bar{x}$ (SE). For each given area, values followed by different letters are significantly different ($P < 0.05$, Scheffé test for multiple comparisons among means).

[a] Area had no effect on seed production ($F = 0.097$; df = 1, 356; $P = 0.755$) or on percentage of seeds consumed ($F = 0.507$; df = 1, 356; $P = 0.477$).

[b] Density significantly affected seed production ($F = 53.049$; df = 3, 356; $P < 0.001$) and the percentage of seeds per plant consumed by moths ($F = 3.912$; df = 3, 356; $P = 0.009$).

[c] No significant relation was found between estimated total seed production per plant and percentage of seeds per plant consumed ($r = -0.69$, $P > 0.05$).

[d] Analyses on percentage seeds consumed were performed on arcsin square root-transformed data, but data are presented before transformation.

Table 6. Effects of *S. europaea* patch size on moth oviposition

Area, m[2]	Density m[-2]	Total no. larvae observed	Total no. larvae per treatment[a]	Estimated larvae m[-2b]
0.0625	160	293	293	469
	1,000	45	284	454
0.25	4	231	231	924
	160	281	1,124	562
	1,000	39	975	488

Values given are the total number of second instar *C. caespititiella* per treatment type (summed over all quadrats in each treatment) and an estimate of the total number of larvae expected to be encountered in a 1-m[2] patch of each density.

[a] Because all quadrats except the lowest-density large quadrats were subsampled (see Methods), total larvae per treatment is extrapolated from the number of larvae actually observed in the subsample.

[b] Because all quadrats are smaller than 1 m[2], the number of moths per square meter is an upward estimation.

Frequency of Parasitism. Eighteen percent of the bagged *C. cratipennella* larvae and 10% of the bagged *C. caespititiella* larvae were parasitized by wasps. Of the 50 *C. caespititiella* larvae bagged, 40 second-generation adults were recovered, whereas five of the larvae died. Of the 41 unparasitized *C. cratipennella* cases, 30 adults moths emerged the following spring. These values for larval parasitism likely underestimate the true parasitism frequency. Parasitoids that emerged from hosts before larvae were bagged would not have been counted, and parasitoids that could have attacked larvae after they were bagged would have been excluded.

Discussion

With the exception of several species of economic importance, coleophorid moths have received little attention from ecologists. Jordan (1958, 1962) and Randall (1982a, 1982b, 1986) described in detail the population dynamics of *C. alticollela* Zeller in the northern Pennines (Westmorland, England). Like *C. caespititiella* and *C. cratipennella* described here, *C. alticollela* and most of the marsh-inhabiting Coleophoridae feed on rushes (*Juncus* spp.) (Heinrich 1923, McDunnough 1942). There is also one report of another coleophorid, *C. salicorniae* Wocke, feeding on *Salicornia* in the Netherlands (Huiskes et al. 1980). Here, I have presented the first report of a single *Coleophora* species feeding on plants in both of these families, polyphagy being uncommon in the Coleophoridae (Heinrich 1923, Jermy 1984).

In their oviposition and feeding behavior, *C. caespititiella* and *C. cratipennella* behave like many other insects (e.g., Root 1973, Kareiva 1983). They are found only in areas where their host plants are common (Table 1), prefer sites of concentrated resources (Tables 2, 3, 5, and 6), rarely move from

sites of high resource density (Table 4), and satiate at extremely high host plant densities (Table 6).

Bivoltinism has not been previously reported for the Coleophoridae. Although multiple-host use is common in phytophagous insects, including the Lepidoptera (reviews in Futuyma & Gould 1979, Jermy 1984, Strong et al. 1984), multivoltine species that obligately use different, unrelated host plants during different generations are infrequent (Jermy 1984).

As a consequence of their diets and life cycles, *C. caespititiella* and *C. cratipennella* also may play a role in structuring the marsh plant community. *Salicornia*, an annual plant, is restricted to disturbed areas lacking in perennial vegetation (patches) because of its inability to outcompete perennial plants for space (Ellison 1987). *Salicornia* seedlings recruit at low densities into patches, and these local *Salicornia* populations persist only until overgrown by the perennial grasses and rush (1–3 yr depending on patch size) (Bertness & Ellison 1987, Ellison 1987). Seedling survival of *Juncus* in similar patches is close to 50%, but *C. caespititiella*, *C. cratipennella*, and the katydid seed predators reduce *Juncus* seed output by three orders of magnitude (Bertness et al. 1987). Consequently, in the presence of seed predators, recolonization of patches by *Juncus* is almost exclusively vegetative (Bertness & Ellison 1987). I hypothesize that, in the absence of the moths, *Juncus* seed production and seed dispersal into *Salicornia* patches would result in more rapid recolonization of disturbed areas by *Juncus* and competitive exclusion of *Salicornia* in the *Juncus* zone at Rumstick Cove. By preying on *Juncus* seeds, the two *Coleophora* species may provide a temporal refuge for *Salicornia*. Relative to *Juncus*, *Salicornia* sustains little seed loss due to insect predation (Tables 3 and 5), and the benefits accrued to *Salicornia* as a consequence of the multiple-host use of *C. caespititiella* may be of selective importance in this marsh plant community. Other polyphagous insects are also known to mediate interspecific plant competitive interactions (Bentley & Whittaker 1979, Whittaker 1979, Louda 1982, Cottam 1985, Parker & Salzman 1985, Cottam et al. 1986, Thomas 1986, Gibson et al. 1987). A similar role for heteroecious rusts and concomitant evolutionary response of trees and shrubs also has been proposed for woodland plant communities (Rice & Westoby 1982).

Parasitoids have been useful in controlling *Coleophora* outbreaks on larch and birch (e.g., Raske 1978, Ryan & Theroux 1981), exert strong population control on *C. alticollela* in parts of its range in England (Randall 1982a), and weakly affect populations of other coleophorids (Schaffner 1959, de Santis & Armesto 1983, Bergelson & Lawton 1988). During 2 yr of captive rearing and one summer studying the parasitoids of *C. caespititiella* and *C. cratipennella*, I recorded a parasitism frequency of 10% for *C. caespititiella* and 20% for *C. cratipennella*. A long-term demographic study of these moths and their parasitoids is needed to determine the effects of the wasps on the moths' population dynamics and the consequent second-order effects on marsh community structure.

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