THE EFFECT OF BAROMETRIC PRESSURE AND OTHER FACTORS ON ECLOSION OF THE CABBAGE BUTTERFLY *PIERIS RAPAE* (PIERIDAE)

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The literature describes various effects of barometric pressure on insects. For example, there is evidence that slightly reduced pressure increases the rate of development of insects while slightly increased pressure has no positive influence (Wellington, 1946). *Pieris rapae* (L.) is said to lay more eggs when the barometric pressure is low (Stephens and Bird, 1949), while low pressure appears to be disadvantageous to at least one insect activity in that a slight depression is reported to prevent the silkworm from secreting silk (Markovic-Giaja, 1957).

Of particular interest is the assertion that lowering of the barometric pressure is necessary for successful eclosion of butterflies (Pictet, 1933), including *Pieris rapae* and *Pieris brassicae* (L.); it was recorded that 91.3% of 1758 pupae eclosed during atmospheric depression. Also, certain Lepidoptera are supposed to be so sensitive to the effect of barometric pressure that they eclose when the pressure falls only 1.7–3.4 mm of mercury below the daily maximum (Mell, 1939).

The present work is in large part an evaluation of the effect of pressure on eclosion of the subject species by means of observations at ambient conditions and also by controlled experiments.

ECLOSION UNDER AMBIENT CONDITIONS

The pressure in the central area of a typical "high" is about 765–773 mm, while a "low" is normally 743–750 mm (Anonymous, 1960). In the New York City area the mean pressure in summer generally is about 762 mm.

The data of Table 1 are for successive broods in a culture started with eggs laid by *Pieris rapae* taken at Flemington, New Jersey on May 1, 1965. It is apparent that the barometric pressure was relatively high, and certainly not considerably depressed, during eclosion. The impression is that the time of eclosion was controlled simply by the time required for maturation of the pupa (7–10 days, approximately). The possibility would seem to remain that eclosion might be delayed by an unusually high pressure, e.g. 788 mm as recorded in New York City for record highs in 1927 and 1949 (Hansen, 1961), and the effect of extremely high pressures was studied m the experiments discussed below.

				Conditions during eclosion ¹			
Num- ber eclosed	Pupa- tion (day)	Eclosion (day)	Date eclosion started	Relative humidity Temperature (%) (°F)		Barometric pressure (mm)	
38 51 37 16	$0-6 \\ 0-5 \\ 0-3 \\ 0-5$	9-15 14-18 ³ 7-10 9-13	June 6, 1965 July 11, 1965 Aug. 11, 1965 Sept. 16, 1965	38-55 49-62 48-60 60-65	75–90 77–87 78–89 72–84	$\begin{array}{c} 754-766^2 \\ 758-766 \\ 761-765 \\ 760-770 \end{array}$	

TABLE 1. BAROMETRIC PRESSURE DURING ECLOSION UNDER AMBIENT CONDITIONS

¹ The barometric pressure readings are corrected to 0° C and sea level. ² The pressure was in the 759–766 mm range except for the last day.

³ The pupae had been refrigerated from day = 6 to day = 12.

ECLOSION UNDER CONTROLLED CONDITIONS—EXPERIMENTAL

Rearing of larvae.—Larvae were reared in cardboard boxes with gauze windows and fed cabbage leaves from refrigerated heads as in previous work (Kolver, 1966).

The pupae used for experiment 1 derived from eggs laid on August 6 and 7, 1966 by females taken at Berkshire Valley and Morristown, New Jersey. Pupation took place 17-21 days after the inception of hatching on August 9. The larvae were reared in a room at 73–91°F and 40-70% relative humidity.

The pupae for the remaining experiments were reared from eggs obtained from N. R. Spencer of the U. S. Department of Agriculture (see Acknowledgment). A minor portion of the final-instar larvae evidenced black spots on the integument, but fortunately there was no effect on pupation or eclosion. Pupation took place 26-29 days after the inception of hatching on April 7, 1967. The room was at 67-79°F and 25-34% relative humidity during the larval period. Incidentally, two male adults from this brood were of the canary-yellow form (one eclosed in experiment 2 and one in experiment 5).

Experiment Number	Pressure (mm)	Photoperiod	Relative Humidity (%)		
1	735-740 and 765-770 ²	no	43 at 72°F		
2	735-740 and 765-770 ²	yes	43 at 72°F		
3	690–700 and 790–800 ²	no	43 at 72°F		
4	825-830	ves	43 at 72°F		
5	ambient	yes	87 at 75°F		
6	ambient	yes	43 at 72°F		

TABLE 2. SUMMARY OF EXPERIMENTAL CONDITIONS

 1 Diffuse sunlight (from windows with southern exposure) from 7:27 AM to 5:03 PM. 2 Cycled from one range to the other every 4 hours and 48 minutes (five times per day).



Fig. 1. Apparatus used for experiments 1-4.

Final-instar larvae were sorted quite reliably into males and females by means of the testes visible in the male as done in previous work (Kolyer, 1966), and the sexes were allowed to pupate in separate boxes.

Apparatus and procedure.—The apparatus shown in Figure 1 was used for experiments 1–4 (summarized in Table 2). This consisted simply of two one-liter flasks connected through their side-arms and fitted with a stopcock (and pinch clamp, not shown, for perfect seal) and mercury-containing manometer open to the atmosphere. Gauze was provided in the flasks so that the emerging butterflies could climb up and expand their wings.

Vials (approximately one inch inside diameter) containing saturated potassium carbonate solution in contact with solid potassium carbonate hydrate were suspended inside the flasks to regulate the relative humidity. A value of 42.8% relative humidity at 77°F is given by Stokes and Robinson (1949), and 43% at 72°F was found experimentally by confining a calibrated hygrometer with the potassium carbonate system. The capacity of the system to absorb water was demonstrated by introducing one milliliter of water into a one-gallon jar containing a hygrometer and the regulating system in a 2.5 inch diameter dish. In about five



Cumulative number eclosed vs. day from start of pupation for experiment 1. A record of temperature is included.

hours the relative humidity had risen to a maximum of 81% and at 50 hours it had fallen back to 50%; in the absence of the system 100% relative humidity was attained about 10 hours after adding the water.

Pupae, detached by clipping the silken girths and pulling free from the silk button at the caudal end, were dropped into the flasks (males in one flask, females in the other) three days before eclosion began, and maintenance of conditions as defined in Table 2 was initiated.



Cumulative number eclosed vs. day from start of pupation for experiment 2.

In the graphs and tables each day is arbitrarily taken to begin at 2:39 AM and is divided into five equal periods (beginning at 2:39 AM, 7:27 AM, 12:15 PM, 5:03 PM, and 9:51 PM). At the start of each period the barometric pressure and the room temperature were noted, and the pressure was cycled in the case of experiments 1–3. The object of cycling was to give the pupae a choice of high or low pressure every five hours.





EXPLANATION OF GRAPH 3

Cumulative number eclosed vs. day from start of pupation for experiment 3.

For reference, the first period of the 8th day on Graph 1 was a high cycle, as was the first period of the 11th day for Graphs 2 and 3.

The data are presented in Graphs 1–7. The temperature record for experiment 1 is included in Graph 1, while the temperature record for experiments 2–6 (all done at the same time) and the barometric pressure record applicable to experiments 5 and 6 are shown in Graph 7.



EXPLANATION OF GRAPH 4 Cumulative number eclosed vs. day from start of pupation for experiment 4.

The barometric pressure readings in Graph 7 were used to adjust the pressure in the flasks. For example, if the atmospheric pressure was 760 mm and a pressure of 740 mm was desired in the flask, a differential of 20 mm on the manometer was produced by drawing out air by lung power and closing off the stopcock and the pinch clamp. A rubber bulb was used to pressure the flasks in the high cycles. To correct the pressure readings, which were taken at Convent, New Jersey at an elevation of 290 feet, to 0°C and sea level, approximately 4 mm must be added (Perry, 1950). The flask pressures listed in Table 2 are ranges because some fluctuations necessarily accompanied temperature variations.

In experiments 5 and 6, wide-mouth jars (approximately 3.5 inches inside diameter by 5 inches deep) contained the pupae and humidity-regulating system. The jars were closed tightly enough to maintain regulated humidity but not to hold a pressure differential relative to the atmosphere. The potassium carbonate system was used in experiment 6, while in experiment 5 a saturated sodium carbonate solution in contact with solid hydrated sodium carbonate was included. The sodium carbonate system gave 87% relative humidity at $75^{\circ}F$ experimentally; Lange (1946) lists 92% at $65^{\circ}F$.

ECLOSION UNDER CONTROLLED CONDITIONS—RESULTS AND DISCUSSION The five factors considered were barometric pressure, light, tempera-

		Nu	umber Eclose		
Experiment Number	Pressure	Male	Female	Total	Theoretical Random Distribution
1	low	7	16	23	25
	high	12	15	27	25
2	low	13	13	26	24
	high	11	11	22	24
3	low	7	13	20	24
	high	17	11	28	24

TABLE 3. ECLOSION DURING ALTERNATING CYCLES OF HIGH AND LOW PRESSURES

ture, relative humidity, and sex. The results are discussed in terms of each of these.

Barometric pressure.—The data summarized in Table 3 show no significant trend with respect to barometric pressure. By the chi-square method of testing goodness of fit (Sinnott and Dunn, 1939) it is found that the differences observed in the total numbers eclosed at high vs. low pressure can very possibly be explained by chance alone (Table 4).

In experiment 3 the low pressure was below one of the lowest on record (721 mm) for New York City (Hansen, 1961), and the high pressure was above a record high (788 mm). In experiment 4, in which the pressure was held constant at an abnormally high level, the butter-flies had no notable difficulty in eclosing (one unexpanded and one with shriveled forewing vs. two imperfect specimens in experiment 1, three in experiment 2, and one in experiment 5). Also, eclosion in experiment 4 was not delayed and proceeded over about the same time interval as in experiments 2, 3, 5, and 6.

In experiment 1 the larvae were diseased, and only 11 specimens (4 males and 7 females) expanded normally. It is interesting that 7 of these (all but 4 of the females) eclosed during the high pressure cycle, showing the lack of advantage of low pressure even when expansion ability was marginal.

Experiment Number	χ^2	Approximate Probability of Observed Deviation by Chance Alone ⁴				
1	.320	58				
2	.333	57				
3	1.33	25				

TABLE 4. SIGNIFICANCE OF DATA (TOTAL ECLOSED) OF TABLE 3

¹ For one degree of freedom.

	Experiment 1			Experiment 2			Experiment 3		
Period ¹	Male	Female	Total	Male	Female	Total	Male	Female	Total
1	0	4	4	1	2	3	1	4	5
2	7	2	9	21	18	39	7	7	14
3	6	14	20	2	2	4	7	9	16
4	5	6	11	0	2	2	4	3	7
5	1	5	6	0	0	0	5	1	6
	Experiment 4			Experiment 5			Experiment 6		
Period	Male	Female	Total	Male	Female	Total	Male	Female	Total
1	0	0	0	0	1	1	2	0	2
2	7	10	17	9	6	15	4	7	11
3	2	2	4	1	4	5	3	2	5
4	0	0	0	0	0	0	1	0	1
5	0	0	0	0	0	0	0	2	2

TABLE 5. ECLOSION VS. TIME OF DAY

¹The day was divided into five equal periods beginning at 2:39 AM.

Pupae which are prepared to eclose appear to be able to wait several hours for the stimulus of light and so might have been expected to take advantage of the occurrence of low pressure cycles every four hours and 48 minutes if reduced pressure also is a stimulus.

As expected, there was no real correlation of eclosion with ambient barometric pressure in experiments 5 and 6. For example, eclosion in experiment 5 was concluded at the high point of the pressure record. In view of the data of Table 1 and the results of experiments 1–4, the fortuitous drop in pressure seen in Figure 7 probably had no bearing on eclosion.

Light.—In experiments 1 and 3 the pupae were kept in darkness except for brief intervals of light when the pressure was adjusted between periods. The data (Table 5) indicate a preference for periods 2-4 (7:27 AM—9:51 PM) in experiments 1 and 3, and the chi-square test (four degrees of freedom) shows less than a 5% probability that the results are due to chance alone. It is possible that temperature variation and/or brief admission of diffuse sunlight at the beginning of the favored periods was responsible. However, David and Gardiner (1962) report a rhythm of eclosion for *Pieris brassicae* in darkness.

In experiments 2, 4, 5, and 6, in which diffuse sunlight was available during periods 2 and 3, there resulted a very marked preference for eclosion during the photoperiod. Only 40% of the pupae should have eclosed during the photoperiod by chance, while the result was 90%. The chi-square test shows that in all cases the deviation from chance



EXPLANATION OF GRAPH 5 Cumulative number eclosed vs. day from start of pupation for experiment 5.

distribution is highly significant. Graphically, the stepwise nature of the curves for experiments 2, 4, 5, and 6 is conspicuous.

The impression is that the mature pupa can wait several hours for the arrival of the photoperiod before eclosing, and it is reported (Mell, 1939) that butterflies generally eclose in the early morning and that the coming of light seems to be the stimulus. In a study including *Pieris rapae*, 85.9% of 1758 pupae eclosed from 8 AM to 6 PM and the remaining 14.1% at night (Pictet, 1933).

Temperature.--In experiments 2-6 the temperature varied over a



TIME, DAYS FROM START OF PUPATION



range of 9° F (Graph 7). Low points occurred at the beginning of period 1 (2:39 AM) in all cases, and high points occurred at the beginning of periods 3 or 4. The fluctuations were similar in magnitude, though less regular, in experiment 1 (Graph 1).

It would seem that the effect of light as a factor is predominant in the experiments having a photoperiod (2, 4, 5, and 6), but some temperature fluctuation may be required for photoperiod to promote eclosion; David and Gardiner (1962) report that for *Pieris brassicae* eclosion takes place in the dark period with photoperiod 6 AM—10 PM when the temperature is constant but that eclosion is delayed until morning or afternoon when the temperature fluctuates.

Relative humidity.—Very high humidity may delay eclosion of certain moths (Mell, 1939). However, in experiment 5 eclosion at 87% relative humidity was certainly not hindered, nor was it judged significantly accelerated or delayed vs. eclosion at 43% relative humidity. As in the other experiments, light appeared to be the dominant factor (though possibly through interaction with temperature fluctuation pattern). Eclosion of the males was completed during the highest phase (763–766 mm, corrected to 0°C and sea level) of the ambient pressure record,



Record of barometric pressure and temperature during experiments 2–6.

and it is suspected, though it was not experimentally demonstrated, that controlled variations of the pressure would have had no more effect at 87% relative humidity than they were found to have in experiments 1–3 at 43%.

At a lower relative humidity under ambient conditions (23-34% relative humidity, $72-76^{\circ}F$), five males eclosed at 764, 763, 761, 766, and 759 mm (corrected to 0°C and sea level). Again, reduced pressure was not required.

Sex.—In Pieris napi (L.) and P. bryoniae (Ochs.) the males are said to tend to emerge before the females (Bowden, 1953). However, in experiments 1–3 the sexes eclosed over almost exactly the same time interval and at about the same rate; if anything, the females tended to eclose a little earlier in experiments 2 and 3. In experiments 4 and 6 the females tended to eclose considerably earlier, though the significance of this is dubious because of the limited numbers involved. Certainly, there was no trend for the males to emerge before the females in any of the experiments. This conclusion is, of course, applicable only to the specific conditions of the tests.

CONCLUSION

Care must be taken in drawing generalized conclusions from the data because of the possibility of the interaction of factors, the possibility of discontinuities in cause-effect relationships, and the possible effect of rate of change of variables. For example, at some critical values for the three variables the relative humidity, temperature, and barometric pressure might interact so that the pressure *does* influence eclosion. Or the effect of pressure might be nil at slight or major depressions but unexpectedly apparent at medium depressions. Or eclosion might be promoted not simply by low barometric pressure but by the dynamic factor of *falling* pressure.

Therefore, the present work does not prove that barometric pressure cannot influence eclosion of *Pieris rapae* but only that it does not influence eclosion under specific ambient conditions or in certain controlled environments. In fact, even the strain of a species conceivably could have an effect. Still, it seems a reasonable conclusion that light is a principal factor (as appears in the literature) and that barometric pressure is not a significant factor under certain typical summer ambient conditions or when cycled between extreme values, or held at a constant high value, in experiments at constant relative humidity, slightly fluctuating temperature ($9^{\circ}F$ maximum variation), and controlled photoperiod.

The indication is that the time of eclosion was controlled to the nearest day or so simply by the rate of development of the pupa (in turn controlled by the temperature history; David and Gardiner (1962), for example, list a pupal period for *Pieris brassicae* of 40 days at 54.4° F and only 7.5 days at 86° F). Then, under the particular conditions of the tests, which involved some temperature fluctuation, the mature pupa showed a strong tendency to await the coming of light as stimulus for eclosion. No obvious effect of sex, relative humidity, or barometric pressure upon this process was seen.

SUMMARY

Under typical summer conditions, pupae of *Pieris rapae* (L.) were observed to eclose at up to 770 mm barometric pressure with no apparent preference for atmospheric depression, although reduced pressure has been described in the literature as a requirement for eclosion of certain Lepidoptera.

Under controlled conditions, male and female pupae were studied separately. The relative humidity was held constant, the temperature fluctuated over a maximum of 9°F with minima at night, and a photoperiod (diffuse sunlight) of either 0 or 9.6 hours was provided. The barometric pressure was held at a constant high level (approx. 830 mm) or cycled from approx. 735 to 770 mm or from approx. 690 to 800 mm five times per day to give eclosing pupae a choice of high or low pressure. No significant dependence of eclosion on barometric pressure or sex was found, but light stimulated eclosion under the test conditions. There was no notable difference in eclosion at 87% vs. 43% relative humidity.

The indication is that the time of eclosion was controlled within a day or so simply by the rate of development of the pupa (dependent on temperature history), and that light, if available, then was the immediate stimulus for eclosion in a very significant proportion of cases. It is emphasized that conclusions must be confined to the particular experimental conditions.

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FOODPLANTS OF CALLOPHRYS (INCISALIA) IROIDES

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In contrast with other members of the subgenus, which are restricted in host selection, *I. iroides* (Boisduval) is polyphagous. The diverse host plants credited to this West Coast butterfly are summarized by Clench (1961), who indicates some of the early records are doubtful.

Recorded foodplants for *iroides* include "young apples" (*Malus*, Rosaceae) in British Columbia (Bethune, 1904) and both *Ceanothus* (Rhamnaceae) and *Cuscuta* (Polemoniaceae) in southern California (Comstock and Dammers, 1933). Field oviposition was observed and larvae reared on *Cuscuta*, a leafless, parasitic plant which lacks chlorophyll. Clench also lists *Gaultheria* and *Arbutus* (Ericaceae) as hosts but does not cite the original source of these records.

Recent investigations during California Insect Survey activities confirm use of two of these foodplants in central and southern coastal California and have disclosed the use by *I. iroides* of *Chlorogalum pomeridianum*, a monocotyledenous plant in the foothills of the Sierra Nevada.

A nearly mature larva was collected on *Arbutus menziesii* at China Camp, Marin County, June 3, 1964, from which an adult *iroides* was reared, emerging on April 19, 1965. *Ceanothus* probably is commonly used by *iroides* over much of its range. One larva was swept from *C*.