

## Body Temperatures and Behavioural Thermoregulation Strategies of Three *Pieris* Butterflies in Relation to Solar Radiation

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**Abstract** — Behavioural thermoregulation of 3 *Pieris* butterfly species, *P. rapae*, *P. melete* and *P. napi*, was examined in relation to the intensity of solar radiation. To evaluate solar radiation intensity, the temperature ( $T_{wr}$ ) was measured with a mercury thermometer whose bulb was covered with white cloth and exposed to direct sunlight. On clear days, the diurnal air temperature was between 16 and 28°C. The  $T_{wr}$  varied between 18 and 45°C, while the temperature in the shade was under 25°C. When the  $T_{wr}$  was under 28°C, the body temperatures ( $T_b$ ) of butterflies closely coincided with it. Butterflies with  $T_b$ 's under 26°C were resting, while those with  $T_b$ 's between 26 and 28°C were basking. When  $T_{wr}$  was between 28 and 40°C, the butterflies were active and their  $T_b$ 's were always lower than  $T_{wr}$ , never exceeding 36°C, though body temperatures could be artificially elevated easily up to the level of  $T_{wr}$ . When  $T_{wr}$  exceeded 40°C, butterflies showed species-specific heat-avoiding behaviour. *P. rapae*, whose habitat resources exist in the sun, intercepted solar radiation by closing the wings over the body. *P. melete* and *P. napi*, however, whose main habitat resources exist in the shade, moved into the shade. Strictly speaking, it is concluded that both butterflies, in many cases, leave shaded habitats for sunny habitats to elevate their  $T_b$  rather than enter the shaded habitats for heat-avoiding.

Insects, like other ectotherms, often regulate their body temperatures by behavioural means, and many of them thermoregulate by varying their exposure to solar radiation and air temperatures (see review by Casey 1981). For example, desert cicada and tenebrionid beetles shuttle between sunny and shady areas (Heath & Wilkin 1970; Edney 1971), dragonflies vary their postures from positive to negative orientation in sunlight (May 1976), and locusts thermoregulate by adopting stiling and crouching postures on heated ground (Waloff 1963). However, in most studies, air temperature, not solar radiation, has been used as the sole index of thermal environmental conditions, and consequently thermoregulation is usually examined only in relation to this factor. It may be impossible to precisely analyze the behavioural responses of insects to thermal conditions using air temperature alone because body temperatures can differ markedly from air temperature when animals are exposed to the direct rays of the sun.

Some authors have measured direct solar radiation to describe the thermal environment (Stower & Griffiths 1966; Hamilton 1971; Douwes 1976; Rawlings 1980; Chappell 1983; etc.). Others have studied behavioural responses of insects, mainly desert insects, to thermal conditions other than air temperature (Waloff 1963; Hadley 1970; Heath &

Wilkin 1970; Edney 1971; Hamilton 1971; Holm & Edney 1973; Edney et al. 1974; Henwood 1975; Casey 1976; Chappell 1983), measuring microclimate conditions of habitats such as temperatures of ground surface, burrows, leaves and shrubs, and attempted to correlate behavioural thermoregulation with these microclimate conditions. However, they have not measured the body temperatures in association with solar radiation.

Although butterfly activity patterns are known to be greatly influenced by direct solar radiation (Clench 1966; Watt 1968; Douwes 1976; Douglas & Guala 1978; Rawlings 1980; Suzuki et al. 1985; Kingsolver 1985), in many cases, butterfly thermoregulation has only been examined in the context of air temperature.

In this paper, I show the different behavioural thermoregulation patterns of 3 *Pieris* butterfly species, *P. rapae*, *P. melete* and *P. napi*, in relation to the intensity of solar radiation. To evaluate the intensity of radiation, the temperature was measured with a mercury thermometer whose bulb was covered with either white or black cloth and exposed to direct sunlight. I then discuss ecological aspects of behavioural thermoregulation, especially the relationship between habitat characteristics and habitat use.

## Materials and Methods

*Pieris rapae crucivora* Boisduval, *P. melete* Ménétriés and *P. napi japonica* Shirôzu occur throughout Japan and have 6, 3 and 3 annual generations respectively in Inabu, Aichi Prefecture (Ohsaki 1982). The forewing lengths of the spring form male of these species are on average  $27.7 \pm 0.9$  ( $\pm$ SD),  $31.1 \pm 1.1$  and  $27.5 \pm 1.0$  mm respectively (Ohsaki 1982). The larvae of all 3 species feed on cruciferous plants and coexist in mountainous areas (Ohsaki 1979).

The research was conducted from late April to early June 1981, in mountainous areas in Kurama, Kyoto, for *P. rapae* and *P. melete*, and in Nose, Osaka, for *P. napi*.

To identify the microhabitat utilization of each butterfly species, the movement pattern of females between sunny and shady areas was observed in field and documented by speaking into a tape recorder for later transcription. Such movement observations were restricted to clear sunny days when many butterflies were active.

Thermal microhabitat conditions were monitored as air temperature and solar radiation intensity at 1.5 and 0.3 m height above ground respectively. To evaluate solar radiation intensity, the temperature was measured with a mercury

thermometer mounted on white board, the thermometer bulb being covered with either white or black cloth which was exposed to the sun's rays. The thermometers measured what I term the "white radiation temperature ( $T_{wr}$ )" and "black radiation temperature" respectively. These temperatures were also measured in the shade. Temperatures were read at 15 min intervals from 7:00 to 18:00.

Body temperature ( $T_b$ ) was measured using a portable digital thermometer (Yokogawa Electric Works, Ltd. Type 2575) with a copper-constantan thermocouple probe of 0.6 mm diameter (Nara Electric Institution Ltd.). Each butterfly captured by a silk net was quickly taken from the net by holding the tips of both forewings and the thermocouple probe inserted to the center of the thorax from its ventral side. If the butterfly's body was touched or if the period from capture to measurement exceeded about 7 s, the reading was discarded.

Behaviours of butterflies were classified into 3 categories as follows: Resting, folding the wings tightly over the back and never orienting the body broadside; Basking, positioning the dorsal surface of the thorax perpendicular to the rays of the sun with the fore- and hind-wing to the sides of the body; Flying, flying or visiting flowers for a short

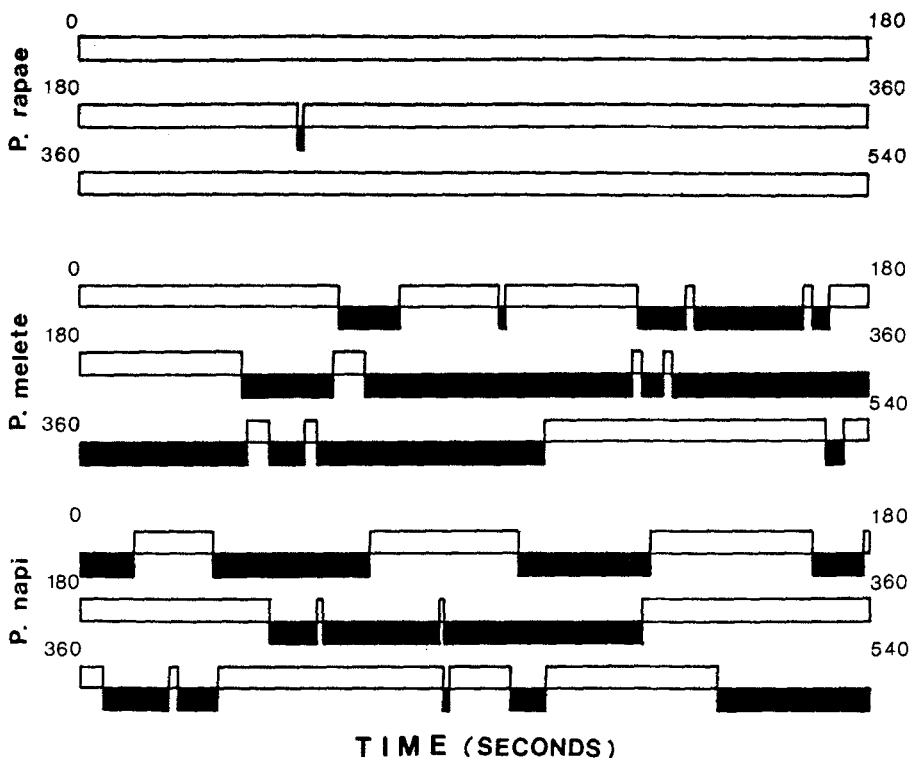


Fig. 1. Examples of movement patterns of individual butterflies (female) between the sun and shade for 9 min. White and black bars indicate sunlit and shaded areas respectively.

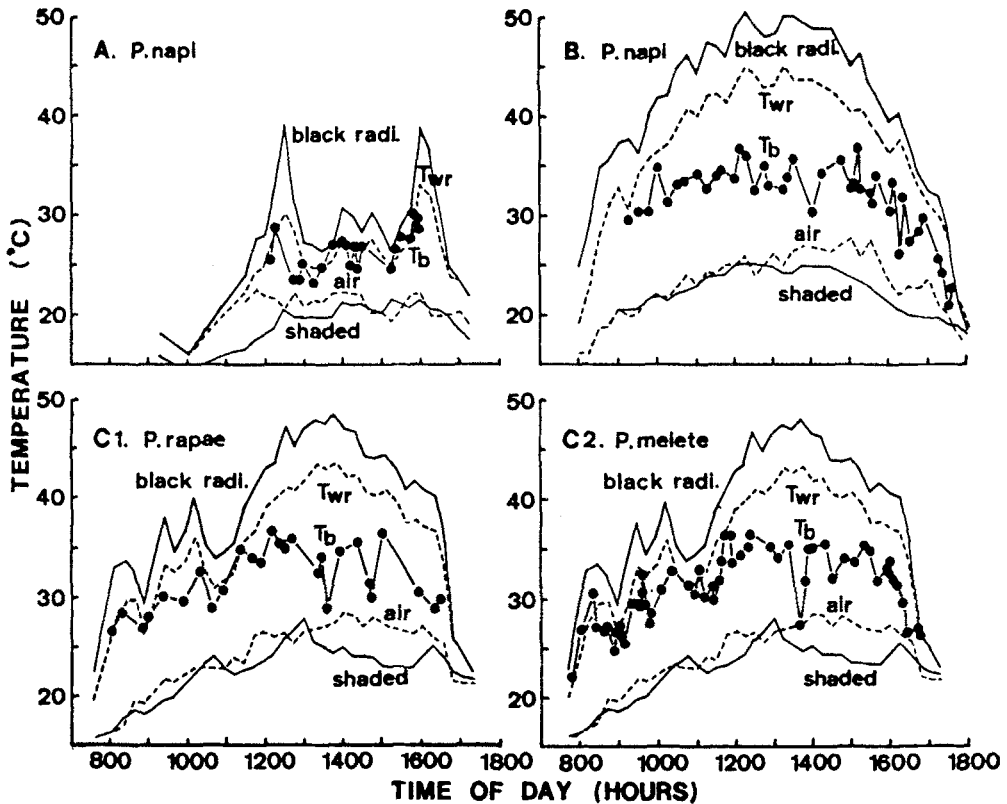


Fig. 2. Thermal conditions and body temperatures of butterflies. Black radi., black radiation temperature;  $T_{wr}$ , white radiation temperature; Air, air temperature; Shaded, shaded temperature;  $T_b$ , body temperature. Each circle indicates the body temperature of a different individual. A) Heavily cloudy day; *P. napi* males (Nose, Osaka, 2nd May). B) Clear sunny day; *P. napi* males (Nose, Osaka, 1st May). C) Cloudy morning, clear afternoon; *P. rapae* males (C1) and *P. melete* males (C2) (Kurama, Kyoto, 9th May).

time.

The effect of microhabitats on thermoregulation and the roles of the wings were examined in both field and laboratory.

In the field, body temperatures were measured under a variety of thermal conditions in sequence of 4 steps: immediately after capture; when closing wings in the sun; when opening the wings and exposing the surface of thorax to the sun's rays; when placing the butterflies in the shade. The butterflies were securely positioned by the thermocouple probe being ventrally implanted between the pro- and meso-thoracic coxae and their wings were held opened or closed by small wooden sticks, one for each wing.

Similarly, the changes of body temperature were measured under an incandescent light bulb (300W, flood lamp) in a constant temperature chamber at 20°C. When the light was on, the white and black radiation temperatures were 44°C and 50°C, respectively, and when the light was off, the temperature was 20°C. These conditions were a rough approximation of the thermal environ-

ment in the sun and shade on a clear day of early May in Kyoto (cf. Fig. 2). Changes of body temperatures were taken by a portable recorder (Yokogawa Electric Works, Ltd. Type 3057).

## Results

### 1. Microhabitat Utilization

Butterfly microhabitats were divided into 2 groups: the sun-drenched and shaded. *P. rapae* used only sunny areas, while *P. melete* and *P. napi* flew from the sun to the shade or vice versa (Fig. 1). The average flying time in the same microhabitat was about 30 s.

### 2. Thermal Conditions and Body Temperature

Thermal conditions in the sun were shown by air temperature and white ( $T_{wr}$ ) and black radiation temperature recordings (Fig. 2). All 3 shade temperatures were very similar, and therefore only the white radiation temperature was used to

Table 1. Numbers of observations of *P. rapae* and *P. melete* butterflies (male) categorized into 3 behavioural patterns in the sun as a function of body temperature.

Body temp. (°C)	<i>P. rapae</i>			<i>P. melete</i>		
	Resting	Basking	Flying	Resting	Basking	Flying
$x < 22$						
$22 \leq x < 24$	2			2		2
$24 \leq x < 26$	1			3	1	9
$26 \leq x < 28$		5	3		3	11
$28 \leq x < 30$		1	10		1	14
$30 \leq x < 32$	1		6			22
$32 \leq x < 34$	4		11			12
$34 \leq x < 36$	1		12			11
$36 \leq x$			2			3

characterize the thermal environment of shaded habitats, and is hereafter called "shaded temperature".

The air temperature was usually slightly higher than the shaded temperature, but was much lower than both radiation temperatures (Fig. 2). The body temperatures ( $T_b$ ) of all butterfly species were always much higher than the air temperature (Fig. 2). When it was very cloudy,  $T_{wr}$  seldom exceeded 30°C and  $T_b$  closely coincided with it (Fig. 2-A). When  $T_{wr}$  was within the range of 30°C to 35°C,  $T_b$  also closely coincided with it (Fig. 2-C). However, when the weather was sunny,  $T_{wr}$  reached 45°C, but  $T_b$  was maintained near 35°C (Figs. 2-B and C). These results indicate that the butterfly regulated its  $T_b$  by using solar radiation, and that  $T_{wr}$  is a useful index of solar radiation intensity.

Further examination of the relationship between  $T_{wr}$  and  $T_b$  will be made in section 7.

### 3. Relationship between Body Temperature and Behaviour

The behaviours of *P. rapae* and *P. melete* in the sun were analyzed in terms of their body temperatures ( $T_b$ ) (Table 1). Most individuals with a  $T_b$  under 26°C were resting. Some individuals with  $T_b$ 's between 26 and 28°C showed typical basking behaviour on grasses, i.e., positioning their black dorsal throat surface perpendicular to the sun's rays with the wings opened. Most individuals with a  $T_b$  above 28°C were actively flying and often visited flowers for a short time and almost all had a  $T_b$  of below 36°C. In individuals with a  $T_b$  between 30 and 36°C, *P. rapae* and *P. melete* showed different behaviours. Some *P. rapae* rested on grass with the wings closed tightly over the back and oriented the dorsal sides to the sun, whereas, in contrast, all *P. melete* were either flying or making short visits to flowers. This strongly suggests a fundamental difference in heat-

avoiding behaviour between these species in that, *P. rapae* avoided solar radiation by perching and closing the wings over the body to prevent solar radiation directly impinging on the dorsal body surface whereas *P. melete* frequently flew into the shade.

### 4. Mean Body Temperature and Range of Activity Body Temperature

Mean  $T_b$ 's of flying butterflies of each species was between 30 and 32°C (Table 2), which was about 5°C lower than the  $T_b$ 's of individuals flying in fine weather (Fig. 2). The range of activity body temperature, defined as the  $T_b$  range of 95% of flying individuals, was about 10°C (Table 2). The upper limits of activity were similar, irrespective of sex and species, but the mean and lower limit of *P. rapae*, which used only the sun, were slightly higher than those of *P. melete* and *P. napi*, which used both the sun and shade.

### 5. Relationship between White Radiation Temperature and Behaviour

The behaviours of *P. rapae* and *P. melete* in the sun were analyzed in terms of the white radiation temperature ( $T_{wr}$ ) (Table 3). When the  $T_{wr}$  was below the lower limit of the activity body temperatures of butterflies, they were resting. When the  $T_{wr}$  was near the lower limit, some butterflies showed typical basking behaviour, and others were flying. When the  $T_{wr}$  was between 30°C and 40°C, most butterflies were flying or visiting flowers for a short time, and the basking and resting behaviours typically found at lower temperatures were not observed. When the  $T_{wr}$  exceeded 40°C, *P. rapae* began resting again, probably because the body temperature was too hot to fly due to high solar radiation intensity, while the number of *P. melete* captured in the sun decreased, suggesting that many were in the shade.

## 6. Effects of Microhabitat and Roles of Wings

The effects of microhabitats on thermoregulation and the roles of the wings were examined in both field and laboratory.

In the sun, the wings of a butterfly were immediately closed after capture, the body temperature ( $T_b$ ) gradually decreased, but the  $T_b$  was higher than the air temperature (Fig. 3). When the wings were opened and the dorsal thorax surface was exposed to the sun's, the  $T_b$  rose to exceed the upper limit of activity  $T_b$ 's. When butterflies were placed in the shade, their  $T_b$ 's fell to that of the shade temperature of under 25°C whether the wings were opened or closed.

In the laboratory, butterflies were securely positioned under an incandescent light bulb in a constant temperature chamber at 20°C (Fig. 4). For *P. melete* whose wings were opened, when the light was on, the  $T_b$  rose quickly and exceeded 45°C (Fig. 4a), but when the light was off, the  $T_b$  fell to the level of the air temperature of the

chamber (Fig. 4b). However, if the light was kept on and the wings were close, its  $T_b$  quickly fell to about 30°C (Fig. 4c). Similarly, for those butterflies with  $T_b$ 's of 20°C whose wings were closed, when the light was on, the  $T_b$  did not rise as high and remained at about 30°C (Fig. 4d). However, the  $T_b$ 's of individuals under the light with wings closed were still within the range of activity  $T_b$ 's.

Thus the data in both field and laboratory indicate that butterflies increase their  $T_b$ 's by solar radiation, and that they cool themselves by reducing the amount of solar radiation intercepted, i.e., *P. rapae* perch and close the wings over the body. Conversely, *P. melete* and *P. napi* fly into the shade and can cool themselves to a greater extent than *P. rapae*.

## 7. Relationship between White Radiation Temperature and Body Temperature

The white radiation temperature ( $T_{wr}$ ) was related to body temperature ( $T_b$ ) as follows

Table 2. Mean body temperature of flying butterfly and range of activity body temperature defined as the range of body temperature of 95% of flying individuals (Mean  $\pm$  1.96  $\times$  SD). 95% C. I. indicates 95% confidence intervals.

Sex	<i>P. rapae</i>		<i>P. melete</i>		<i>P. napi</i>	
	♂	♀	♂	♀	♂	♀
N	44	8	85	48	80	6
Mean $\pm$ 95% C.I. (°C)	31.9 $\pm$ 0.9	32.3 $\pm$ 2.1	30.1 $\pm$ 0.8	30.7 $\pm$ 0.8	30.0 $\pm$ 0.8	31.1 $\pm$ 3.0
Activity Range (°C)	26.5 – 37.4	27.4 – 37.3	23.1 – 37.1	25.2 – 36.2	22.7 – 37.2	24.6 – 37.6

Table 3. Numbers of observations of *P. rapae* and *P. melete* butterflies (male) categorized into 3 behavioural patterns in the sun as a function of white radiation temperature.

White radi. (°C)	<i>P. rapae</i>			<i>P. melete</i>		
	Resting	Basking	Flying	Resting	Basking	Flying
$x < 22$				1		
$22 \leq x < 24$	1			1		1
$24 \leq x < 26$	2			1		8
$26 \leq x < 28$		4	2	2	3	6
$28 \leq x < 30$		2	1		1	5
$30 \leq x < 32$			1			8
$32 \leq x < 34$			11		1	16
$34 \leq x < 36$			5			10
$36 \leq x < 38$			6			11
$38 \leq x < 40$			10			8
$40 \leq x < 42$	2		6			8
$42 \leq x < 44$	4		2			3
$44 \leq x$						

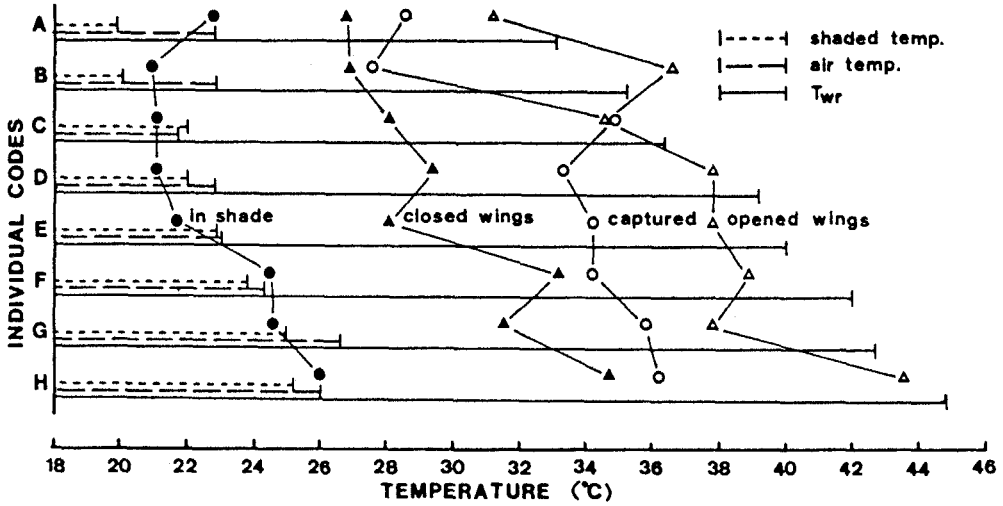


Fig. 3. Body temperatures of *P. napi* (males) in a variety of field conditions. o, Body temperature immediately after capture; ▲, Body temperature wings closed in the sun; △, Body temperature wings open and dorsal surfaces of thorax exposed to the sun's rays; ●, Body temperature placed in the shade. Bars indicate, from the top, shaded, air and white radiation temperatures ( $T_{wr}$ ), respectively.

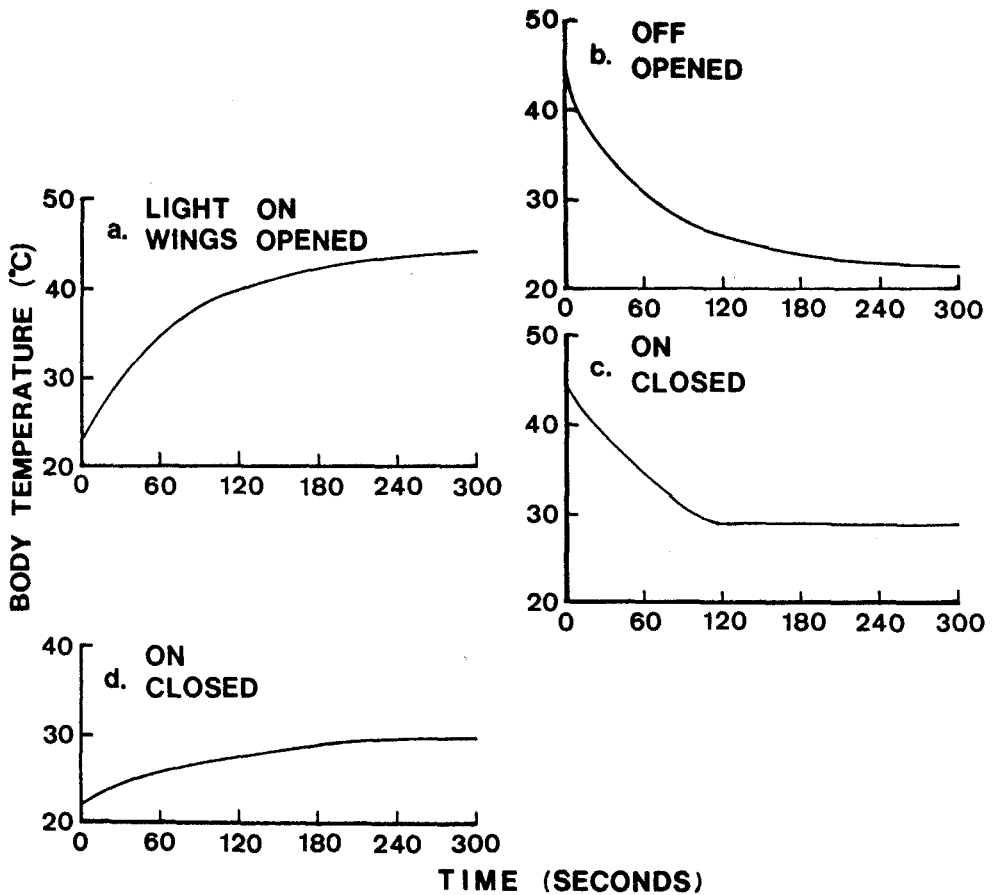


Fig. 4. Examples of heating and cooling curves of body temperature of *P. melete* (female) in spring from under an incandescent light bulb in a constant temperature chamber at 20°C. When the light was on, the white radiation temperature was 44°C.

(Fig. 5): when the  $T_{WR}$  was below  $28^{\circ}\text{C}$ , the  $T_b$  was equal to or exceeded the  $T_{WR}$ . When the  $T_{WR}$  was between  $28^{\circ}\text{C}$  and  $40^{\circ}\text{C}$ , the  $T_b$  gradually increased to about  $34^{\circ}\text{C}$ . However, when the  $T_{WR}$  exceeded  $40^{\circ}\text{C}$ , the  $T_b$  began to decrease inversely, and rarely exceeded  $36^{\circ}\text{C}$ .

From these observations the following hypothesis may be proposed. Typical heating behaviour occurred when the intensity of solar radiation was around the lower limit of the activity  $T_b$  of the butterfly, and it could increase its  $T_b$  to above the lower limit by orientation in sunlight. When the intensity of solar radiation increased and was enough to fly, flight was frequent and vigorous and then the  $T_b$ , which had gradually increased, was kept within the range of activity  $T_b$ . When the intensity of solar radiation further increased and an active butterfly could not maintain the  $T_b$  below the upper limit of the range *P. rapae* began

to rest, while *P. melete* and *P. napi* frequently flew into the shade. Consequently, the  $T_b$ 's of both species became lower.

#### Discussion

Three *Pieris* butterfly species regulate their body temperatures ( $T_b$ ) by behavioral means using solar radiation. *P. rapae* thermoregulate  $T_b$  only by body orientation in the sun. Whereas *P. melete* and *P. napi* do so by shuttling between the sun and shade. Why do the mechanisms by which they thermoregulate  $T_b$ 's differ among them?

This cannot be understood only from the behavioural aspects, and I will therefore discuss ecological aspects of behavioural thermoregulation, especially the relationship between habitat characteristics and habitat use.

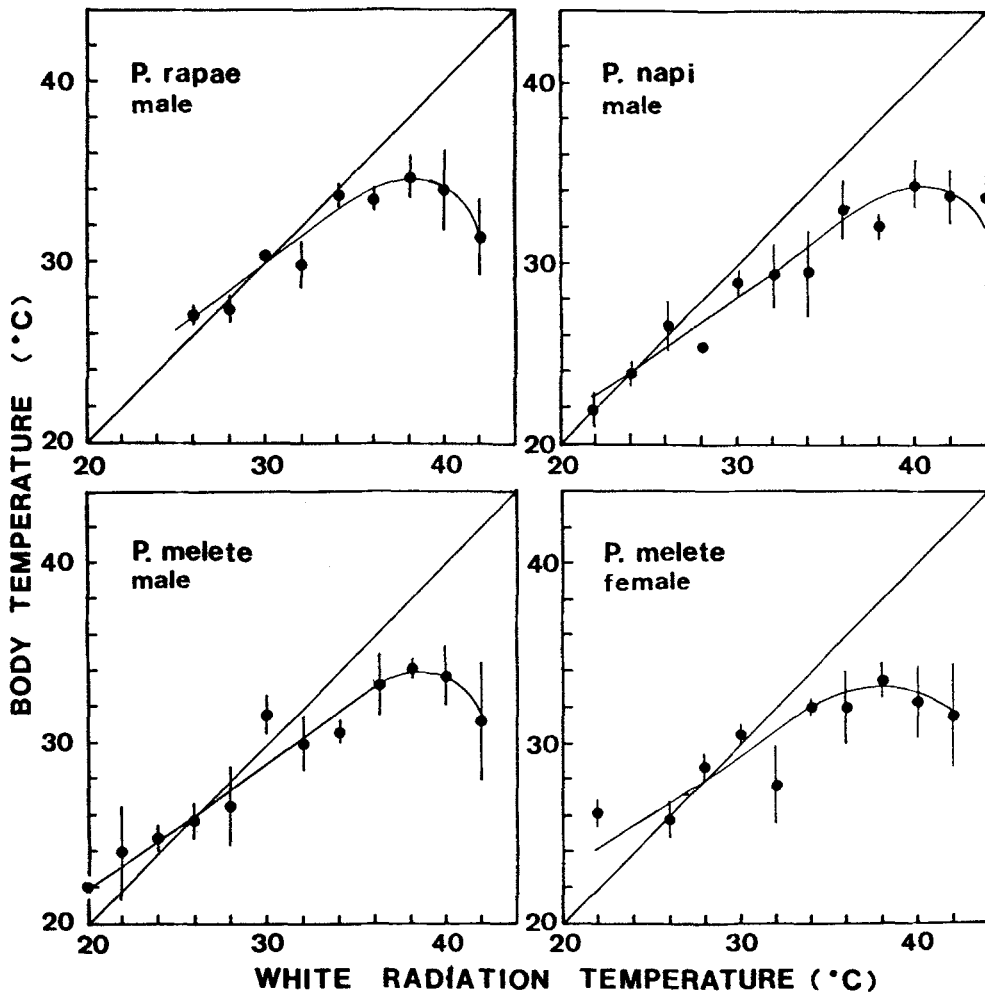


Fig. 5. The relationship between white radiation temperature and butterfly body temperature. Each circle indicates the mean butterfly body temperature for respective  $2^{\circ}\text{C}$  intervals of white radiation temperature. The bars indicate SD.

The larval habitat of *P. rapae* is both unpredictable and unstable (Ohsaki 1979), and its life mode is adapted to such a habitat (Ohsaki 1980, 1982). Although its egg volume is only half of those of *P. melete* and *P. napi*, *P. rapae* achieves a much higher reproductive potential than these species due to high fertility and a reduction of the generation time (Ohsaki 1982). This latter feature especially, greatly effects an increase in the value of the intrinsic rate of increase,  $r$  (Cole 1954; Lewontin 1965; Ohsaki 1982). *P. rapae* attains a short generation time by laying eggs in the sun (Ohsaki 1982). The duration of this short generation time is about two thirds that of eggs laid in the shade, and theoretical results suggest this increases the reproductive potential about 40 times (Ohsaki 1982). Thus, *P. rapae* can live in a temporary habitat only in the sun and consequently, all habitat resources for adult *P. rapae*, such as oviposition sites, emerging sites of females and nectar plants occur in the sun, and adult butterflies are active only in sunny habitats where they regulate  $T_b$  by body orientation.

Conversely, the larval habitat of *P. melete* and *P. napi* is predictable and stable, being mainly in the shade under trees (Ohsaki 1979). The life mode of *P. melete* and *P. napi* is adapted to such a habitat (Ohsaki 1980, 1982). These species lay larger eggs, which, although the total number of eggs laid is fewer than that of *P. rapae*, may be expected to increase the survivorship of individual larva immediately after hatching (Ohsaki 1982). Therefore, the main habitat resources for adult butterflies such as oviposition plants and emerging sites of females exist in shaded places, though most nectar plants exist in the sun (Ohsaki 1979, 1982). Consequently, adult butterflies may shuttle between the sun and the shade to achieve thermoregulation.

Strictly speaking, it is concluded that the flight of *P. melete* and *P. napi* into the shade, in many cases, is not a heat-avoiding behaviour. Their main habitats are in the shade, but the intensity of solar radiation in the shade is lower than the lower limits of activity  $T_b$ 's and it thus appears that they leave shaded habitats for sunny habitats in order to elevate their  $T_b$ 's rather than enter shaded ones for heat-avoiding.

*P. melete* and *P. napi* have seasonal dimorphism, producing dark-veined adults in spring and light-veined adults in other seasons (Yokoyama & Wakabayashi 1954). The lateral wing base is particularly dark and such seasonal variations may be thermoregulatorily adaptive, as noted in *P. napi* by Shapiro (1975), i.e., their dark wing base must be able to elevate the  $T_b$  rapidly under weak solar radiation in the sun in spring or even under weaker the solar radiation found in the shade. Under such conditions they may use not only dorsal but also lateral basking.

Thus the behavioural responses of *Pieris* butterfly species to thermal conditions can be analyzed more precisely by using the white radiation temperature or the index of intensity of direct solar radiation.

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