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PATTERNS OF OVIPOSITION IN *HEMILEUCA LUCINA* (SATURNIIDAE)

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ABSTRACT. *Hemileuca lucina* (Saturniidae) is a batch-layer, ovipositing on stems of *Spiraea latifolia* (Rosaceae) in the fall, three months after larval development is completed. Eggs hatch the following spring. Patterns of oviposition and choice of oviposition site were determined by sampling three natural populations of this moth in Massachusetts. Mean number of eggs per mass was 146, with no decrease in the weight of eggs laid later relative to earlier in the mass. Females made few mistakes in choice of hostplant, and chose stems in sunny locations near the edge of *S. latifolia* clumps. Egg masses were deposited near the ground at a mean height of 33 cm, and on twigs between 1 and 5 mm diam.

Additional key words: eggs, *Spiraea latifolia*.

Choice of oviposition sites may be critical for the reproductive success of an individual insect. Although mistakes in the selection of appropriate oviposition substrates occur (Chew & Robbins 1984), generally females are discriminating in where they lay their eggs (Rausher 1979a, 1979b, Stamp 1982, Singer 1983, 1984, Williams 1983, Grossmueller & Lederhouse 1985). Appropriate choices may be particularly important for insects that lay eggs in batches, because they may make only one to a few decisions of where to oviposit. This is in contrast to species that oviposit eggs singly, where females may make hundreds of such decisions.

Most studies on oviposition behavior have dealt with species in which eggs are deposited the same season in which the larvae feed, when cues are available that indicate appropriate larval host plants and environ-

ment. For example, Rausher (1979a) demonstrated that ovipositing *Battus philenor* (L.) (Papilionidae), whose offspring feed in that same season, discriminate among host plants and benefit by choosing plants that will not senesce before the larval period ends. Williams (1981) found that ovipositing *Euphydryas gillettii* Barnes (Nymphalidae) butterflies chose leaves of the host plant with an orientation towards the sun that minimized larval development time, a critical component of larval survival in the montane habitats with short growing seasons where these butterflies occur. In contrast, cues such as hostplant quality and microclimate, which are directly related to offspring survivorship, may not be available to species that deposit eggs in the growth season prior to that in which larvae feed. Some of these species deposit eggs a few weeks after the larval period [gypsy moth, *Lymantria dispar* (L.) (Lymantriidae), and tent caterpillars, *Malacosoma americana* (Fab.) and *M. disstria* (Hübner) (Lasiocampidae)], whereas others oviposit months after the larval period (species of tribe Hemileucini in Saturniidae) (Ferguson 1971, Tuskes 1984).

Our objective was to examine oviposition behavior and site selection of *Hemileuca lucina* Hy. Edw. (Saturniidae), an insect that lays batches of eggs three months after the larval period and in the growth season before that in which larvae feed.

Like other hemileucines, *H. lucina* is univoltine. The flight period occurs in mid to late September and lasts about two weeks. Females eclose laden with eggs. They attract males by producing a pheromone, apparently as soon as their wings expand, as Tuskes (1984) noted for other hemileucines. In the laboratory (at about 22°C), copulation lasts 1 to 2 h ($\bar{x} = 92 \text{ min} \pm 50 \text{ SD}$, $n = 13$). Females begin depositing eggs shortly afterwards.

Females deposit usually 1, but occasionally 2 (less than 5% deposit 2), clusters of eggs in a ring around stems of the host plant, *Spiraea latifolia* (Ait.) Borkh. (Rosaceae) (Fig. 1). The female climbs onto a twig and curls the abdomen up and to the side around the twig for each egg deposited. She alternates from side to side, with two depositions made swinging the abdomen to the left and then two to the right. The first few eggs are laid in a sparse half-circle around the twig. The female then works her way up the twig, carefully inserting eggs into the gaps among the others, thus making a tightly packed egg ring. Usually, several rows are deposited, with the rows progressing up the stem.

The eggs overwinter and, in Massachusetts, hatch sometime in May, depending on local weather conditions. Larvae are gregarious in the first four instars. Group size declines, and by the fourth or fifth instars solitary individuals are observed in the field (Cornell et al. 1987). Factors such as parasitoids and predators, weather, and food availability con-

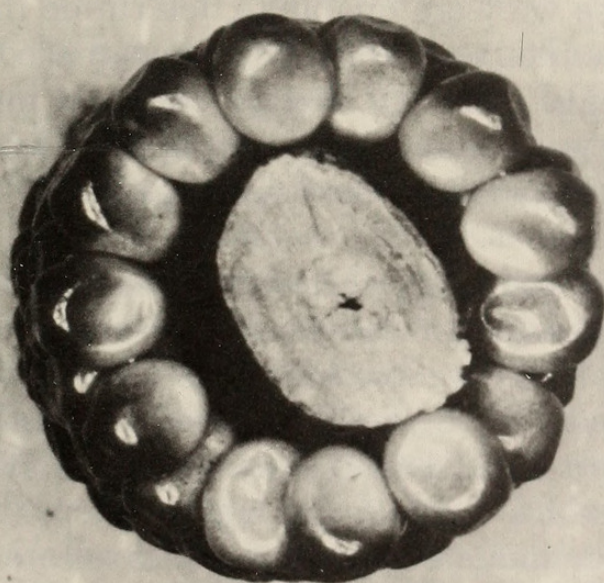
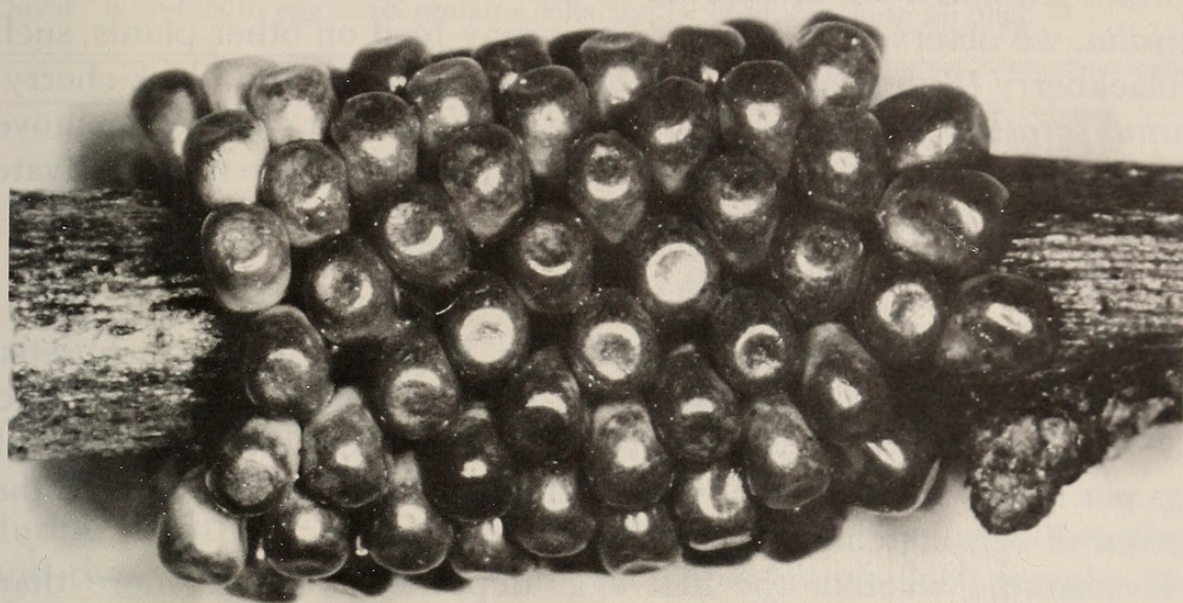


FIG. 1. Egg mass of *H. lucina*. Top, longitudinal view. Bottom, stem of *Spiraea latifolia* cut to show arrangement of eggs around it.

tribute to reduction in group size. Larvae are black with spines in the first five instars. The spines cause painful dermatitis when larvae are handled, particularly in the penultimate and ultimate instars. Larvae are solitary in the sixth instar and usually have a lateral yellow stripe

and yellow mottling, but can be quite variable (D. F. Schweitzer pers. comm.). Although larval feeding in the early instars is confined to *S. latifolia*, we observed that later instars may feed on other plants, such as blackberry (*Rubus* sp.), cinquefoil (*Potentilla* sp.) and black cherry, *Prunus serotina* (Rosaceae). The larvae leave the host plant, often move some distance, and burrow into the soil to pupate, where they aestivate through the rest of the summer.

MATERIALS AND METHODS

Egg masses were collected from Dover, Norfolk Co., Massachusetts, in 1983 and 1984; Belmont, Norfolk Co., Massachusetts, in 1984; and Leverett, Franklin Co., Massachusetts, in 1984 and 1985. Number of eggs per mass was counted at these 3 sites. In 1985, we determined the percent of eggs hatching at Leverett.

To examine whether the first eggs deposited weighed more than those deposited later, as has been found in other lepidopterans (Wellington 1965, Leonard 1974, Richards & Myers 1980, Jones et al. 1982, Wiklund & Persson 1983, Karlsson & Wiklund 1984, Harvey 1985), eggs from newly laid egg masses were detached from twigs and weighed individually. Because we were unable to determine the exact order of deposition but knew that eggs were laid from the bottom to the top, we removed nine eggs from the bottom ring and nine from the top ring of each of five egg masses. The null hypothesis was that no difference in egg weight occurred between eggs laid first and those laid last.

At Leverett in 1984 and 1985, we described the location of egg masses. We first measured the height at which they occurred on *S. latifolia* stems. On 19 May 1985, we measured, to the nearest 10 cm, their distance from the edge of *S. latifolia* clones. In addition, we noted whether masses were located in the sun or shade. We also searched outside dense clones of *S. latifolia* for egg masses.

To determine what diameter of stem females selected for oviposition, and whether that reflected what was available, we compared diameter of stems containing egg masses with that of stems that were available. On 14 April 1985, the diameter of available stems was measured by establishing transects through clones of *S. latifolia* at Leverett. A transect was set up through the middle of each of two clones, and another transect along the edge of these same clones, for a total of four transects. The height used for sampling diameter of available stems was based on mean height above ground of egg masses the previous year (1984) at that site ($\bar{x} = 24.9 \text{ cm} \pm 11.4 \text{ SD}$, $n = 33$). Every stem within 5 cm of the transect was measured at a height of 25 cm. We assumed that relative availability of stems of different diameters did not change

TABLE 1. Number of eggs in egg masses of *Hemileuca lucina* from three sites in Massachusetts. Dover "a" refers to egg masses collected in 1983, hatching that year, and Dover "b" refers to egg mass remains collected in 1984, hatching in 1983.

Location	Year	Mean \pm SD	n
Dover	1983a	156.4 \pm 44.1	17
	b	142.1 \pm 43.9	53
	1984	135.2 \pm 44.5	34
Belmont	1982	157.4 \pm 39.1	5
	1983	121.0 \pm 19.8	2
Leverett	1983	147.4 \pm 50.8	32
	1984	149.9 \pm 47.8	33
Total		145.8 \pm 44.7	176

during the study. New stems are produced each year, old ones grow, and there are thousands of stems available from which females may choose.

Power of the statistical tests (probability of not committing a type II error, $1 - \beta$) was calculated as described by Cohen (1977).

RESULTS AND DISCUSSION

Description of the egg mass. A typical egg mass is shown in Fig. 1. Mean weight of an egg from a single mass was $1.63 \text{ mg} \pm 0.16 \text{ SD}$ and ranged from 1.13 to 1.89 mg ($n = 118$). Such variation in egg weight may or may not relate to larval fitness (Wellington 1965, Richards & Myers 1980, Wiklund & Karlsson 1984, Karlsson & Wiklund 1984, Harvey 1985). In general, weight of eggs when laid declines as lepidopteran females age (Wellington 1965, Leonard 1974, Richards & Myers 1980, Jones et al. 1982, Wiklund & Persson 1983, Karlsson & Wiklund 1984, Harvey 1977, 1985, Boggs 1986). Accordingly, for those species laying only one or two egg masses, egg weight would be predicted to decline from first to last eggs laid in a single mass, as Wellington (1965) found for *Malacosoma californicum pluviale* (Dyar) (Lasiocampidae). However, we found that the first eggs deposited in an *H. lucina* egg mass were not significantly different in weight from eggs deposited last (Wilcoxon paired sample test, $n = 5$, $P > 0.05$). Because *H. lucina* females do not feed as adults, often mate and oviposit within a few hours of eclosion, and usually lay only a single egg mass, they may emerge with all eggs yolked and allocate resources to eggs randomly (Wiklund & Karlsson 1984).

The mean number of eggs per mass was 145.8 (Table 1), and ranged from 42 to 235. Of 36 egg masses collected in Leverett in 1984, 2 did not hatch; of 33 egg masses collected there in 1985, again 2 failed to hatch. Even within an egg mass, not all eggs hatched. Of the 31 egg

NUMBER OF EGG MASSES

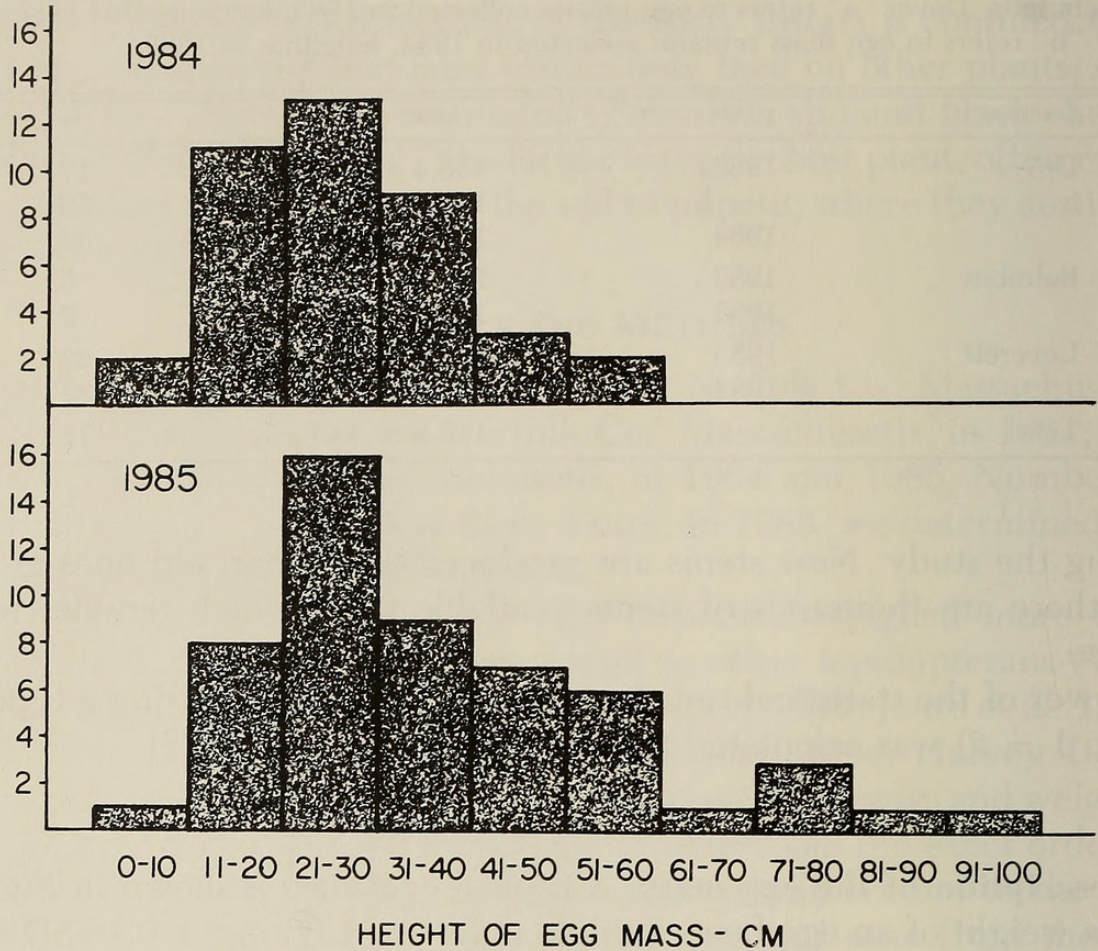


FIG. 2. Distribution of above-ground height of *Hemileuca lucina* egg masses in 1984 ($n = 40$) and 1985 ($n = 53$) at Leverett.

masses from Leverett that hatched in 1985, a mean of 12.9% (± 16.5 SD, range 1.1–93.5%) of eggs per mass did not hatch.

Location of egg masses. Females were quite specific about where they laid eggs. Of 38 egg masses at Leverett in 1985, only 2 were on nonhost plants, 1 on blackberry (*Rubus* sp., Rosaceae), and 1 on goldenrod (*Solidago* sp., Asteraceae). Both “mistakes” were located in the midst of dense clumps of *Spiraea latifolia*, and probably did not adversely affect larval survival. Newly hatched larvae may move more than 100 cm to find food. Mean height of egg masses at Leverett was 32.8 cm (± 17.3 SD, $n = 93$) (Fig. 2). Height distribution of masses did not differ significantly between 1984 and 1985 (χ^2 , $df = 6$, $P > 0.10$, $1 - \beta = 0.55$, $\alpha = 0.05$). Stem height of *S. latifolia* ranged up to about 200 cm; thus, females were avoiding the higher sites. Eighty-five percent of the masses occurred below 50 cm (Fig. 2).

Females chose stems of a particular diameter (Fig. 3). Egg masses occurred on stems between 1 and 5 mm diam., whereas the available stems ranged from less than 1 mm to 12 mm. The size categories of

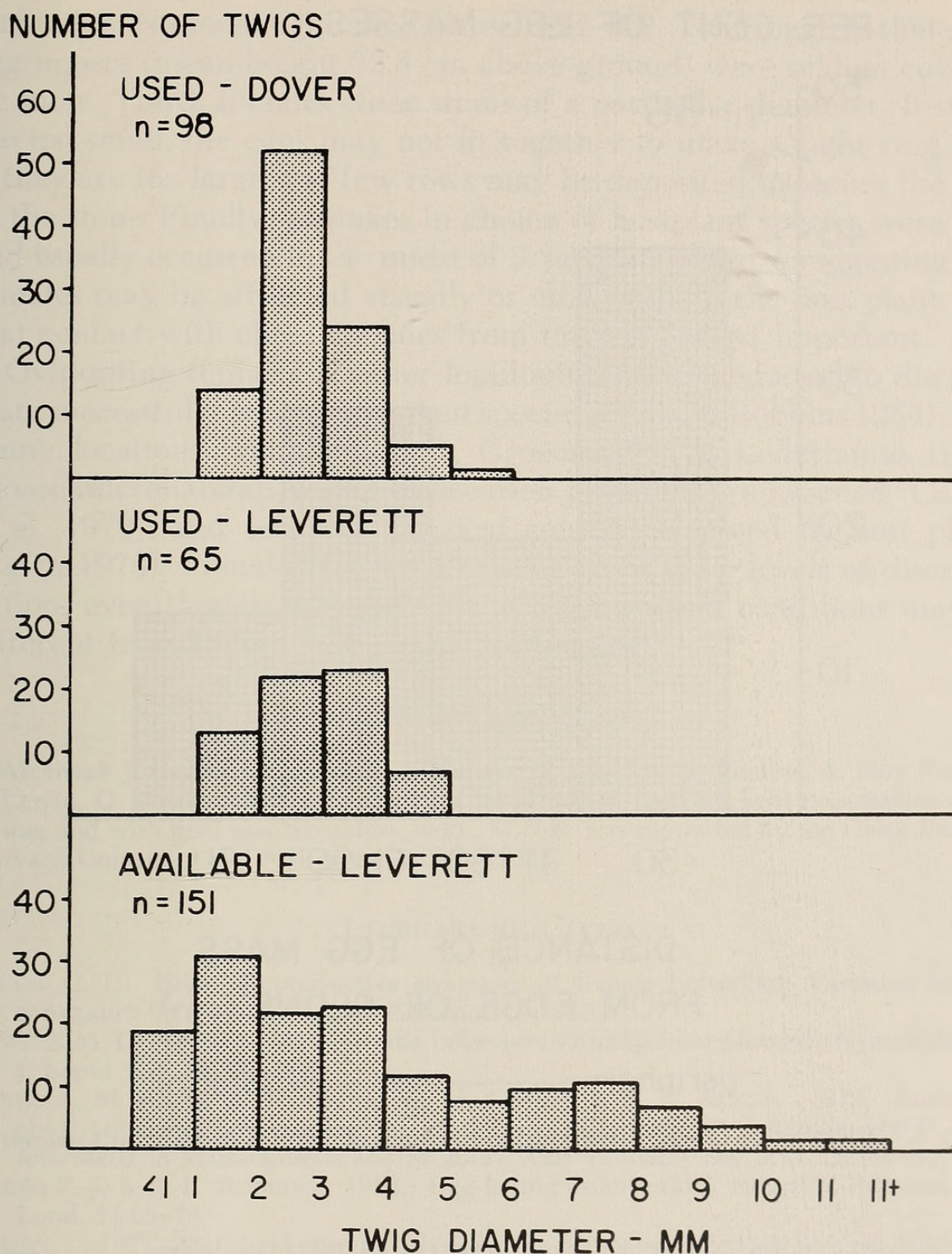


FIG. 3. Diameter of stems at height of 25 cm available to ovipositing *Hemileuca lucina* females compared to diameter of stems chosen for oviposition.

stems used and those of available stems at Leverett were significantly different (χ^2 , $df = 4$, $P < 0.001$) (Fig. 3). Diameter of stems chosen by females at Leverett and Dover were not significantly different (χ^2 , $df = 4$, $P > 0.05$, $1 - \beta = 0.57$, $\alpha = 0.05$) (Fig. 3).

All egg masses occurred in portions of *S. latifolia* clones not shaded by trees or shrubs during the day ($n = 38$, Leverett 1985). Thus, females appeared to avoid shady locations. In addition, females chose oviposition

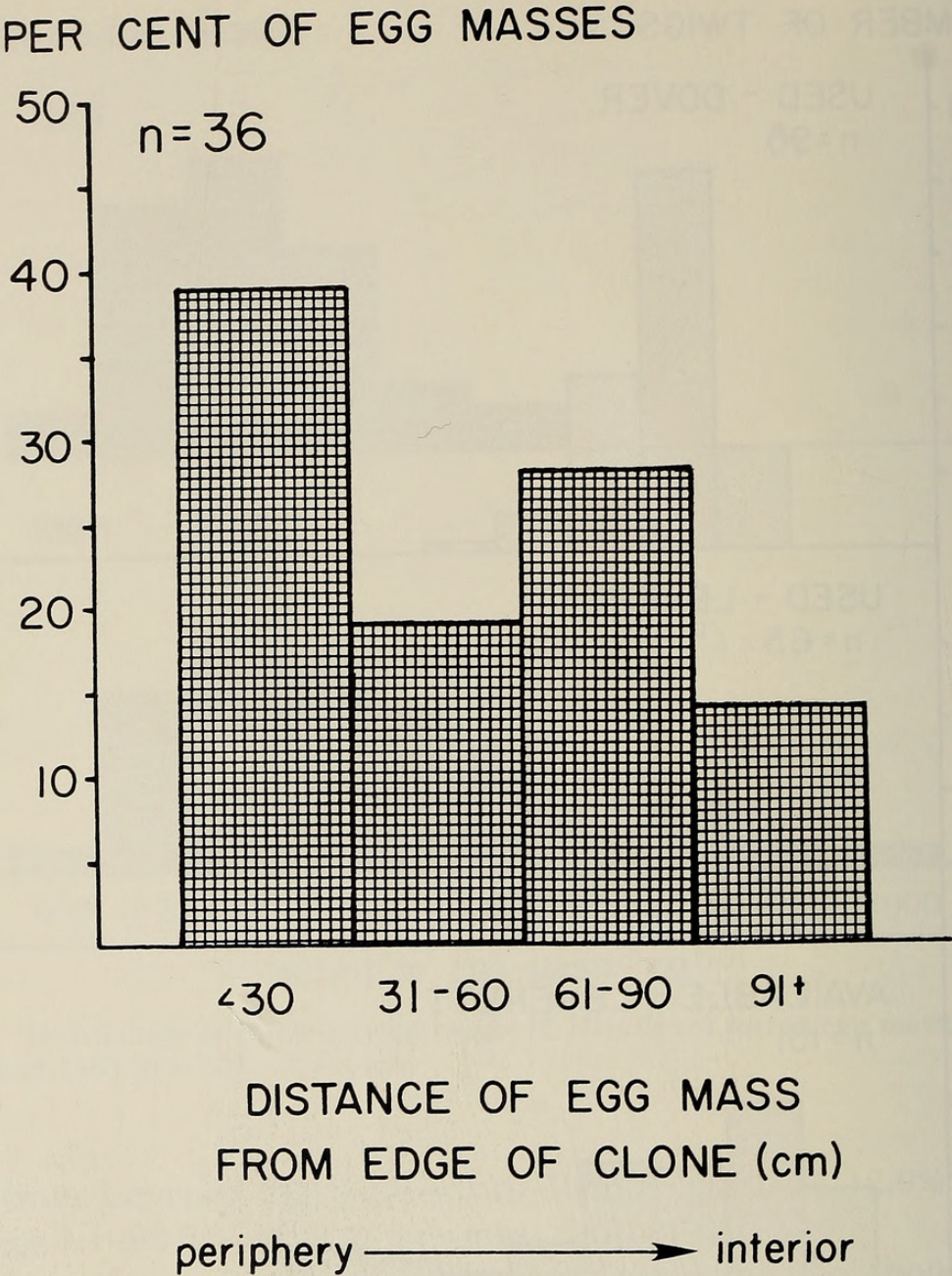


FIG. 4. Distribution of egg mass position in clones of *Spiraea latifolia* at Leverett in 1985.

sites on the periphery (0–60 cm) of *S. latifolia* clumps (Fig. 4), where more sunlight was available.

Our results show that *H. lucina* females chose stems of *S. latifolia* that were a specific subset of those available for oviposition. First, such stems were located near the periphery of a clump and in the sun. This may aid in synchronizing egg hatch with bud burst, which is important in other species (Feeny 1970, Williams 1981). Second, egg masses were low on the stem, which may keep at least some under snow during the winter and ensure a more even microclimate. However, mean maximal monthly snow depth was 21.7 cm (± 20.7 SD; $n = 102$ months, 1971–80 for 2 sites, Blue Hill Observatory near Dover, and Worcester, Mas-

sachusetts; National Climatic Center 1971–80). That suggests that most egg masses (mean height 32.8 cm above ground) were seldom covered by snow. Third, females chose stems of a particular diameter. If stems are too small, the eggs may not fit together to make a tight ring, and if they are too large, too few rows may be deposited to secure the ring to the stem. Finally, mistakes in choice of hostplant species were rare and usually occurred in the midst of *S. latifolia* clumps, suggesting that females may be attracted visually or olfactorily to the host plant, and that contact with chemical cues from the stem is less important.

Ovipositing females of other lepidopterans are reported to discriminate successfully among hostplant species (Chew & Robbins 1984), seek sunny locations (Williams 1981, Grossmueller & Lederhouse 1985), choose microhabitats where desiccation problems are lessened (Carroll et al. 1979), and confront physical constraints posed by host plants (Levin 1973). Female *H. lucina* exhibit all of these levels of discrimination, even though they oviposit at a time when conditions may be different from those when larvae are feeding.

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