

## IS 'REFLECTANCE' BASKING REAL?

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### Summary

Various kinds of butterflies raise both (or sometimes one) of their pairs of wings while basking with their body at approximately right angles to the incident solar radiation and with their wings held at an acute angle to the incident sunlight. I here test the effects of wing posture on thoracic temperature in so-called 'reflectance' basking.

1. Butterflies with pale yellow or white dorsal wing surfaces held with their wings at 45, 90 or 180° with respect to each other (or 22–23, 45 and 90° with respect to the solar radiation) heated to mean thoracic temperatures ( $T_{th}$ ) of 38.2, 39.5 and 39.9°C, respectively, in direct sunlight. These closely similar values of  $T_{th}$  are significantly different ( $P < 0.02$ ) from each other, but the difference is in the opposite direction to that predicted by the solar reflectance hypothesis.

2. The  $T_{th}$  of butterflies tested under a sun lamp in the laboratory showed the same trend of  $T_{th}$  with wing angle. Reflectance from the wings thus makes little or no practical contribution to the animal's heating response.

3. Butterflies with wings at 45° that were heated from above with a sun lamp showed an immediate increase in  $T_{th}$  when turned at right angles to a gentle air stream. Thoracic temperature immediately declined when they were again turned to face the air stream.

4. Those butterflies that were at right angles to the air stream showed an immediate increase in  $T_{th}$  when the wings were raised from 180 to 45°, and their  $T_{th}$  again declined to previous values when the wings were again lowered. However, little or no effect of wing angle on  $T_{th}$  was observed when the wing angle of butterflies *parallel* to the air stream was altered.

These results indicate that wing elevation in basking butterflies does not increase  $T_{th}$  by way of solar reflection from the wings. Instead, the raised wings increase  $T_{th}$  by reducing convective cooling. 'Reflectance' basking is a form of dorsal basking used by species of butterflies that perch above vegetation rather than above a heated substratum.

### Introduction

Numerous species of lycaenid and pierinine butterflies typically bask in sunshine by opening their wings at angles of 5–75° to the incident solar radiation. As indicated in a number of recent publications (Kingsolver, 1985*a,b,c*, 1987, 1988),

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this wing-opening behaviour is considered to be a mechanism for using the wings as mirrors to reflect the solar radiation striking the wings onto the body. The behaviour has thus been coined 'reflectance' basking and is considered to be 'a new mechanism for behavioral thermoregulation not previously described in animals' (Kingsolver, 1985*a*). Although supported by extensive mathematical and biophysical modelling (Kingsolver, 1985*b*, 1987, 1988), the empirical support for this hypothesis is circumstantial. I here provide empirical evidence which is incompatible with the prevailing hypothesis, but which instead provides support for an alternative thermoregulatory function of the same behaviour.

### Materials and methods

Heating experiments on freshly killed butterflies as a function of wing angles were performed from 14:30 to 16:25 h under a bright sunny sky (no overcast visible) on an apparently windstill day in mid-September in Hinesburg, Vermont. Some heating experiments were conducted in a glass-enclosed space (to reduce convection currents).

To examine the reflectance hypothesis, I created a butterfly rack out of two lengths of stiff wire that were held erect by being inserted into holes drilled into two boards (Fig. 1). Each of the two wires was bent to form three sides of a rectangle, with the fourth and bottom side of the rectangle being the supporting board. The top of the rectangle had two 'notches' bent into it with angles of 45 and 90°. These notches, plus a level or 180° portion of the wire, served as receptacles for three strips of stiff paper bent into the same angles (45°, 90°, 180°) that were laid across the two wires. The legs of the rack were adjusted in length so that the strips (serving as butterfly holders) were at right angles along their length to the direct solar radiation. The butterflies were far enough above the substratum (15–20 cm) so that no heat could be trapped around and beneath the body (see Wasserthal, 1975). Each of the three holders was folded along the midline (reinforced with bent inserted insect pins) and they had 10 cut-outs, so that each of the 10 butterflies put onto or above each cut-out was supported by its head, the outside and tips of its wings, and the tip of its abdomen.

Body temperatures were allowed to equilibrate (6–10 min) and the animals were then grasped by the wings and  $T_{th}$  measured (within 2 s) to the nearest 0.1°C with a BAT-12 Sensortek digital thermometer using a micro-probe thermocouple probe (type MT-29/1, time constant 0.025 s, needle diameter 0.33 mm).

Approximately 10 animals for each of the three treatments were tested simultaneously so that radiation and convection effects would be equalized between treatments (Table 1). Furthermore, within any one run,  $T_{th}$  measurements of the butterflies were rapidly alternated between the three treatments, rather than reading all of the  $T_{th}$  of any one treatment before reading those of another. The position of the angles was varied on the rack between runs. The special precautions were necessary to control for the random effect of possible extraneous convection currents and radiation differences. Prior to the experiments

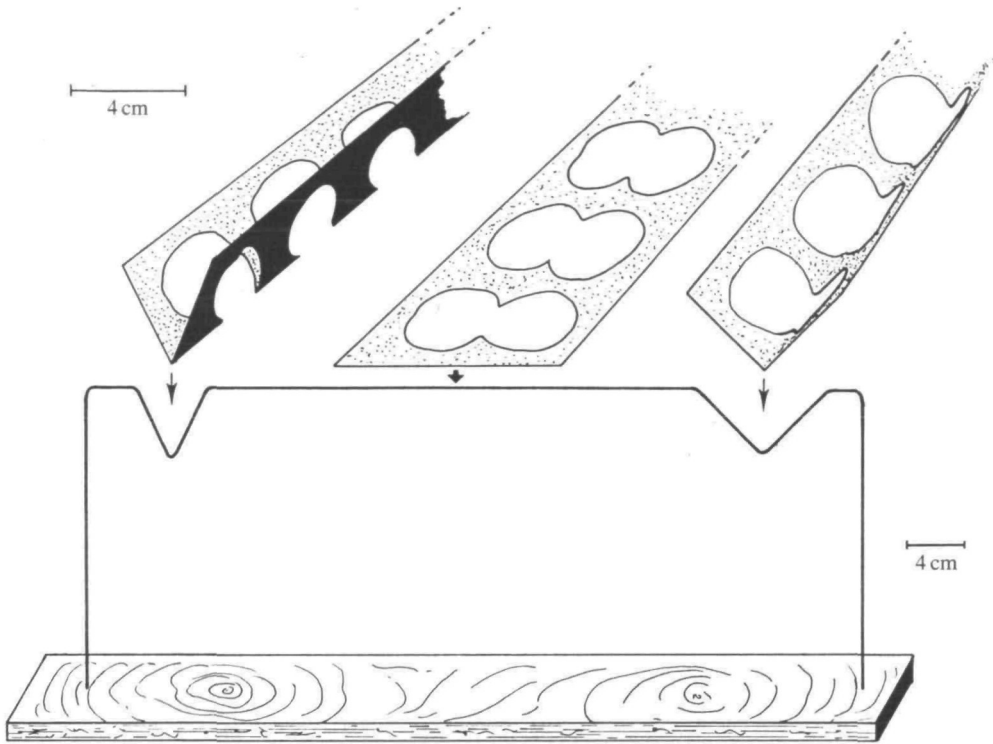


Fig. 1. The rack used for holding butterflies in direct sunshine until their thoracic temperature ( $T_{th}$ ) equilibrated. (The second wire frame for holding up the distal portion of stiffened paper trays is not shown.)

the freshly captured butterflies were stored in a refrigerator at 2–5°C and killed by freezing just before use, and then thawed.

Convective cooling as a function of wing angle and angle to a gentle air current ( $20 \text{ m min}^{-1}$ ) was examined in the laboratory. Wing angles in the wind tunnel were controlled by mounting each butterfly in a frame made by glueing together 1 mm wide slivers of wood and using thread for hinges (Fig. 2). The two square frames (one for each wing) were reinforced by one piece of flexible wire, which could be bent to spread the frames to the desired angle, one with respect to the other. The wings were raised or lowered with the frames, and the frames were attached to a wooden matchstick and stuck into a piece of styrofoam at the desired angle to the air flow.

Continuous measurements of thoracic temperatures were taken with 0.03 mm diameter copper–constantan thermocouples insulated except for the tip and inserted into the approximate centre of the thorax. Thoracic temperatures were printed out at 10 s intervals or less with a Honeywell thermocouple potentiometric recorder. The butterflies in the wind tunnel were heated from directly overhead with an incandescent sun lamp. The location of the thorax of the butterfly was

Table 1. Thoracic temperatures of butterflies at three different wing angles ( $45^\circ$ ,  $90^\circ$  and  $180^\circ$ ) in direct sunshine

Run	$45^\circ$			$90^\circ$			$180^\circ$			Run means		Conditions $T_a$	time
	Mean	Range	N	Mean	Range	N	Mean	Range	N	of runs	$T_a$		
1	44.1	(40.0-48.6)	10	45.1	(41.5-49.3)	10	45.7	(43.2-47.4)	9	44.9	28°C	14:30 h	
2	37.4	(34.3-39.2)	11	39.8	(36.9-42.9)	10	41.7	(37.8-46.0)	9	39.6	28°C	15:00 h	
3	40.1	(35.0-41.8)	10	41.9	(39.0-44.4)	9	42.2	(37.1-45.0)	13	41.4	28°C	15:20 h	
4	35.9	(33.2-38.6)	10	34.7	(33.0-36.4)	10	36.0	(33.1-38.0)	10	35.5	27°C	15:45 h	
5	36.6	(33.2-39.8)	12	38.5	(35.6-41.8)	10	38.1	(35.4-40.3)	10	37.7	28°C	16:05 h	
6	35.9	(32.7-40.0)	11	37.0	(34.8-39.0)	7	36.4	(34.5-40.5)	10	36.4	26°C	16:25 h	
Grand means of treatments										<u>39.49</u>			
										<u>38.22</u>			
										<u>39.90</u>			

$T_a$ , ambient temperature.

There is a highly significant difference in  $T_{th}$  between runs ( $P < 0.0001$ ).

The difference in  $T_{th}$  between wing angles is also highly significant ( $P = 0.020$ ), although in the opposite direction to that predicted by the reflectance hypothesis, when the difference between runs is removed by randomized block two-way ANOVA.

Note, the temperature excess ( $T_{th} - T_a$ ) averaged 10-17°C, in the same range, although this was usually higher than those of Kingsolver (Table 2). These higher temperature excesses indicate more solar radiation, and they should therefore show amplified reflectance effects, if they occur.

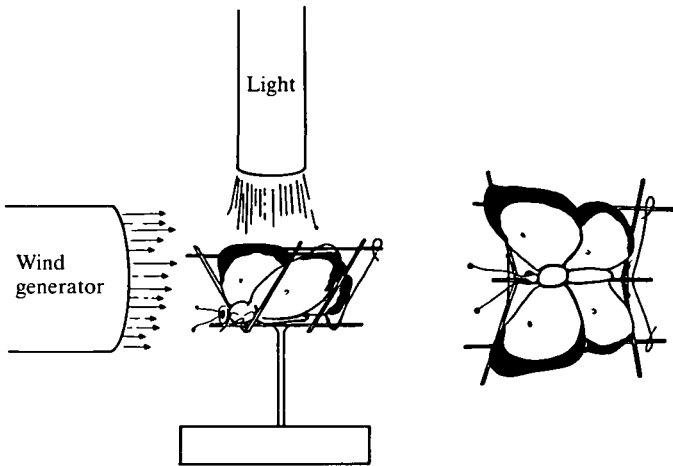


Fig. 2. Sketches of a *Colias* butterfly (laterally and dorsally) mounted on a rack in an air stream and under illumination. Wing angle was adjusted by the rack, and direction with respect to the air stream was varied by rotating the mount. A thermocouple was chronically implanted in the thorax.

maintained within 1 mm between (generally continuous) runs at different wing angles and angles of orientation to the air current.

All temperatures were referenced to a US Bureau of Standards-calibrated mercury thermometer.

The butterfly used, *Colias eurytheme*, is normally a lateral basker (Watt, 1968), and it might be argued that the results are not biologically relevant. However, the butterflies only served as more realistic models than previous models made out of steel and yellow paper to study effects of convection on *Colias eurytheme* (Kingsolver and Moffat, 1982), or out of copper and paper to study models of reflectance basking in *Pieris* (Kingsolver, 1987). I chose *Colias* butterflies because their almost totally white or pale yellow upper wing surfaces should maximize any reflectance effect on heating (Kingsolver, 1987, 1988) if it occurs. Butterflies with closed wings ( $0^\circ$  wing angle) were excluded, because by this well-known (Casey, 1981) heat-avoidance posture butterflies shade the thorax from direct radiation and, at the same time, the wings are unavailable for possible reflectance basking.

## Results

### *Wing angles and thoracic temperature*

If the partially open wings function in reflectance basking, then butterflies with partially open wings should achieve higher  $T_{th}$  than those with wings fully open ( $180^\circ$  or more). To test for possible reflectance basking I heated six groups of approximately 30 dead butterflies. Each group of 30 was equally divided between individuals with wings at  $45^\circ$ ,  $90^\circ$  and  $180^\circ$  to each other (or  $22-23^\circ$ ,  $45^\circ$  and  $90^\circ$  with respect to the incident solar radiation).

Despite making the conditions as uniform as possible (see Materials and methods), there were nevertheless differences in the final  $T_{th}$  of as much as 8.6°C within any one treatment of any one run. (Such large differences reflect the great thermal lability of very small bodies to slight perturbations in air flow, as well as possible thermal gradients within the body and inability to repeat the precise thermocouple placement with respect to these gradients.) However, such variations should have cancelled out since the  $T_{th}$  measurements of the three different treatments (wing angles) were always taken within several seconds of each other to control or reduce potential error from temporal variation in local convection and radiation.

Pooling the results of six separate runs of the same experiment (using a total of 60 butterflies for each of the three treatments) failed to show an enhanced heating effect in the butterflies with raised wings (Table 1). The final  $T_{th}$  values of butterflies in the three treatments were remarkably similar (mean 38.2°C, 45°; 39.5°C, 90°; 39.9°C, 180°). Nevertheless, the large sample size ( $N=181$ ) revealed a statistically significant difference (ANOVA,  $F=6.24$ ,  $P=0.0024$ ), although only between 45 and 180°. Surprisingly, however, this difference was opposite to the direction predicted by reflectance basking. Nevertheless, as expected there was a significant difference between runs ( $F=153$ ,  $P=0.0001$ ). These results show that variations of wing angle have a minimal, if not trivial, effect on  $T_{th}$  by reflection.

#### *Wing angles and convective cooling*

Reflectance baskers, unlike dorsal baskers, typically do not hug the substratum. Instead, they perch on vegetation near the ground where they are exposed to turbulent and unpredictable air currents. (My experiments were performed at elevations above the substratum similar to those normally chosen by reflectance baskers.) Owing to their small body mass (typically 10–100 mg), reflectance baskers could very rapidly lose body heat through convection even in very slight air movements. Convection should be decreased, however, when the air currents are partially blocked, as they would be by raising the wings.

I tested the hypothesis that raising the wings while basking increases the equilibrium thoracic temperature (by reducing thoracic cooling rather than by effects on warming) by placing dead butterflies in a uniform gentle air stream (20 m min<sup>-1</sup>) of a wind tunnel and then altering both their wing angles and their orientation to the air flow, while at the same time heating them with a heat lamp to  $T_{th}$  values near those normally encountered in the field (Figs 3 and 4).

Ten butterflies were each tested in the wind tunnel at different wing angles (45 or 180°) and orientation to the air flow (parallel or perpendicular with respect to the long body axis). In each of the 20 trials on butterflies with wings held at 45°, there was an increase in  $T_{th}$  of 1.0–4.8°C (mean +2.40°C) when the butterfly was changed from a parallel to a perpendicular position with respect to the air flow. Conversely, in each of the 20 trials where the butterflies were turned from a perpendicular to a parallel position there was an immediate decline in  $T_{th}$  of 0.5–4.6°C (mean -2.3°C).

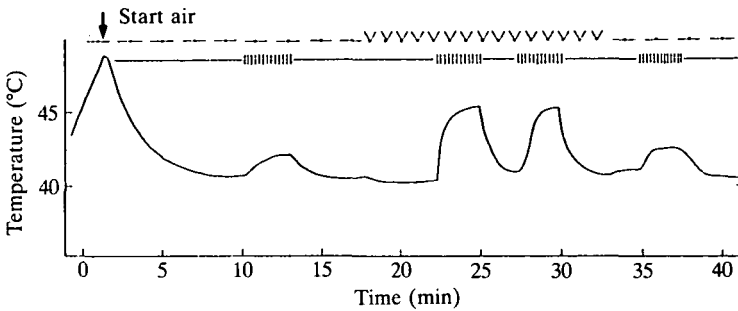


Fig. 3. Thoracic temperature of a butterfly in the wind tunnel at  $20 \text{ m min}^{-1}$  while subjected to a sun lamp from above. The butterfly had its wings spread out at  $180^\circ$  (—) or the wings were lifted upwards to form an angle of  $45^\circ$  ( $\nabla$ ). It was either facing the air stream (—) or perpendicular to it (||||) with respect to the long axis of the body. Note that the angle with respect to the air stream had little effect on  $T_{\text{th}}$  when the wings were at  $180^\circ$ . However, there was an immediate large increase in  $T_{\text{th}}$  when the butterfly with raised wings was turned perpendicular to the air flow (centre).

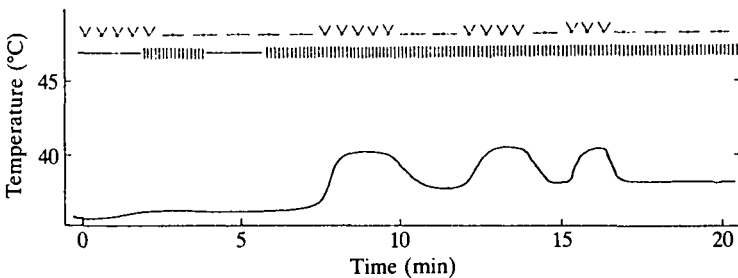


Fig. 4. As Fig. 3, except that here the butterfly with raised wings was turned to be perpendicular to the air stream, rather than being already perpendicular to it and then raising the wings. The same effect – an immediate increase of  $T_{\text{th}}$  in the 'basking' butterfly – occurs when the animal is perpendicular to the moving air. The effect is very large when the wings are raised, and it is very small (see Fig. 3) or not evident (at left) when the wings are spread at  $180^\circ$ .

In another version of the above experiment the butterflies were maintained at a constant orientation in the air stream (either perpendicular or parallel to it) and the wing angles were varied instead. When the butterflies were maintained perpendicular to the air stream, raising the wings from  $180$  to  $45^\circ$  immediately resulted in an increase in  $T_{\text{th}}$  ( $1.0$ – $3.0^\circ\text{C}$ ) in all five trials (mean  $+1.86^\circ\text{C}$ ). Conversely, when the wings were again lowered to  $180^\circ$  the  $T_{\text{th}}$  in all five trials resulted in an immediate drop in  $T_{\text{th}}$  of  $0.5$ – $2.2^\circ\text{C}$  (mean  $-1.32^\circ\text{C}$ ). The results were entirely different when the butterflies were parallel to the air stream. Raising the wings to  $45^\circ$  had a negligible effect in butterflies parallel to the air flow; average  $T_{\text{th}}$  declined by  $0.15^\circ\text{C}$  (range  $= +0.5$  to  $-1.4^\circ\text{C}$ ,  $N=9$ ). Conversely, when

the wings were lowered again,  $T_{th}$  showed a variable effect (range = +1.6 to -1.0°C,  $N=10$ ) with again only a negligible effect on mean  $T_{th}$  (mean +0.22°C). These very small temperature effects nevertheless show the same trend as those previously observed in the field; they are opposite to those predicted by reflectance basking.

### Discussion

Many butterflies typically open their wings dorsally while basking. When the wings are fully open at 180° (or 90° with respect to the direct solar radiation) the behaviour is called dorsal basking (Casey, 1981). Dorsal baskers typically perch on the ground or other substratum, and they achieve a high  $T_{th}$  because of the direct solar radiation striking the thorax, as well as the reduced convective cooling as a result of warm air trapped under their spread wings (Wasserthal, 1975).

Other butterflies of typically small size (lycaenids and pierinines) usually perch on grass or other vegetation rather than on a warm substratum such as the ground. These butterflies generally do not open their wings to 180°, but instead elevate them at some angle less than 90° to the sun. It has been concluded that these butterflies heat themselves by reflecting solar radiation off the wings onto the thorax, and they have thus been designated as 'reflectance baskers' (Kingsolver, 1985*a,b*, 1987, 1988). However, the skippers (Hesperiidae) raise their forewings while keeping their hindwings horizontal, at 180°. The reflectance hypothesis obviously is not applicable to them because in almost all hesperiids the wings are darkly pigmented. No explanation for their elevated forewings has so far been given.

If reflectance heating occurs, then butterflies with light-coloured fully open wings (180° with respect to each other) should achieve lower  $T_{th}$  in sunshine than those with wings at some angle to the incident solar radiation. I found no such effect. My relatively simple results contrast markedly with the established hypothesis of Kingsolver (1985*a,b*, 1988) that is buttressed by a wide range of observations and models. It is inappropriate to ignore the contrary evidence and I therefore here make a detailed comparison so that the hypothesis as a whole can be evaluated.

The reflectance hypothesis is physically suspect; if the angle of reflection is equal to the angle of incidence, then the body of the butterfly (at the point of the V of the wings) is not available for such heating unless all or most of the light is reflected each time it strikes the wing surface. Given the extremely slow circulation (Wasserthal, 1983) and heat conduction (Wasserthal, 1975) within the wings, possible wing heating will probably also not be available for body heating.

Kingsolver (1985*b*) proposed that the wings reflect light onto the abdomen and hence into a position where heat can be absorbed, and that there is then haemolymph flow from the abdomen to the thorax during such basking to increase 'body' (thorax?) temperature. However, to my knowledge there are no data in



existence showing a higher abdominal than thoracic temperature in any insect, as would be required for the model to apply. Also, there is no convincing evidence that butterflies as small as *Pontia*, *Artogeia*, *Pieris* and other so-called reflectance baskers are capable of physiological heat transfer between abdomen and thorax. The only experiment designed to address the issue was done on 'a' butterfly in which a thread was tied between thorax and abdomen. This individual then had a lower 'body' temperature than when it was not constricted in another heating run (Kingsolver, 1985*b*, Fig. 7*b*). However, such experiments do not differentiate between physiological heat transfer involving the tracheal (Heinrich, 1975) or circulatory systems (Heinrich, 1970, 1971), and take no account of the likely disruption of physical heat transfer due to the thread or the physical constriction itself. (It would be necessary to ligate the heart itself, leaving all else intact).

Kingsolver's (1985*a*) primary evidence for reflectance basking is the observation that *Pieris* orient to sunshine with opened wings when attempting to heat up. However, wing opening to expose the thorax is also expected if the animals are dorsal basking. In a companion publication, Kingsolver (1985*b*) examined body temperature excess as a function of wing angle in laboratory experiments with pierid butterflies. In two individual *P. napi* and two specimens of *Pontia occidentalis* (Table 2), temperature excess varied from 5°C (wings closed) to about 10–12°C (wings at 45–180°). However, low temperature excess with closed wings is to be expected, simply because the thorax is shaded. Furthermore, since the difference in temperature excess between any two treatments (wing angles) is less than the variation between any two individuals he compared in a run, it is not valid to attribute the slight differences to treatments. Also, since the treatments were not run concurrently they are also not strictly equivalent.

Kingsolver (1985*b*) buttresses his reflectance hypothesis on the observations that there is a correlation between wing colour and wing angles during basking in the pierid butterflies *Pontia* and *Artogeia* (both are subgenera of *Pieris*). Average wing angles are 96° in *Pontia* and 46° in *Artogeia*. (These angles for 'basking during flight behavior' refer to total wing opening, not angle to solar radiation, which are half those values.) Furthermore, in *Pontia* the wing angles used in basking during flight behaviour show a mean angle of 114° for females and 72° for males. Kingsolver (1985*b*) states that *Artogeia* are 'largely white on the dorsal wing surfaces, except along the wing bases and on one or two small medial or distal patches'. In contrast, *Pontia* 'generally have extensive dorsal melanization along the outer wing margins', and females 'tend to be more extensively melanized than males at the dorsal wing margins and elsewhere'. However, given the accompanying photograph (his Fig. 6) all the butterflies look closely similar to the naked eye. Nevertheless, he states: 'Measurements with a spectroreflectometer (Kingsolver, 1983*a*) for *Pieris* show that the white dorsal wing surfaces have a solar reflectivity of more than 0.8 while the reflectivity of the black melanic wing regions is less than 0.3'. Unfortunately, it is not known to what extent the reflectivity of specific spots or 'wing regions' has on the reflectivity of the whole wing. It could perhaps be debated whether significant (with regard to wing reflectivity) overall

Table 2. Thoracic temperature excess as a function of wing angle (here converted to be with respect to each other, or double that with respect to solar incidence) in *Pieris butterflies*

Runs	0°			45°			90°			180°			Species
	Mean	Range	N	Mean	Range	N	Mean	Range	N	Mean	Range	N	
Kingsolver (1985b) Fig. 8	3.3	(3.0-3.5)	2	11.5	(11.0-12.0)	2	12.0	(11.0-13.0)	2	12.8	(11.0-14.5)	2	<i>Pontia occidentalis</i>
Kingsolver (1985b) Fig. 7a	5.3	(4.5-6.0)	2	10.8	(10.5-11.0)	2	11.0	(10.0-12.0)	2	9.5	(9.0-10.0)	2	<i>Pieris napi</i>
Kingsolver (1985b) Fig. 7b	4.8	(4.0-5.5)	2	10.3	(9.0-11.5)	2	12.0	(11.0-13.0)	2	9.3	(8.5-10.0)	2	<i>Pontia occidentalis</i>
Kingsolver (1987) Fig. 5	Same data as Kingsolver (1985b) Fig. 7a,b.												
Grand means of treatments	<u>4.47</u>			<u>10.8</u>			<u>11.7</u>			<u>10.5</u>			

These data are derived from the figures listed and estimated to the nearest 0.5°C.

Note that treatments within runs are not equivalent (as in Table 1) because the different wing angles had to be changed (i.e. they could not have been run simultaneously since they refer to the same individuals).

Analysis of variance shows no significant effect of wing angle on temperature excess ( $P=0.37$ ) when 0° wing angles (thoracic shading) are excluded.

melanization differences exist among these taxa; if they do, then they are slight while wing angles differ hugely.

Kingsolver (1985b) states that higher maximum body temperatures can be attained with longer reflective wing surfaces. However, his data contradict this model prediction: the longer reflective wing lengths of *Artogeia* produced lower  $T_{th}$ . Furthermore, to achieve maximal heating rates by reflection, wing angles should be strictly independent of colour. The only way to argue that wing angles are altered for reflectance basking is to conclude that the butterflies bask in postures so as to *reduce* solar input! I conclude that the hypothesis that wing angles are varied as a function of colour because of differential heating rates is unsupported by either physiological or behavioural observations.

The primary experimental evidence for the hypothesis that sexual dimorphism in dorsal wing melanization in *Pontia* produces differences in basking angle at which body temperature is maximized is derived by comparing body temperature excess (his Fig. 8) of 'a' female with that of one male *Pontia occidentalis* and noting a difference in body temperature ( $T_b$ ) between the two as a function of wing angle.

With the same individual, in the same position, at nearly the same time of day, with the thermocouple chronically implanted (i.e. in the same position) it is to be expected that all runs in any one individual would be nearly identical (and also different from those of another). The next individual (such as one with slightly darker wings) would be expected to have a different temperature even if wing colour makes no difference, because most of the other variables could be different. In small animals such as these, extrinsic factors (radiation, slight air movement, thermocouple placement, etc.) have huge effects that could easily mask any other effects. I used a sample size of approximately 60 individuals per treatment and ran the different treatments simultaneously to cancel out all the anticipated extraneous effects.

Kingsolver (1987, 1988) extrapolates the reflectance hypothesis to generate a 'functional map of melanization patterns to thermoregulation performance'. The functional map of wing colours in *Pieris* butterflies for reflectance basking was used further to predict that populations of *Pieris* from cold environments would have melanin on the basal dorsal fore- and hindwings and on the basal-ventral hindwings (Kingsolver and Wiernasz, 1987). This pattern was found. However, dorsal melanization is equally compatible with dorsal basking. (Ventral melanization supports neither the reflectance nor the dorsal basking hypotheses, and some of the other correlations could conceivably support other ideas unrelated to thermoregulation, such as aposematicism or sexual signalling).

Aside from the classic and elegant experiments by Wasserthal (1975) showing the importance of wing positioning on convection and thermal balance in dorsal baskers, there have been other, more recent, papers examining the role of convection in other butterflies. Two of these (Kingsolver and Moffat, 1982; Polcyn and Chappell, 1986) are particularly pertinent to this study.

Kingsolver and Moffat (1982) examined convective heat loss in real and model *Colias* butterflies. Their results are expressed primarily in terms of Nusselt

numbers (dimensionless heat transfer coefficients) and Reynolds numbers (dimensionless wind speed), which are then plotted one as a function of the other. The authors conclude from these studies that convective heat loss from resting *Colias* is independent of yaw angle. Their observation of the independence of heat loss from yaw angle is consistent with field observations indicating no behavioural orientation to wind direction. But *Colias* are lateral baskers; their wings are closed dorsally. Therefore, yaw angle represented both wing and body orientation to the wind direction and the effects of wing angle and heat loss on  $T_{th}$  cannot be generalized to dorsal baskers, where body and wing angle can vary independently with respect to sunshine.

Both body and wing orientation were independently examined by Polcyn and Chappell (1986) in a typically dorsal-basking butterfly *Vanessa cardui*. Using dead, thermocouple-equipped butterflies with wings dried in three different wing positions, it was convincingly shown that wind-to-body angle has a marked effect on temperature excess, especially at low wind speed. At a wind speed of  $0.25 \text{ m s}^{-1}$ , for example, butterflies (all wing angles combined) have an average thoracic temperature excess (when heated with a 150 W incandescent lamp) of about  $3.5^\circ\text{C}$  when facing the wind, and nearly double that when the wind is from the rear of the butterfly. My results, like theirs, show that there is 'no consistent trend in temperature excess between wing positions' (provided the insects are parallel to the air stream). Although the studies of Polcyn and Chappell (1986) convincingly show that body position is an important component of convection in achieving equilibrium body temperatures, they are nevertheless somewhat equivocal regarding the role of wing angle, especially for hydrated butterflies with light-coloured wings, where reflectance basking might play a role in the overall thermal budget.

In summary, a dorsal basking butterfly with fully open or with partially raised wings is obviously heated by the direct solar radiation striking the thorax. If the butterfly is on a flat substratum, then raising the wings should result in cooling because the warm air trapped under the wings dissipates and thus increases the thermal gradient for convective cooling. In contrast, if the butterfly is perched on vegetation such as grass or small leaves, where there are air movements, then raising the wings can result in apparent heating.

Elevation of the wings in butterflies perched above the substratum has a very profound thermal effect. When butterflies are oriented at right angles to a very gentle air stream they achieve a considerably greater  $T_{th}$  when the wings are raised than when the wings are open, at  $180^\circ$ . These results by themselves are in accord with the reflectance basking hypothesis. However, immediately after butterflies with raised opened wings are turned so that they are parallel with the same air stream, their  $T_{th}$  declines to control levels. The enhanced heating of butterflies with partially raised wings is therefore not due to reflectance heating, but instead to reduced convective cooling; the raised wings serve not as solar reflectors for heating, but as convection baffles that reduce cooling. Given these results, it is therefore appropriate to delete the term 'reflectance' basking, and to consider

butterflies with raised wings to be engaging in a variation of the well-known dorsal basking behaviour.

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