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BODY TEMPERATURE, BEHAVIOR, AND GROWTH OF EARLY-SPRING CATERPILLARS (*HEMILEUCA LUCINA*: SATURNIIDAE)

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ABSTRACT. Buckmoth caterpillars (*Hemileuca lucina*: Saturniidae) hatch in May, are then exposed to considerable variation in spring thermal conditions, and thus may benefit by basking. We found that larvae exposed to full sunlight reached body temperatures as much as 5°C above ambient temperatures. When sunlight was obscured by clouds, their body temperatures rapidly cooled to that of ambient. However, during partly sunny conditions, larvae in groups were often warmer than solitary larvae. The advantages for buckmoth caterpillars in attaining body temperatures warmer than ambient are discussed in terms of their food plant and predators.

Additional key words: basking, gregarious, predators, *Spiraea latifolia,* Massachusetts.

Thermal conditions affect the foraging patterns of and food plant exploitation by herbivorous insects. For example, raising the body temperature by basking may speed up physiological processes enabling larvae to consume and digest food faster and, thus, develop more quickly (Sherman & Watt 1973, Casey 1976, Grossmueller & Lederhouse 1985). Shortened developmental time for larvae may decrease availability to parasitoids (Porter 1983) and predators (Evans 1982) and maximize the intake of high quality food, which may be available only for a limited time during the growing season (Feeny 1970, Stamp & Bowers 1990a).

Our objective was to examine, under natural conditions, body temperature, behavior, and growth of buckmoth caterpillars (*Hemileuca lucina* Hy. Edw.: Saturniidae), which are typical of gregarious caterpillars feeding early in the spring. Larvae of *H. lucina* are specialists on meadowsweet (*Spiraea latifolia* Ait. Bork.: Rosaceae), a shrub common in wet fields in New England. In late September in Massachusetts, buckmoths deposit egg masses around stems of their hostplant. The eggs hatch in May. Although the mean size of egg masses was 146 eggs (Bowers & Stamp 1987), larval aggregations found in the field were often much smaller (Stamp & Bowers 1988). Reduced group size reflects the declining tendency to aggregate, subdivision as a result of escape responses to predators and parasitoids, and mortality (Cornell et al.

1987, Stamp & Bowers 1988). The caterpillars are conspicuous due to aggregation and aposematic coloration (i.e., black with urticating spines). Like many other early spring feeders (Porter 1982, Capinera et al. 1980, Knapp & Casey 1986), they bask. The larvae develop in early spring over 6–8 weeks, pupate in late June in the soil, and remain there through the summer.

METHODS

Depending on local larval densities, we used various sites over the three year study period (1983–85). To assess foraging behavior of first instar larvae, we used a population in 1985 at Leverett (Franklin Co.), Massachusetts. To determine larval temperatures, we used populations in 1984 and 1985 at Leverett and Gardner (Worcester Co.), Massachusetts. We used a population in 1983 at Dover (Norfolk Co.), Massachusetts, to examine growth rate of larvae under natural conditions.

To determine the feeding location of first instar larvae, 58 aggregations were observed on 19 May 1985 at Leverett. The following were recorded: height of the stem used by larvae, height of aggregation above the ground and relative to foliage, and behavior of larvae.

To ascertain maximal body temperatures of larvae under field conditions and to compare the thermoregulatory ability of solitary versus aggregated larvae, we observed aggregations of third and fourth instar caterpillars at two field sites (Leverett and Gardner). The size (wet weight) of mid-instar third and fourth instar larvae is 191.7 mg ± 34.5 SD (n = 36) and 216.0 mg ± 38.7 SD (n = 36), respectively. An infrared thermometer (Everest Interscience) was used to measure surface temperature of larval groups and air temperature at the corresponding microsites, 3 cm from the aggregations (with air temperature determined by a shielded sensor on the antenna of the infrared thermometer). This instrument allowed thermal measurements (of an area with a 2.5 mm diameter) without disturbing the larvae, which thrash and drop off the food plant with the slightest provocation. In 1984, a black-body instrument was used to estimate solar radiation (Porter 1982). Black-body measurements represent a combination of factors: radiation (solar and thermal), convection, and conduction. Although such measurements have limited value when the geometry and reflectance properties of the probe in the black-body instrument are different from those of the animals being measured (as is usually the case), black-body measurements do serve as an indicator of the thermal input available. In 1985, a pyranometer (LI-COR 200SB sensor attached to a LI-COR 185B radiometer) was used to determine solar radiation and to calibrate the black-body instrument used the previous year. Temperatures of live individuals were determined with a calibrated thermistor probe inserted into the thoracic segments (Porter 1982). These larvae were

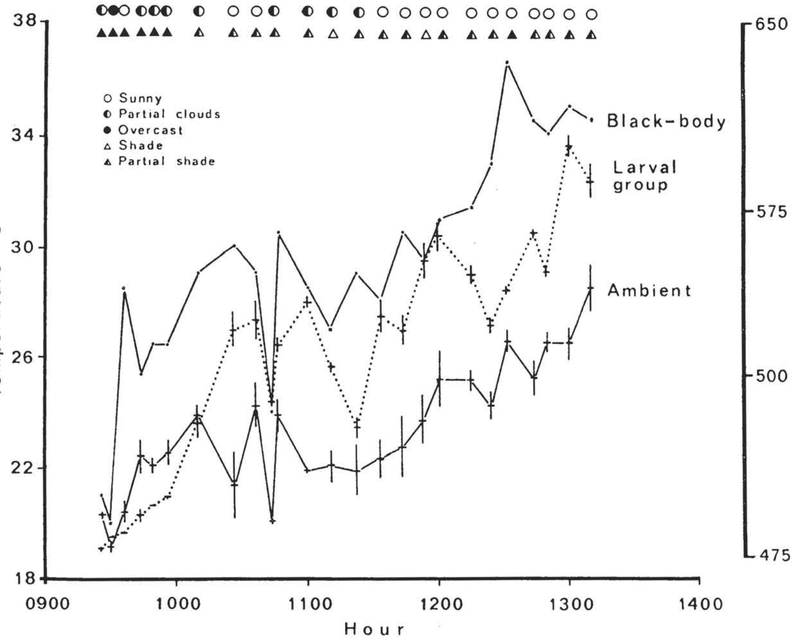

FIG. 1. Thermal measurements of aggregated third instar caterpillars at Leverett, Massachusetts, on 15 June 1984. Mean ambient temperature and surface temperature of the aggregation are shown with ± SE. Solar radiation (W m^{-2} = watts per square meter) was measured with a black-body instrument. Available sunlight is indicated with: open circles = full sunlight, half circles = partial clouds, and dark circles = overcast. Triangles represent shading by vegetation, with open triangles = no shade, half triangles = partial shade, and dark triangles = full shade.

placed 2.5 cm away from the group to be measured and in a vertical position, the most common position of buckmoth larvae whether they are feeding on leaves or massed during molting; larvae remained in this position throughout the measurements.

To examine the growth rate of caterpillars under natural conditions, five aggregations of buckmoth larvae were monitored in spring 1983 at Dover. Starting on 14 May, then again on 25 May, 1 June, 9 June, and finally on 14 June, 10 larvae from each aggregation were taken to the laboratory, weighed individually, and returned to the aggregation the next day. Monitoring began with first instar caterpillars and continued until the fifth instar, after which it was no longer possible to determine from which aggregation individuals had come.

RESULTS

Buckmoth caterpillars hatch in May in Massachusetts, for example, 7 May 1983 and 20 May 1984 at Dover, 15 May 1986 and 20 May 1987 at Belchertown, and 17 May 1985 at Leverett. The phenology of the

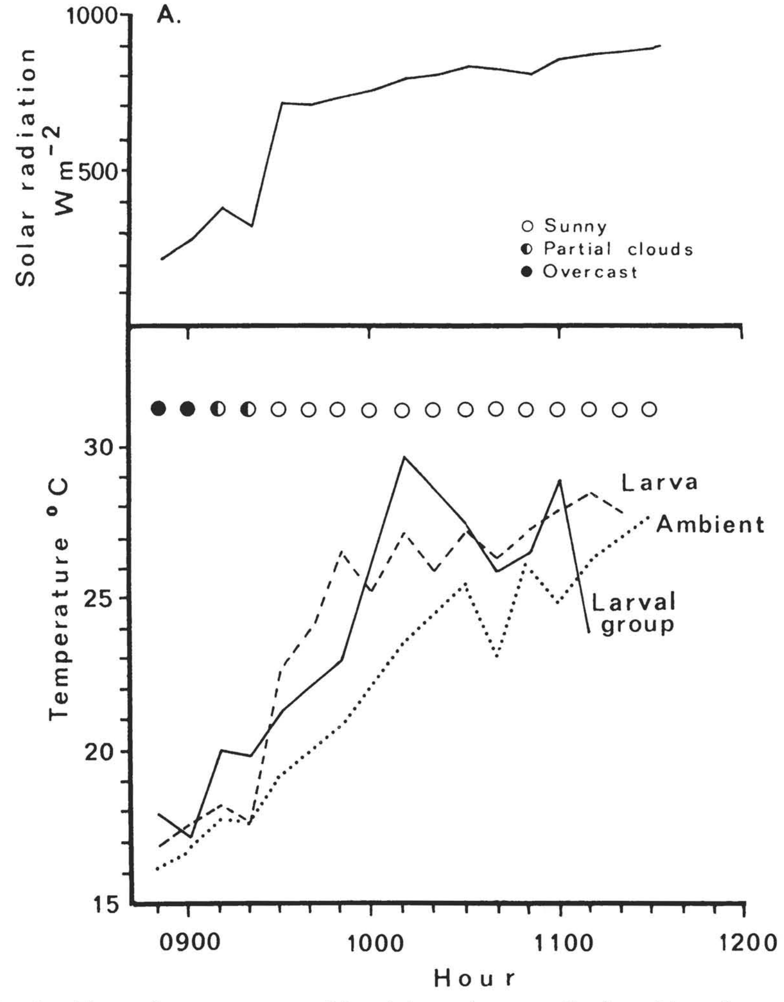

FIG. 2. Thermal measurements of fourth instar larvae at Gardner, Massachusetts, on 9 June 1985. A. The larval group (7 larvae) was 56 cm above the ground at the top of a branch. B. Relationship of larval body temperature (T_b) and ambient temperature (T_a), with black dots for grouped larvae (G) and open circles for solitary larva (S). Lines were fit by least squares method.

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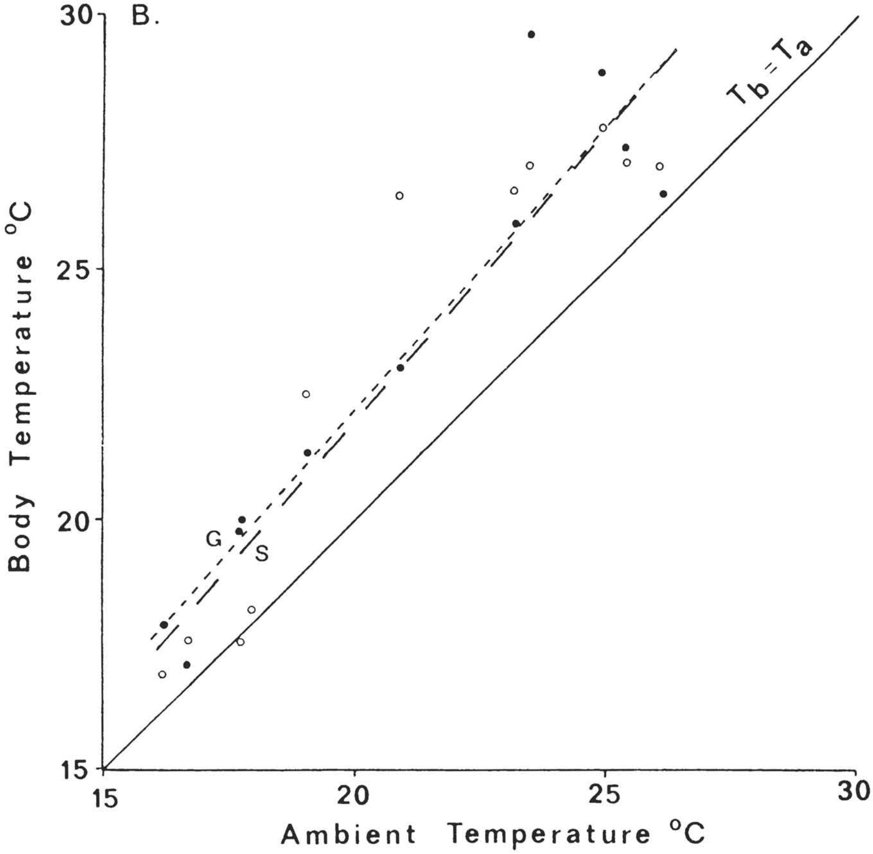
H. lucina larvae parallels that of the food plant (*S. latifolia*), with larvae hatching about a week after budbreak. The newly-hatched larvae move up the stems, about 30 cm, to the top of branches and begin feeding. First instar larvae spend considerable time basking. Observations of 58 aggregations in mid-May (on a day with alternating full sunlight and



clouds, and air temperatures of 13–16°C at the height of the aggregations) showed that all aggregations were exposed on stems, either at the height of the uppermost leaves or above them. The mean height of the stems was 92 cm (±36 SD) and larvae were located at a mean height of 76 cm (±32 SD). Thus, the groups were located on the top fifth of the stems. Of 58 aggregations, 12.1% were molting to the second instar, and 65.5% were resting (i.e., massed with some on top of others and not feeding or moving around). The other groups (22.4%) were feeding gregariously on new leaves.

Fluctuations in temperature of aggregations of mid-instar larvae corresponded to changes in availability of direct sunlight, which depended upon the degree of cloudiness and the amount of shade from vegetation. For example, one morning (at 1044 h), conditions changed from full to partial sunlight and both the black-body and larval aggregation temperatures dropped several degrees (Fig. 1). When in full sunlight

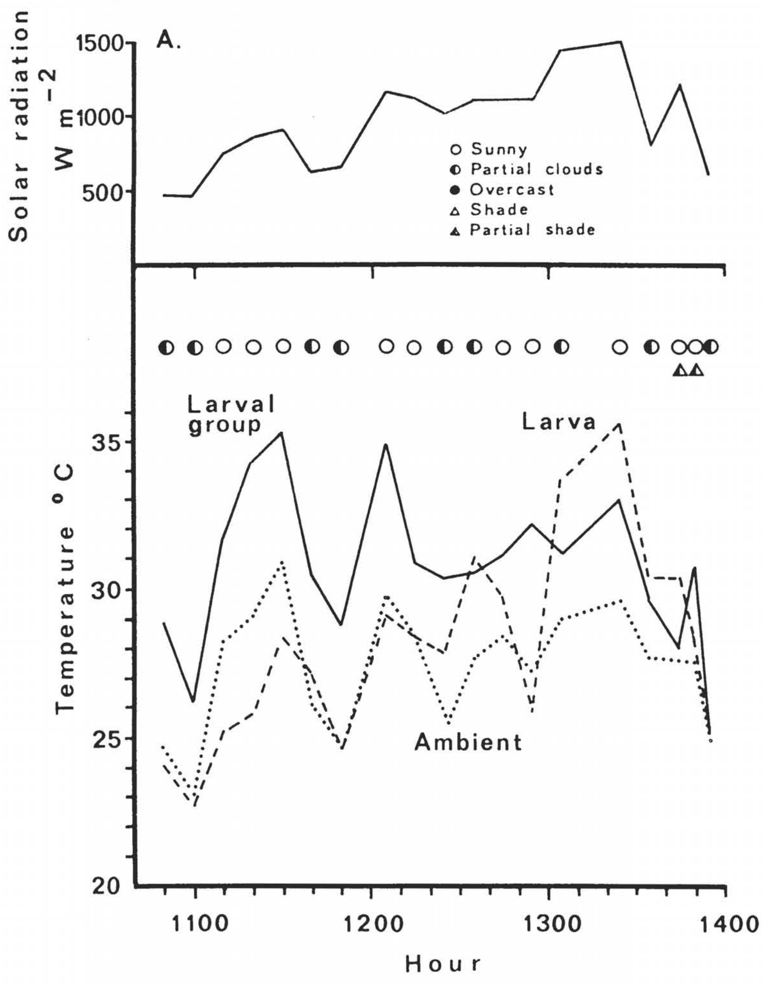


FIG. 3. Thermal measurements of fourth instar larvae at Gardner, Massachusetts, on 11 June 1985. A. The aggregation of 15 larvae was feeding on new leaves at the top of a branch, 39 cm above the ground. B. Relationship of larval body temperature (T_b) and ambient temperature (T_a) for larvae, with black dots for grouped larvae (G) and open circles for solitary larva (S). Lines were fit by least squares method.

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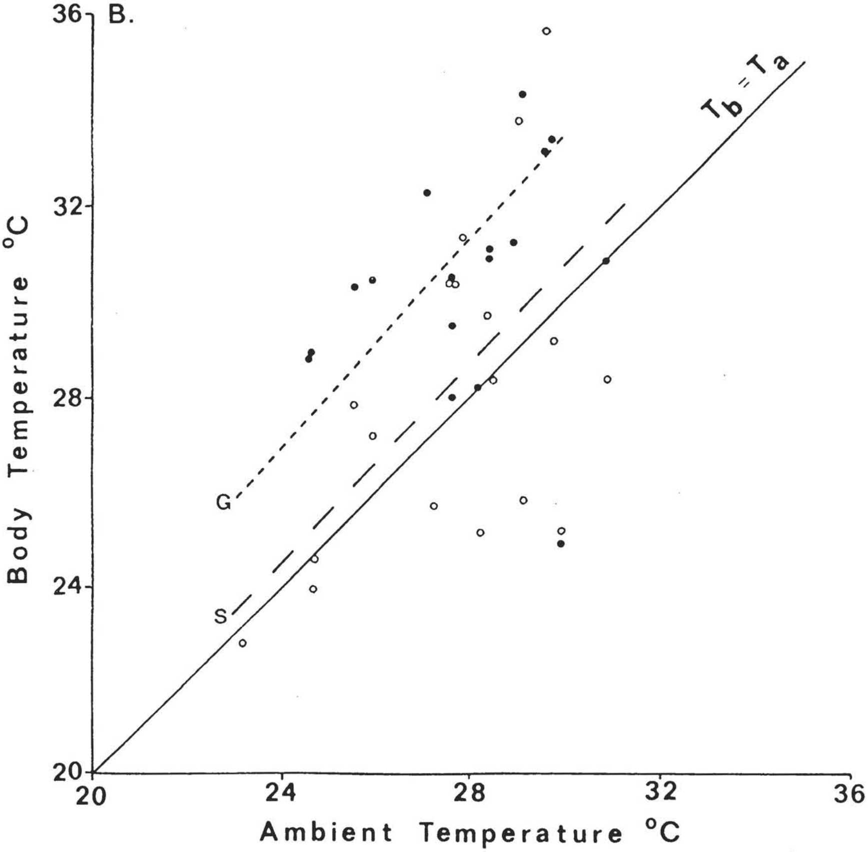
(e.g., from 1153 to 1201 h, with no clouds and no shade), the larval aggregation temperatures approached that of the black-body measurements. Without direct sunlight (e.g., around 0930 h), the aggregation temperature was similar to ambient temperature (Fig. 1).

With full sunlight and steadily increasing solar radiation through the morning, groups and individuals quickly warmed from 17°C at 0900



h to 25°C by 1000 h (Fig. 2A) and, during this morning observation, maintained body temperatures that were above ambient temperatures (Fig. 2B). On a day with partial cloudiness, both groups and individuals cooled rapidly when cloud cover occurred, thereby reducing solar radiation and ambient temperature (Fig. 3A). Consequently, throughout this observation period, isolated individuals' temperatures oscillated around ambient temperature, whereas group temperatures were higher (Fig. 3B). Partially shaded larvae had body temperatures similar to ambient (Fig. 4A), but, for a while at least, grouped larvae were warmer than solitary larvae (Fig. 4B). Data points for body temperatures that were below those of ambient temperature probably were due to high levels of evaporative cooling.

The growth rates (slopes of larval weight regressed on days) were the same for all five field aggregations in spring 1983 at Dover (ANOCOVAR, $P > 0.20$, df = 4, 14; Fig. 5A). The slopes were 0.053, 0.054,

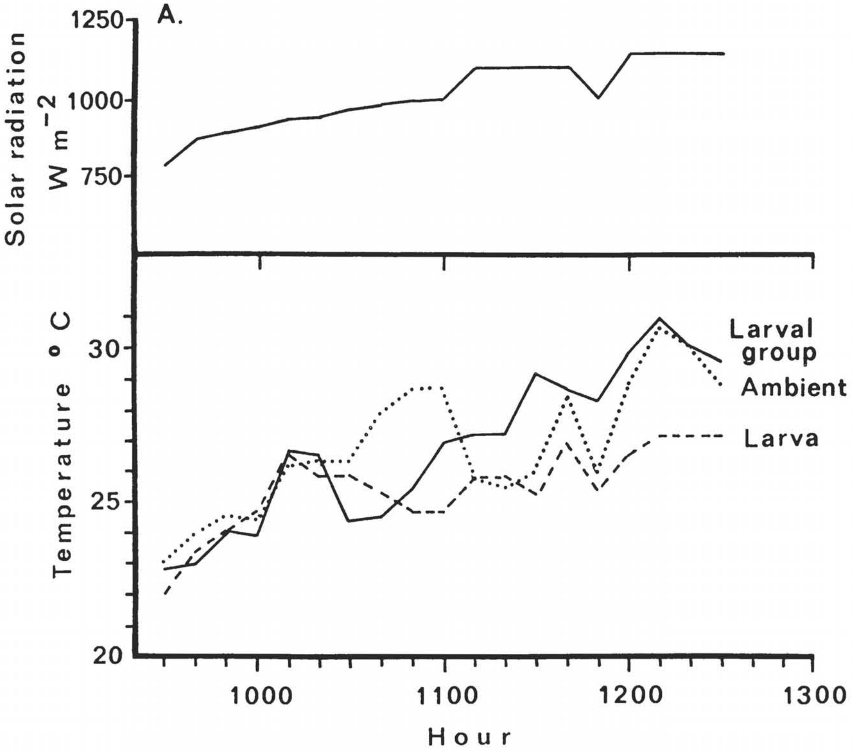


FIG. 4. Thermal measurements of pre-molt, non-feeding fourth instar larvae at Gardner, Massachusetts, on 10 June 1985. A. The aggregation of 26 larvae was 13–29 cm above the ground and in partial shade, and there were no clouds. B. Relationship of body temperature (T_b) and ambient temperature (T_a). S1 and G1 refer to temperatures before 1100 h of solitary (open circles) and grouped larvae (black dots), respectively; S2 (open stars) and G2 (black stars) refer to temperatures of those same larvae, solitary and grouped respectively, after 1100 h.

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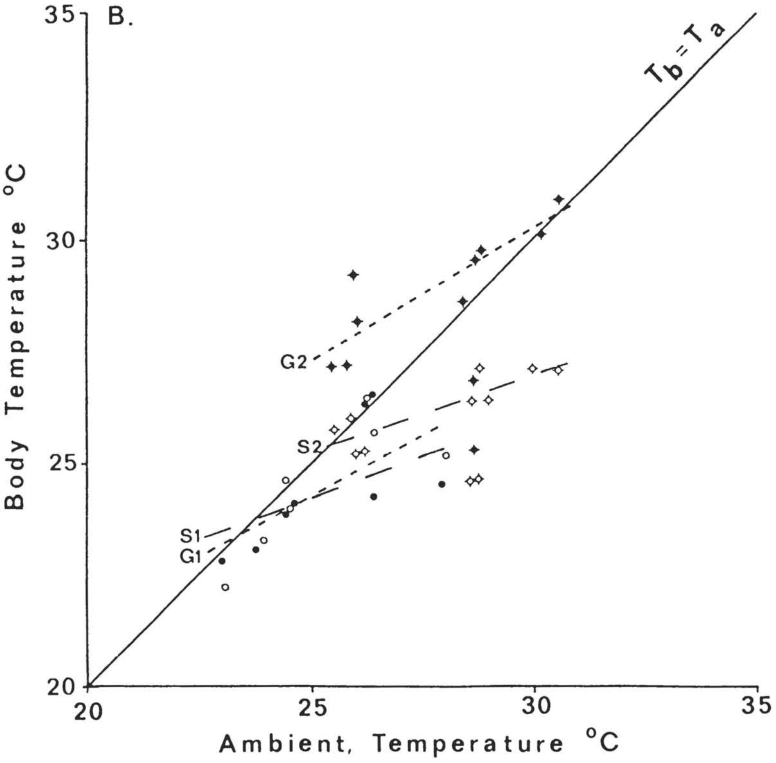
0.062, 0.064 and 0.067. The hatch dates of the egg masses, estimated by extrapolating the regression lines, were 2–10 May. Although the larvae hatched about 1–2 weeks earlier than usual that year, they were subject to typical (and considerable) fluctuations in temperature and available sunshine (National Climatic Center 1979, 1983; Fig. 5B, C). In May in particular, caterpillars were frequently subject to days with either less than 10% of potential sunshine or more than 85% of potential sunshine. By the fifth week (14 June), larvae in the field aggregations were in the fifth instar, and the aggregations had become subdivided into smaller groups.



Discussion

Buckmoth caterpillars that were exposed to full sunlight reached body temperatures as much as 5°C above ambient temperatures (Figs. 1, 2A, 3A) and, during partly sunny conditions, larvae in groups were warmer than the solitary larvae (Figs. 3B, 4B). Growth is faster at warmer temperatures; for instance, relative growth rate of buckmoth caterpillars doubled when the daytime rearing temperature was increased from 20 to 30°C (Stamp & Bowers 1990b). By growing faster, larvae can spend more of the developmental period eating when leaves are highest in nutritional quality, which is the first few weeks after budburst in May (Stamp & Bowers 1990a). By basking during cool but sunny springs, larvae may escape predators and parasitoids temporally. For instance, stinkbugs, such as *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), are important predators of gregarious caterpillars (Mukerji & LeRoux 1965; including *H. lucina,* Stamp, pers. observ.) but are relatively few in number early in the spring (Evans 1982).

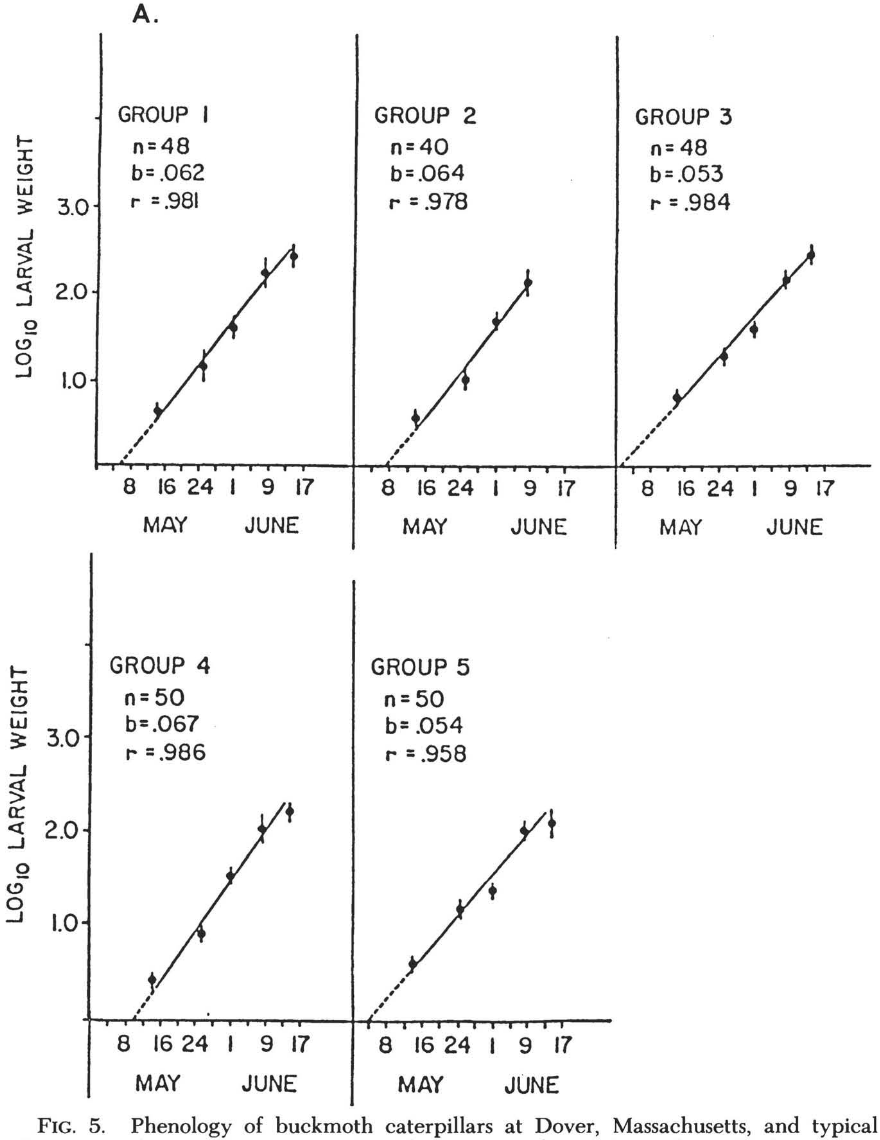


FIG. 5. Phenology of buckmoth caterpillars at Dover, Massachusetts, and typical climatic conditions in spring 1983. Data shown in B and C are from Blue Hill Observatory, 14 km from Dover, Massachusetts (National Climatic Center 1983). A. Growth of larvae under natural conditions at Dover, Massachusetts, with mean ± SE shown. Dashed portions of lines indicate extrapolation to determine hatch date. B. Availability of sunshine during growth period of larvae shown in A. C. Air temperatures during growth period of larvae shown in A. Developmental stages are indicated: estimated hatch (H), larval instars (II–VI) as observed, and estimated pupation (P).

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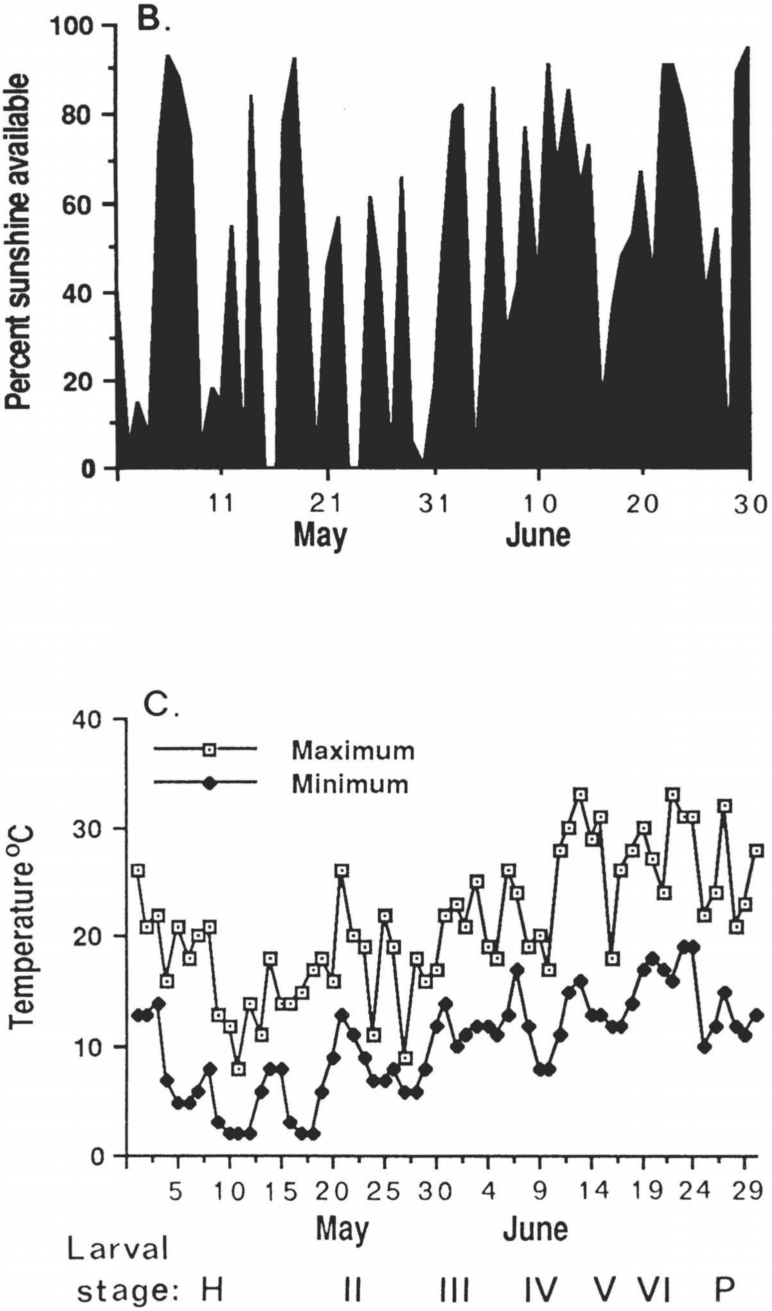
B.
Percent sunshine available
100
80
60
40
20
0
11
21
31
10
20
30
May
June
C.
Maximum
Minimum
Temperature °C
40
30
20
10
0
5
10
15
20
25
30
4
9
14
19
24
29
May
June
Larval stage: H
II
III
IV
V
VI
P

Consequently, when the thermal conditions are in their favor, tent caterpillars, which also bask (Knapp & Casey 1986), can more quickly grow beyond the size in which they are vulnerable to these predators (Evans 1982). Another lepidopteran species (*Euphydryas aurinia*; Nymphalidae), by basking and thus growing quickly in cool sunny springs, is better able to avoid parasitism by braconid wasps than in overcast springs, in which caterpillar development is much slower (Porter 1982, 1983).

Buckmoth larvae were subject to considerable variation in maximal body temperatures from day to day, especially in May, which may have important consequences for growth and survival. In addition, our results show that buckmoth caterpillars were subjected unpredictably to periods of relatively cool temperatures during the daylight hours (Figs. 3A, 5). Cool temperatures slow down molting rate more than growth rate (Ayres & MacLean 1987; Stamp 1990). Thus, larvae that enter the molting phase during an overcast period are likely to have an extended developmental period compared to those that are feeding then and molting during warmer periods.

The pattern of local populations of *Hemileuca lucina* becoming extinct (Bowers & Stamp, pers. observ.) and the "boom and bust" phenomenon of *Euphydryas phaeton* (Nymphalidae) (Clench 1979; Stamp & Bowers, pers. observ.), another species with larvae that feed early in the spring and bask, may be largely a function of consecutive springs with favorable conditions (cool but sunny) followed by a series of unfavorable springs (overcast). It is in the latter case that natural enemies and deteriorating food quality are likely to have the greatest negative impact on growth and survival of early spring feeding caterpillars.

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