

The Thermal Ecology of Some *Colias* Butterfly Larvae

Paul W. Sherman and Ward B. Watt

Department of Biological Sciences, Stanford University, Stanford, California and
The Rocky Mountain Biological Laboratory, Crested Butte, Colorado

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Summary. The thermal ecology of *Colias* butterfly larvae has been studied, using simple modifications of previous thermistor implantation technology. Like their adults, these larvae rely on a repertoire of thermoregulatory behavior to control body temperature in relation to external heat sources and sinks. They neither heat nor cool by metabolic means. They display narrow, well-marked body temperature ranges for their major activity, feeding. These are 10–15°C lower than the maximum activity temperatures of the adults. Also in contrast to the adults, the locations of the larval activity maxima differ by several degrees C between the taxa studied. In each taxon studied the rate of feeding reaches a maximum in a body temperature range corresponding roughly to the temperature range maximizing the occurrence of feeding. The overall larval growth rate is maximized under constant temperature regimes corresponding to the maximum feeding range. A qualitative model for larval activity in the field in relation to daily temperature changes is constructed and apparently supported in its essentials. These results are discussed in relation to other aspects of larval ecology, notably predator pressure, and some speculation on their meaning for larval metabolic organization is raised.

Introduction

It is now clear that the adults of numerous insect groups maintain close regulation of their body temperatures during activity. In many Lepidopterans, ranging from Sphingid and Saturniid moths to *Colias* butterflies, the preferred body temperature for adult activity is 34° or 35° to 38° or 39°C, and complex and rigidly stereotyped behavior is associated with achieving and maintaining body temperature in this range. This may take the form of internal heat generation by voluntary muscular activity, as in various moths (Heath and Adams, 1967; Hanegan and Heath, 1970; Heinrich and Bartholomew, 1971), apparently by desynchronization of normally coordinated muscle groups (Wilson, 1968; Kammer, 1968). Alternatively, other insects, such as *Colias*, may orient to absorb much or little sunlight, to heat up or avoid overheating (Watt, 1968, 1969). The immature stages of insects are of course already known to differ from their adults in many ways. It thus becomes of interest to examine the immatures in regard to thermal physiological ecology.

How similar are they to the adults, both with regard to narrowness and stereotypy of general thermal requirements and with regard to details and precise ranges of body temperature preferences?

Colias butterflies offer several advantages as subjects for such study. As holometabolous insects, their larval stages are fundamentally different in morphology and behavior from their adults (see Fig. 1 for illustrations of larvae), and they are large enough (fifth instar larvae are 0.5 cm in diameter and 3–4 cm long) to make chronic implantation of temperature sensors feasible. Extensive information is already available on the behavioral thermoregulation (solar orientation) and related adaptations of *Colias* adults (Watt, 1968, 1969). Similar information on the larvae would thus be very useful in enlarging total knowledge of this organism's thermal niche. This paper begins the thermal-biological study of *Colias* larvae, examining two closely related taxa, *C. eurytheme* Boisduval and *C. philodice eriphyle* Edwards, in the "temperate lowland" species complex of the genus. We will show that while larvae appear just as stereotyped in their thermal requirements as the adults, the temperature ranges in which they display maximum activity are drastically different.

Materials and Techniques

Animals. Laboratory strains of *Colias eurytheme* and *C. p. eriphyle*, originating from Los Banos, Merced Co., California, and from Hotchkiss, Delta Co., Colorado, respectively, were reared on *Vicia* (vetch) as the larval food plant. Rearing temperature was 25°C unless otherwise noted, and a photoperiod regime of 16 L:8 D was maintained.

Thermistor Instrumentation. Construction and operation of temperature sensors was essentially as described by Watt (1968). Bead thermistors, 0.25 mm in diameter, were embedded at the tips of J-shaped rods of epoxy resin, 0.5 mm diameter x 0.5 cm in length, and connected to Wheatstone Bridges via No. 42 magnet wire. Larval temperatures were continuously recorded from these bridges with Heath EU-20 V strip chart recorders. All temperature measurements had a resolution of $\pm 0.1^\circ\text{C}$ and an absolute accuracy, over the range 0–50°C, of better than 0.5°C at any point in the range.

Larval Probe Implantation. Only fourth and fifth instar larvae were implanted with thermistors. Earlier instars are too small to withstand the surgery, and further are so small that the probes would form significant portions of the larval mass and thereby distort larval thermal balance.

Deep anesthesia of larvae is necessary to relax their internal hemolymph pressure (due to tension of transverse muscle bands) and thus prevent extensive loss of hemolymph through the implantation wound. This was achieved by exposing larvae to 95% carbon dioxide gas for 5 minutes prior to start of surgery. Larvae were maintained under anesthesia with a slow stream of carbon dioxide. Each larva was placed on its side and a small perforation made in its cuticle with sterile forceps and pin, off the dorsal midline (to avoid the heart) and between the last thoracic leg and first abdominal proleg. The probe tip, having the same diameter as the thermistor itself, was inserted through this wound to a depth of 2 mm. The external edges of the wound were sealed around the probe with water-soluble ("Elmer's")

glue; the larva itself sealed the wound internally. The stream of carbon dioxide was continued for 20-30 minutes to facilitate glue drying while keeping the larva quiet. After postoperative recovery, larvae were usually physiologically unaffected by the experience. Indeed, several molted to the pupal stage successfully with probes still implanted. Those few larvae which remained sluggish or otherwise abnormal 1 hour after surgery were discarded.

Data Reduction and Analysis. Distributions of the occurrence of larval behaviors as functions of larval temperature were tested as $i \times j$ contingency tables with the χ^2 test, and cooling curves were reduced to Newton's Law plots, as before (Watt, 1968, 1969). Regression lines were fitted to the latter data, and to feeding rate data, with the UCLA Biomed Multiple Regression Program for Stanford's IBM 360/67 computer. Significances and differences of the regression coefficients were evaluated with F and t tests (Sokal and Rohlf, 1969; Rohlf and Sokal, 1969).

Experimental Designs and Results

Comparability of Different Larvae. The thermal experience of size-matched larvae under similar environmental conditions is extremely reproducible. Pairs of such larvae, with probes implanted, were examined side by side for a total of $8\frac{1}{4}$ hours under a variety of controlled ambient air temperature and radiant energy load conditions. The paired larvae showed identical temperatures 87% of the time; the maximum difference ever observed was 1.2°C , and differences were explainable by obvious minor differences in exposure of the two larvae to air currents or the radiant energy source, whether sunlight or spot lamp.

Thermal Balance of Larvae in Their Environment. It is known that *Colias* adults do not significantly alter their body temperatures by metabolic heating or evaporative cooling (Watt, 1968, 1969). Rather, they act as passively heated or cooled objects, changing their relationships to sun, shade, and air circulation to change behaviorally the position of their thermal balance. In this way, they can attain body temperatures 20°C or more above ambient, thus reaching their thermal optimum for activity. What of the larvae? Are they as thermally passive?

In the first place, larvae do not spontaneously heat by metabolic or mechanical means. No larva has ever shown a significant rise in body temperature in the absence of a radiant energy source sufficient to account for the temperature change. The larvae, indeed, never normally attain a temperature as far above ambient as do the adults, and only do so at all when placed under intense radiant load and prevented from escaping.

Secondly, larvae show no sign of cooling by evaporative water loss. Probed larvae, heated above ambient by sunlight or spot lamp, were shaded and allowed to cool while their temperatures were recorded. These raw cooling curves were transformed to plots of cooling rate against insect temperature excess above ambient. The scatters thus generated were tested for the linearity predicted by Newton's Law of Passive Cooling, using the Multiple Regression Program. Plots from

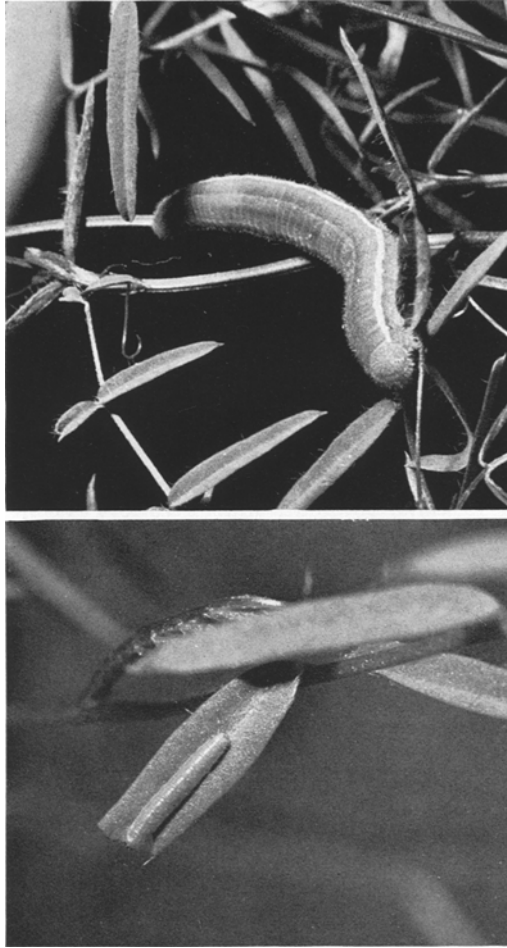


Fig. 1. *Colias eurytheme* larvae on *Vicia* food plant. Below, mid-first instar larva, 2.5 mm long. Above, mid-fifth instar larva, 4.2 cm long

6 *C. eurytheme* and 4 *C. p. eriphyle* larvae, ranging from 9 to 27 data points each, were thus tested. Each was fitted by a linear regression equation whose significance, evaluated by F test, was far beyond the $P = 0.001$ level. One such plot is shown in Fig. 2. This is strong evidence against the presence of evaporative or other non-Newtonian cooling.

The larva, in short, heats and cools as a thermally passive body. To confirm this even further, a simulated larva, matching a fifth instar larva in size, was made of plastic tubing and filled with water to approxi-

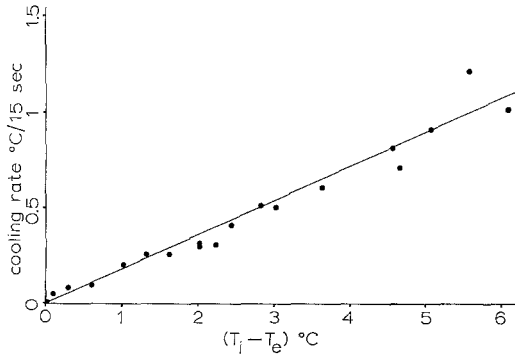


Fig. 2. Typical Newtonian cooling plot of a *C. eurytheme* larva (fifth instar). T_i insect temperature, T_e environmental temperature. Linear regression coefficient $b = 0.179$, $F_{1,18} = 392.1$, $P \ll 0.001$. There is no evidence whatever for evaporative or other non-passive cooling

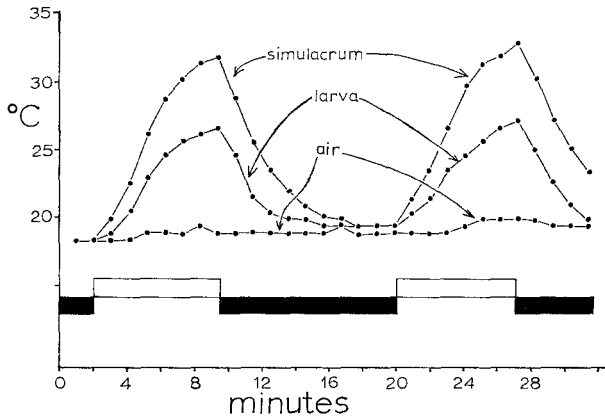


Fig. 3. Geometric similarity of heating and cooling curves of a *Colias* larva and the simulacrum-larva described in the text. White bar represents radiant load source (spot lamp) on, black bar represents the source off

mate the mass and thermal properties of insect hemolymph. This simulacrum, after being sealed and painted flat black (Krylon Nr. 1607), was provided with a thermistor probe and exposed to various radiant heating and shaded cooling conditions in company with one or more probed live larvae. Invariably the geometries of heating and cooling curves were similar between actual larvae and the simulacrum, though the latter always heated to a much higher equilibrium temperature than real larvae under radiant load, because of its maximal absorptivity. An example of this is shown in Fig. 3.

Description of Behaviors Studied. Larvae of *Colias*, like those of other holometabolous insects, are essentially "eating machines". Except for specialized behaviors connected with periodic molting, their only activities are feeding and movement to and from food, or escape from predators or unfavorable microclimate.

Young larvae feed by gnawing away the upper surfaces of leaves, creating small "pinholes"; they rest between feedings in the centers of leaves. Their avoidance of leaf edges may be important in eluding the search patterns of certain predators. It may also be involved in thermal balance, since a larva which is small compared to a leaf would be more subject to cooling air currents at the edge of the leaf than in the center. It may even be simply a means of avoiding falling off the leaf, since, for a small larva, falling clear of the food plant could pose difficulties in finding the food again. In any event, as the larvae grow they turn to eating the distal third or half of leaves, on both sides of the midrib. This pattern gives way in turn to the last instars' practice of selecting a suitable leaf, then first eating one side evenly down to the midrib and then as methodically consuming the other half. Large larvae consume several leaves in succession until satiated, then retire to the central stems of the food plant for a period of digestive processing. This ends with several defecations and the start of a new round of feeding on leaves. This pattern of retreat to the center of the plant when not feeding appears to be an adaptation to minimize the time spent by large, relatively conspicuous larvae at the leafy periphery of the plants, where they would be far more exposed to visually searching predators such as birds. Such predators are a major source of selective pressure on larvae (see below, and Gerould, 1921).

When subjected to decreasing or consistently low temperatures below 15°C, larvae move directly but not precipitously down food plant stems and seek shelter at the stem bases and among the ground litter. As ambient temperature rises to and above 15°C, they move upward again. Whether these are positive and negative geotaxes or phototaxes has not yet been determined.

If subjected to sudden heating by a strong radiant energy source (sunlight or spot lamp), first, second, and third instar larvae move immediately from the exposed upper surfaces of leaves to the shaded undersurfaces. Larger larvae move rapidly down the food plant stems and either remain motionless at the stem bases or seek further shelter among ground litter. In extreme heat stress, larvae "rear up" the head and the thoracic segments, cast these back and forth violently, then convulsively release the grip of the abdominal prolegs on the plant and drop to the ground. The distribution of both levels of heat avoidance behavior as a function of larval body temperature is shown in Table 1.

Table 1. Heat avoidance in fifth instar *Colias eurytheme* larvae. Occurrence of heat-avoiding behavior, as described in text, as a function of larval body temperature

Larval body temperature °C	Heat-avoidance behavior		Total observations	% avoidance
	Yes	No		
< 17		> 100	> 100	0
17-17.9	0	54	54	0
18-18.9	0	108	108	0
19-19.9	0	130	130	0
20-20.9	0	122	122	0
21-21.9	0	90	90	0
22-22.9	0	162	162	0
23-23.9	0	93	93	0
24-24.9	0	171	171	0
25-25.9	0	174	174	0
26-26.9	0	219	219	0
27-27.9	0	180	180	0
28-28.9	0	201	201	0
29-29.9	0	72	72	0
30-30.9	12	162	174	6.9
31-31.9	5	130	135	3.7
32-32.9	20	116	136	14.7
33-33.9	12	100	112	10.7
34-34.9	5	61	66	7.6
35-35.9	70	17	87	80.5
36-36.9	57	12	69	82.6
37-37.9	29	7	36	80.6
38-38.9	48	0	48	100.0
≥ 39				100.0

(The “extreme” heat avoidance behavior appears to be the same as that elicited by poking or other abrupt mechanical disturbance; either extreme heat conditions stimulate the same physical irritation sensors, or thermal receptors independently elicit the same response under “emergency” conditions.)

Under both temperature extremes, then, *Colias* larvae appear to seek refuge in the thermal buffering of ground mass and cover. Microclimate and behavioral data presented below further support this view.

Feeding Occurrence as a Function of Body Temperature. We know now that *Colias* larvae rely on behavioral interaction with their environment for thermoregulation. We ask next what, if any, is the thermal dependence of eating, their major function in life? Do the larvae have a range of preferred body temperatures for feeding, as the adults have for flight and activities dependent on flight? If so, do larvae of different populations have the same or different temperature preferenda?

Table 2. Thermal distribution of *Colias* larval feeding. Comparisons, and statistical degrees of freedom in χ^2 tests. P = probability of as much

°C	<i>C. eurytheme</i>						<i>C. p. eriphyle</i>		
	No probe			Probe			Feed	No feed	% feed
	Feed	No feed	% feed	Feed	No feed	% feed			
< 15	No feeding by any larvae								
15-16				0	94	0.0	17	791	2.1
17-18	8	224	3.4	3	310	1.0	36	844	4.1
19	12	161	6.9	8	210	3.7	34	423	7.4
20	7	193	3.5	12	233	4.9	59	438	11.9
21-22	14	611	2.2	20	565	2.4	194	1215	13.8
23	36	396	8.3	41	379	9.8	108	696	13.4
24	45	416	9.8	60	366	14.1	115	650	15.0
25	65	439	12.9	78	409	16.0	77	518	12.9
26	71	421	14.4	86	371	18.8	40	440	8.3
27	74	432	14.6	75	415	15.3	9	488	1.8
28	67	470	12.5	81	478	14.5	3	287	1.0
29	36	395	8.4	30	399	7.0	0	263	0
30	17	434	3.8	11	330	3.2	0	521	0
31	7	315	2.2	4	306	1.3			
32 ≤	No feeding by any larvae								

Before answering these questions, we must deal with yet another: Does the implantation of a probe alter the occurrence or thermal distribution of feeding behavior, even though the animals are not grossly injured physiologically? Ultimately, there is an uncertainty principle involved here, but we took advantage of the close thermal similarity of adjacent size-matched larvae (see above) to answer this question as far as possible. Size-matched fifth instar *C. eurytheme* larvae with and without implanted thermistors were, while closely adjacent on the same food plants, exposed to a variety of ambient temperature and radiant load conditions. Feeding or abstention from feeding was noted for both classes of larvae over 15-second intervals, and tabled as a function of the body temperatures of the larvae bearing thermistors, which represented as well the body temperatures of the larvae without thermistors to within the match of thermal experience noted above. The resulting distributions were tested for heterogeneity and, as Table 2 shows, no significant difference in frequency or thermal distribution of feeding is seen with and without thermistors. The probes, implanted by our methods, do not produce artifacts in the behavior studied.

evaluations, of feeding occurrence as a function of larval body temperature. $n =$ or greater heterogeneity in the data being due to chance

Heterogeneity tests					
<i>C. eurytheme</i> Probe vs. no probe			<i>C. eurytheme</i> vs. <i>C. p. eriphyle</i>		
χ^2	n	P	χ^2	n	P
—	—	—	1.04	1	$0.30 < P < 0.50$
3.02	1	$0.05 < P < 0.10$	6.21	1	$0.01 < P < 0.02$
1.50	1	$0.20 < P < 0.30$	2.98	1	$0.05 < P < 0.10$
0.24	1	$0.50 < P < 0.70$	8.43	1	$0.001 < P < 0.01$
1.13	1	$0.20 < P < 0.30$	47.03	1	$P \ll 0.001$
0.37	1	$0.50 < P < 0.70$	3.14	1	$0.05 < P < 0.10$
3.56	1	$0.05 < P < 0.10$	0.13	1	$0.70 < P < 0.80$
1.71	1	$0.10 < P < 0.20$	1.82	1	$0.10 < P < 0.20$
2.41	1	$0.10 < P < 0.20$	21.22	1	$P \ll 0.001$
0.04	1	$0.80 < P < 0.90$	55.99	1	$P \ll 0.001$
0.78	1	$0.30 < P < 0.50$	37.28	1	$P \ll 0.001$
0.38	1	$0.50 < P < 0.70$	17.57	1	$P \ll 0.001$
0.05	1	$0.80 < P < 0.90$	} 10.15	1	$0.001 < P < 0.01$
0.07	1	$0.70 < P < 0.80$			

Table 2 also presents a comparison of *C. eurytheme* and *C. p. eriphyle* larvae. Both show well-marked feeding maxima; however, these are not the same. *Eurytheme's* feeding is maximized between 23 and 29°C body temperature, but *eriphyle's* is maximized between 20 and 26°C. This difference is underscored by the tests of the two distributions: feeding activities of the two taxa are homogeneous only at the thermal extremes, where neither feeds, and in the zone of overlap of the two maxima. These larval responses differ from adult *Colias* behavior both in the dramatically lower temperature for activity (adult *Colias* are, in all species tested, most active at body temperatures of 35–39°C; Watt, 1969) and in the existence of significant differences between taxa in the zone of maximum activity.

Thermal Effects on Feeding Rate. We now know the temperatures at which larvae are willing to feed. We next ask: within this temperature range, how does the rate of feeding vary? Fifth instar larvae bearing thermistors were deprived of food for three hours to assure uniform emptiness of their guts, then placed on food plant under air temperature and radiant load conditions appropriately manipulated to generate

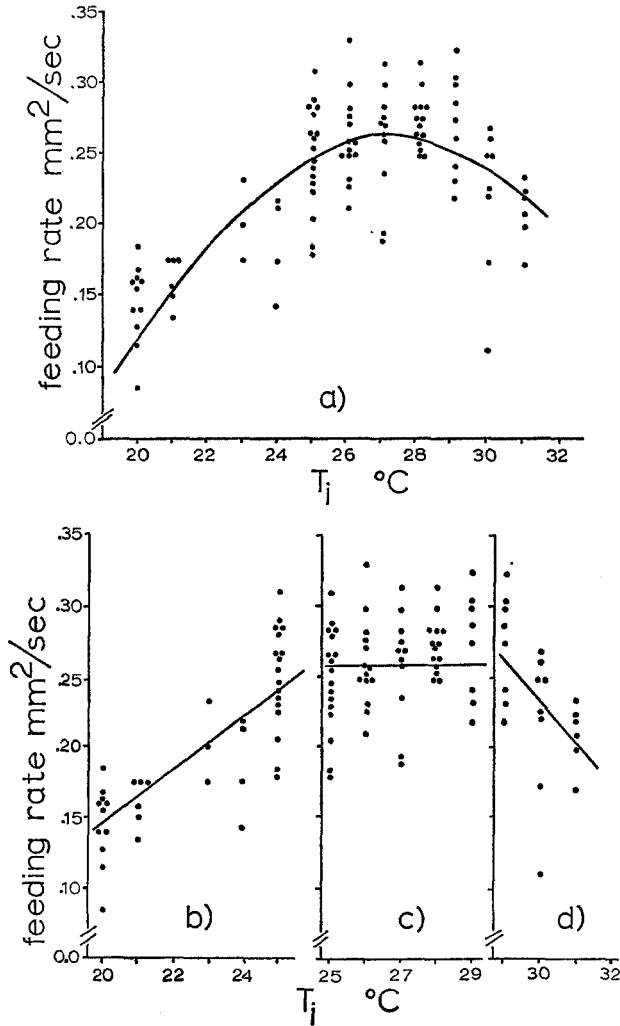


Fig. 4a—d. Feeding rates (ordinate), as mm² leaf surface eaten/sec, as functions of *Colias eurytheme* body temperature (abscissa). a) All data, best fit by a quadratic equation (computer-calculated, see text); b—d), same data, three separated body temperature ranges, each best fit by a linear equation. See text for comparative analysis of these treatments of the data.

various larval body temperatures. Leaf area consumed per bout of feeding was measured and plotted, as in Fig. 4 for *C. eurytheme*, against larval body temperature at the time of feeding. Data were then examined with the Multiple Regression Program (see above).

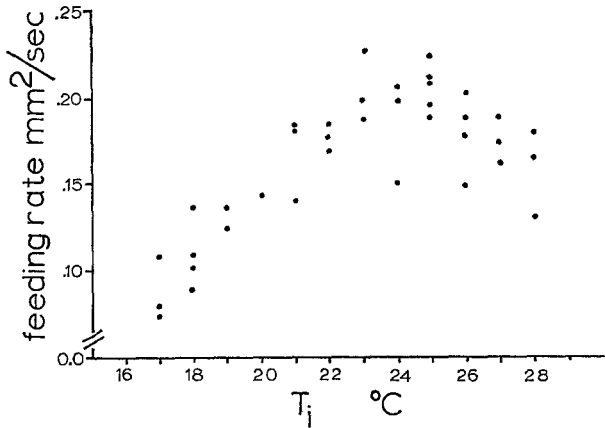


Fig. 5. Feeding rate as a function of *C. p. eriphyle* body temperature. Compare Fig. 4 and see text

The equation best fitting the *C. eurytheme* data, taken all together, is a quadratic, concave downward ($y = 1.53 + 0.131x - 0.0024x^2$; $F_{2,100} = 60.6$, $P < 0.001$). No obvious single molecular or physiological mechanism could generate such a relation between feeding rate and body temperature. Further data analysis reveals that significant straight lines can be unequivocally fit by the computer to two narrower ranges within these data. For 20–25°C, b (linear regression coefficient) = +0.019, $F_{1,39} = 58.5$, $P < 0.001$; for 29–31°C, $b = 0.030$, $F_{1,22} = 8.1$, $0.001 < P < 0.005$. A straight line is also the best fit to the intermediate range, 25–29°C, but its regression coefficient is not significantly different from zero: $b = +0.005$, $F_{1,64} = 3.1$, $0.05 < P < 0.10$. These facts strongly suggests that different processes, of different thermal dependence, are limiting feeding rate at different temperatures. It is noteworthy that the region 25–29°C, across which the maximum feeding rate occurs, also roughly coincides with the thermal maximum for the occurrence of feeding, and that in this range feeding rate is not a significant function of body temperature. Either some mechanical upper limit of feeding rate has been reached, or a process of active thermal compensation is at work.

Data of similar form, though lesser extent, are shown for *C. p. eriphyle* in Fig. 5. The area of maximum feeding rate is shifted downward in body temperature so as, again, to roughly coincide with the feeding occurrence maximum of this taxon.

Thermal Influence on Growth Rate. Since thermal effects on feeding are so striking and complex, we examined the effects of temperature on overall *Colias* larval growth rate. *C. eurytheme* larvae were reared at

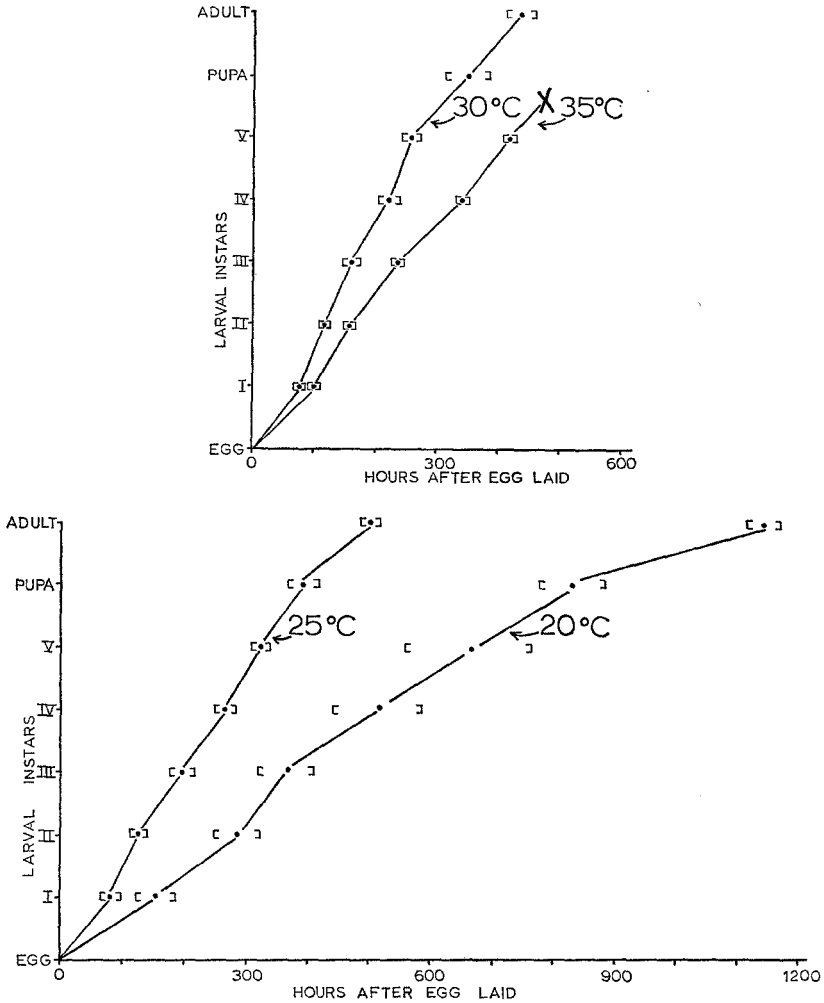


Fig. 6. Development rates of *C. eurythema* larvae at different rearing temperatures. Developmental stages on ordinate, time on abscissa. Dots indicate means, and brackets extremes, of times of entry into the stage in question. The smallest sample size for any stage and temperature is 9 (adult eclosion, 20°C); most are 20 to 30 or more. "X" in the 35° plot indicates death during the fifth instar of all larvae reared at that temperature

20°, 25°, 30°, and 35°C; temperatures of all rearing chambers were verified with the same micro-environment sensors used in field thermal work. Growth was measured by noting the time of each molt, starting with egg hatch. Fig. 6 shows the resulting data. It is striking that growth

rates are essentially the same at temperatures at both ends of the feeding maximum, and lower at temperatures above and below that. No larvae survived to pupation at 35°C. Preliminary experiments indicate that these effects of temperature on growth rate, whatever their detailed nature, are not subject either to acclimation within the individual life span or to influence by maternal experience. More work will be needed to verify fully the absence of acclimatization phenomena in growth rate control and to look for them in other aspects of larval thermal biology.

Interaction of Colias Larvae with Thermal Microclimate. It is clear from the above that *Colias* larvae have: a) a surprisingly narrow common temperature range for maximizing the rates of various vital processes; b) a repertoire of behavioral responses capable in principle of maximizing time spent in that temperature range. If the behavior does in fact operate in this way, one should be able to predict wherein its natural microhabitat a larva would be found during the day, given data on thermal parameters of that microhabitat over the same time. To do this quantitatively will require biophysical studies of solar energy absorption by larvae, etc., beyond the present work. However, we can already predict roughly as follows:

Having taken refuge during the night in the thermal buffering capacity of the ground, larvae should make their way up the plant as air temperature and solar load increase during the morning. They should feed when and where their internal temperatures become optimal. If air temperature and solar load increase so as to raise exposed larvae above their optimum, they will retreat into shade, but even in shade they will cease to feed if ambient temperature rises above optimum.

Fig. 7 presents microclimate and behavioral evidence to show that these predictions are confirmed in practice. Larvae do indeed climb up to feed in those parts of the plant where they can first achieve their thermal preference range, and are later driven downward by excessive solar load. When even the best air temperature is too high, they take such shelter as is available on or near the ground and remain inactive. If clouds interrupt the afternoon heat, further activity in upper parts of the plants is allowed.

Discussion

Why is it that *Colias* larvae are adapted to function at far lower body temperatures than their adults? Further, why do larvae of different populations or taxa show different thermal preferences, in contrast to the adults, which are invariant in this respect?

The answers may well lie in the fact that *Colias* larvae are exposed by their mode of feeding to severe pressure from visually searching predators,

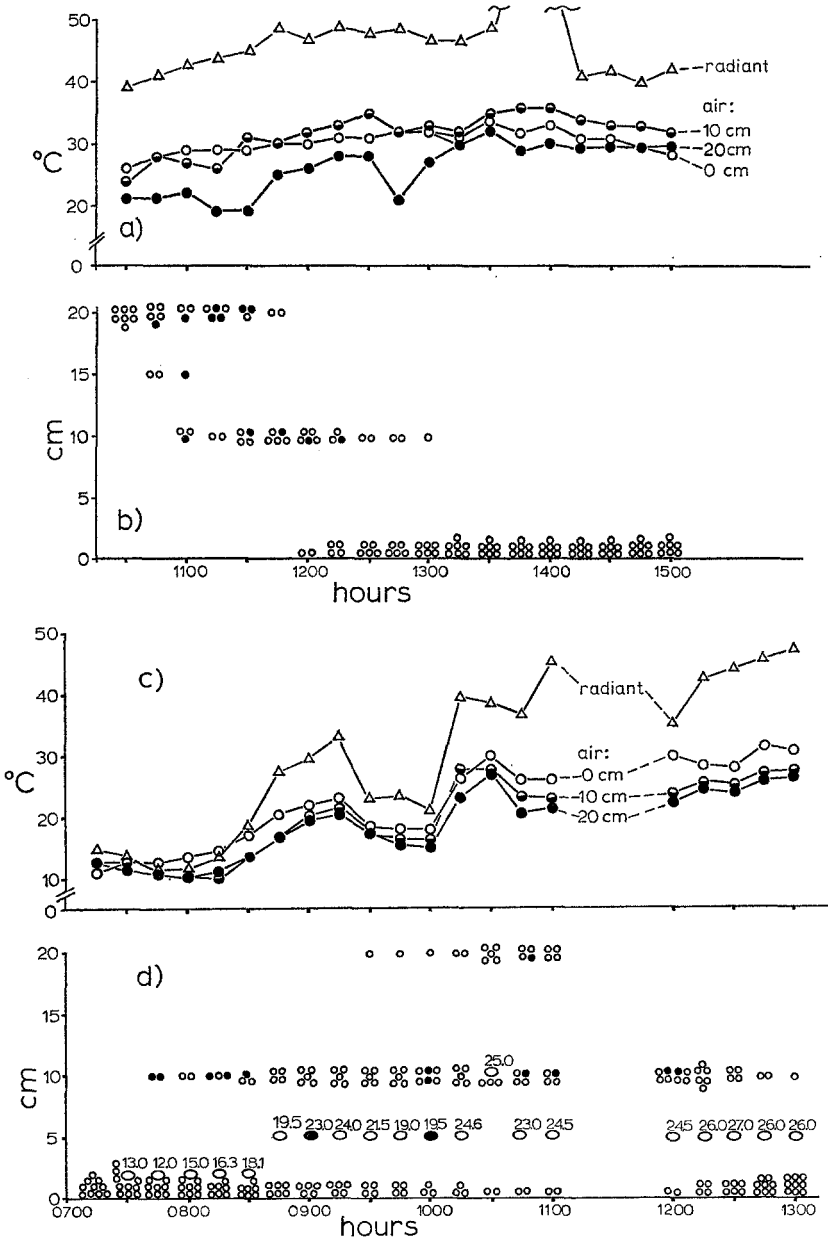


Fig. 7a—d. Movement and feeding of *C. glaucaria* larvae in wild food plants in relation to microclimate through the day. a) and b), data of 23 August 1971. a), thermal microclimate: Black body temperature at 20 mm above ground as measure of solar radiant heat load, triangles; air temperature, 0, 10, and 20 cm above ground,

notably birds. To this they have adapted by evolving a cryptic green coloration, with lateral and dorsal stripe patterns mimicking highlights on plant stems, which is highly stereotyped throughout the genus (see Fig. 1). Gerould (1921) showed its effectiveness, finding that sparrows efficiently consumed *Colias* larvae mutant to a blue coloration (the trait, a simple Mendelian recessive, segregated from inbreeding of a wild stock), when these were placed outside on food plants. These same sparrows failed to find normally colored larvae placed on the same plants at the same time in similar numbers. One can then argue that such predator pressure for cryptic coloration has kept larvae from evolving darker or lighter pigmentation for solar energy absorption or reflection, as the adults have done (Watt, 1968, 1969). The larvae, denied this adaptive option, have had to "grin and bear" differences in temperature, adapting to function at habitat-specific body temperature ranges, which are lower than those of the adults.

This explanation would predict an orderly relation between larval thermal biology of *Colias* populations and the thermal properties of their microclimates: the lower ambient temperature, radiant energy load, etc., go, the lower should be the thermal preferences of resident larval populations. The two populations studied so far agree with this prediction, but that is hardly a sufficient test; more need to be examined. It is of interest that so far no evidence for the use of "acclimation" as an adaptive response has been found. This suggests, so far as the present data go, that all local thermal adaptation of larvae is due to natural selection upon relevant genetic variability. There might well be some lower limit below which a given species could not adapt. If so, this might be an important factor limiting the distribution of arctic-alpine or other cold-habitat *Colias* and related insects.

Given that *Colias* larvae are thermally distinct from their adults in many ways, the nearly equal narrowness of the thermal optima of these developmental stages is striking. If the larvae are going to vary their thermal optima with microhabitat anyway, why not evolve a far wider range of thermal tolerance? It is tempting to speculate that key aspects

open, half open and filled circles, respectively. b), positions of larvae in the plants ± 2.5 cm. Filled circle, larva feeding; open circle, larva not feeding. c) and d), data of 25 August 1971. c), thermal microclimate. Symbols as in (a). d), positions of larvae in the plants ± 2.5 cm. Filled and open circles as in (b). Filled oval, larva feeding with thermistor implanted. Open oval, larva with thermistor not feeding. The number above each oval is the temperature, in $^{\circ}\text{C}$, of the probed larva at that time. Note that feeding position and temperature were recorded only on strict 15-minute intervals, so that additional feeding, and minor changes of position frequently took place in between

of their metabolism simply cannot be organized to operate at maximal efficiency over a range of more than a few degrees Centigrade, wherever on absolute temperature scales that range may lie. Other speculations might be developed. This one should be testable once we know more than we now do about the overall metabolic organization of these insects, and about mechanisms of their thermal adaptation at the biochemical level.

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Paul W. Sherman
 Department of Zoology
 University of Michigan
 Ann Arbor, Michigan 48104, U.S.A.

Dr. Ward B. Watt
 Department of Biological Sciences
 Stanford University
 Stanford, California 94305, U.S.A.