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## Thermoregulation and flight activity in territorial male graylings, *Hipparchia semele* (Satyridae), and large skippers, *Ochlodes venata* (Hesperiidae)

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**Abstract** Some male butterflies defend specific mating sites, e.g. sandy patches (*Hipparchia semele*) or plants (*Ochlodes venata*). When perching within its territory, a male orients the body axis and tilts its wings and body in order to control the body area exposed to the sun, and thereby keeps its body temperature ( $T_b$ ) as close to a preferred level as possible. In accordance with a model presented here, these behaviours can be separated into three successive phases. At low temperatures, the males maximized the heat load by exposing the maximum body area (sun-basking). This raised  $T_b$  above the temperature of a non-regulating animal by c. 3° C. At an intermediate range of temperatures,  $T_b$  was kept constant at the preferred level by means of a gradual change of body orientation and posture (graded phase). At high temperatures, the heat load was minimized by exposing the minimum body area. This lowered  $T_b$  below that of a non-regulating animal by c. 2.5° C. *H. semele* went through all three phases, but *O. venata* only reached the basking phase due to a more moderate microclimate. Three types of thermoregulation in ectothermic animals and their functions are discussed. Thermoregulation in territorial male butterflies serves to prepare the animal for efficient flight performance if another male should try to take over the territory, or a predator attacks. The males also made frequent short flights, spontaneously or elicited by other insects. Their duration was independent of temperature, and they may function as a sexual signal.

**Key words** Behavioural thermoregulation · Time budgets · Butterflies · Territoriality · Sexual selection

### Introduction

Behavioural thermoregulation in ectotherms serves to keep the body temperature as close as possible to some preferred level, and thereby maximize a relevant activity

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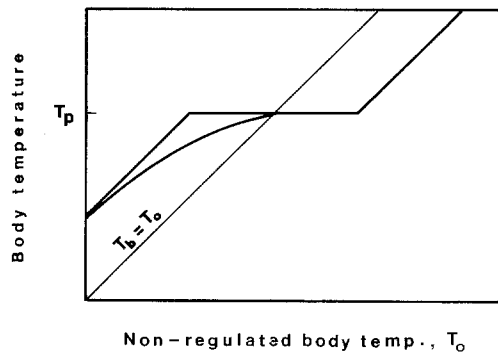
or physiological process. The means used are basking, changes of body orientation and posture, and shuttling between sun and shade. Differences in morphology and in behavioural and environmental constraints give rise to an adaptive diversity of thermoregulatory strategies (Heinrich 1993). It is believed that the model presented here can be used for a comparative analysis of such strategies. Here it is used to analyse thermoregulation in territorial male butterflies, while earlier it has been used to describe thermoregulation in foraging tiger beetles (Dreisig 1984, 1990).

Thermoregulation serves many different functions. In the present case, it may be important for the mating success of the males (Willmer 1991). A number of male insects use a “perch-and-pursue” mating strategy: they occupy and defend specific sites which serve as mating stations, and respond to the passing of males, females and other insects by alighting and approaching them. The appearance of a conspecific male usually results in a contest during which the combatants engage in aerial manoeuvres (e.g. Baker 1972; Davis 1978; Wickman and Wiklund 1983). The outcome of these contests may depend on the ability to regulate the body temperature near the optimal level for flight, and thermoregulation is thus an important component of sexual selection in these insects.

### A model of behavioural thermoregulation

The model relates the body temperature ( $T_b$ ) of a regulating animal to the body temperature of a hypothetical non-regulating animal ( $T_0$ ) (Fig. 1).  $T_0$  represents the null situation, and if  $T_b$ s vary less than  $T_0$ s during the day, thermoregulation is inferred. Although  $T_0$ , of course, increases with the daily increase of ambient temperatures,  $T_b$ s should not be related to some arbitrary ambient temperature, since this cannot show if thermoregulation occurs, and also precludes a meaningful comparison with other studies (see also Herz et al. 1993).

Behavioural thermoregulation keeps  $T_b$  as close to some preferred temperature ( $T_p$ ) as possible, i.e. as close



**Fig. 1** A model of the daily course of the body temperature of a regulating ectothermic animal.  $T_b$  is related to the body temperature of a non-regulating animal ( $T_0$ ), i.e. the line of equality ( $T_b=T_0$ ) indicates no regulation. At low  $T_0$ s,  $T_b$  increases above  $T_0$  (the basking phase: linear increase in a continuous basker, curvilinear increase in a shuttling basker). At an intermediate range of  $T_0$ s,  $T_b$  is kept constant at a preferred level ( $T_p$ ) by means of some graded behaviour (graded phase). When the graded behaviour reaches its ultimate value,  $T_b$  increases again, but now below  $T_0$  (the heat avoidance phase)

as various constraints allow. This is done by maximizing the heat load at low temperatures, gradually reducing it over an intermediate range of temperatures, and minimizing it at high temperatures. Thus, three successive phases can be recognized: the basking, the graded, and the heat avoidance phases. These are described in more detail in the following.

At low temperatures,  $T_b$  is raised above  $T_0$  by the adoption of a basking posture which maximizes the body area exposed to the sun and the conduction of heat from the substrate (the basking phase). Two types of baskers have been recognized. Some animals bask continuously in a stationary position, and  $T_b$  is, therefore, an equilibrium temperature ( $T_0 < T_b < T_p$ ).  $T_b$  increases with  $T_0$ , and in Fig. 1 the temperature excess ( $T_b - T_0$ ) is assumed constant, i.e.  $T_b$  increases in parallel with  $T_0$ . The phase terminates when  $T_b = T_p$ . The second type are animals which bask in order to maximize some activity which is not compatible with basking, e.g. searching for prey. These animals shuttle between sun-basking and activity (intermittent basking). Thus,  $T_b$  is not an equilibrium temperature, but increases during basking bouts and decreases during activity bouts (Dreisig 1984, 1985). Mean  $T_b$  will be intermediate between  $T_p$  and  $T_0$ , but lower than  $T_b$  in a comparable continuous basker (Fig. 1: curvilinear function). The temperature excess decreases with the increase of  $T_0$  (Dreisig 1984). Basking bouts get shorter and the activity bouts longer as  $T_0$  increases, i.e. the fraction of time spent basking decreases with an increase of  $T_0$ . The phase terminates when  $T_b = T_0 = T_p$  during activity bouts, i.e. the animal stops basking when it can be active at the preferred temperature.

During the graded phase, the animal regulates  $T_b$  at  $T_p$  by means of some graded behaviour which keeps the heat load constant in spite of an increase of  $T_0$ . Stationary animals gradually reduce the body surface area (silhouette) exposed to the sun, while mobile animals use a

stilted posture, and thereby gradually increase the distance between the body and the hot ground surface (Dreisig 1990). If there is a cost to the graded behaviour for some reason,  $T_b$  may also increase during this phase, but at a slower rate than during the previous phase. Eventually, the graded response reaches an ultimate value (projected body area minimal, or stilted height maximal), and this terminates the phase.

During the heat avoidance phase, the graded response stays at its ultimate value, which means that  $T_b$  increases with a further increase of  $T_0$  ( $T_0 > T_b > T_p$ ). In Fig. 1, the increase is assumed to be parallel to that of  $T_0$ , but it may be slower if some additional heat-reducing mechanism is used, e.g. stilted, increase of perching height (Vielmetter 1958; Rawlins 1980; Findlay et al. 1983), sun-shade shuttling or evaporative cooling. Eventually,  $T_b$  reaches some upper tolerance limit, and the animal must escape to a more protected environment. It should be noted that the number of phases an animal goes through depends on how far  $T_0$  progresses during its daily increase. When temperatures decline in the afternoon, the sequence may be repeated in reverse order.

## Materials and methods

Grayling males, *Hipparchia semele* L., and large skipper males, *Ochlodes venata* (Bremer & Grey), were studied near Molslaboratoriet, a field station at Århus, Denmark. The graylings were sitting singly in patches of bare sand, e.g. on roads in the area. They are lateral baskers (Clench 1966; Findlay et al. 1983), i.e. they fold the wings over the back, and expose the side of the body and the underside of the wings to the sun. A combination of body orientation and tilting of the wings controls the body area exposed to the sun. The orientation ( $O$ ) is defined as the angle between the horizontal projection of the body axis and the sun's azimuth. It varies from  $0^\circ$  (parallel) to  $90^\circ$  (perpendicular) (no distinction is made between orientations to the left or right of the sun, or between orientations with the head turned towards or away from the sun). The bearing of the head from magnetic north along the longitudinal body axis was measured with a hand-held compass ("Silva") at a distance of about 1 m. The azimuth of the sun was obtained from a solar location chart ("The Air Almanac"), and was also measured directly on occasion. The inclination ( $I$ ) of a lateral basker is defined as the angle between wing-plane and vertical. It is  $0^\circ$  if the animal is sitting in an upright position (wing-plane vertical), and  $90^\circ$  if it is lying flat on the ground. The angle is positive if tilting is away from the sun, and negative if it is towards the sun. It was measured with the inclinometer of the compass at a distance of c. 1 m.

The skippers were studied in a meadow where males were sitting singly on large isolated plants of the common alkanet, *Anchusa officinalis* L. Skippers are dorsal baskers, i.e. they spread their wings and expose the dorsal side of the body to the sun. However, they hold the wings in a way which differs from other dorsal baskers: the hind wings are fully opened, but the forewings are only half opened. At rest, the wings are folded vertically over the body. In a dorsal basker, the orientation is defined and measured as in a lateral basker. The inclination is defined as the angle between vertical and the longitudinal body axis, i.e. it is zero if the body axis is vertical, and  $90^\circ$  if it is horizontal. The angle is positive if the body axis points away from the sun, and negative if it points towards it, but no distinction is made between tilting with the head up or down.

The combined effect of orienting and tilting can be expressed as the angle ( $\gamma$ ) between the direction to the sun and the normal to the wing-plane (hindwings in skippers) (Findlay et al. 1983). The exposed body area is maximal when  $\gamma=0^\circ$ , and minimal when

$y=90^\circ$  (sunrays striking the wing-plane edge-on). Findlay et al. (1983) showed that  $y$  can be calculated for a lateral basker by means of the following expression (re-written in accordance with the present definitions):

$$\cos y = \cos \varnothing \sin (90 - I) [\cos (90 - O) - 1] + \sin (\varnothing + 90 - I)$$

where  $\varnothing$  is the altitude of the sun (obtained from the solar location chart). For a dorsal basker, the term  $[\cos (90 - O) - 1]$  is replaced by  $(\cos O - 1)$ .

In order to test the model,  $T_b$ s were estimated from operative temperatures ( $T_c$ ) (for a discussion of this method, see Bakken 1992).  $T_c$  is the equilibrium temperature of a model with the same thermal properties as the study animal, usually a dead specimen of the species. This method was preferred because the usual "grab-and-stab" method would have meant killing a large number of animals, and, furthermore, may be too imprecise for the present purpose. In comparisons performed under identical conditions, operative temperatures are usually close to the temperatures of the live animals (Bakken 1992). A disadvantage is that possible physiological effects like metabolic heat production, evaporation and hemolymph circulation can not be measured. However, the effect of the first two is normally negligible in insects, and hemolymph circulation plays an insignificant role in butterfly thermoregulation (Kingsolver 1985).

Operative temperatures were also used to estimate the temperature of a hypothetical animal not regulating its  $T_b$ . Since this is a special set of operative temperatures, they have been given a special symbol,  $T_0$ , in the model above and in the following. In the present case,  $T_0$  is the operative temperature of a model animal with a random body orientation and a normal body posture (which can be observed e.g. when the sun is not shining).

A freshly killed grayling was provided with a thermistor inserted through the hole made by cutting off the head of the butterfly, and positioned in the middle of the thorax. The hole was closed by a drop of glue, which also securely fastened the thermistor. The lead was connected to a digital thermometer accurate to  $0.1^\circ$ , and to a potentiometric recorder. The butterfly was glued to a thin wooden stick (diameter 2 mm) and fixed in a position with the wings folded above the body. The stick was placed as an extension of the horizontal arm of a holder, the vertical arm of which was pushed into the sand until the horizontal arm and the stick touched the surface of the sand. By rotating and turning the horizontal arm, the model could be oriented and tilted as desired. In order to estimate  $T_0$ , the model was placed in an upright position and oriented randomly, i.e. intermediate between the orientations maximizing and minimizing the radiative heat load from the sun (body axis  $45^\circ$  to the left or right of the direction of the sun). Each recording usually lasted 2 min, and was later used for the computation of an average  $T_0$  during this period. Measurements were only done on calm days.

In order to estimate  $T_b$ s of regulating animals, the posture of the model mimicked that of animals maximizing and minimizing the radiative heat load from the sun. The grayling model was rotated through  $360^\circ$  and its temperature measured for each  $45^\circ$ , starting with the model facing the sun. Readings were monitored for 1 min at each position. The temperatures of an animal minimizing  $T_b$  was the mean of the two measurements with the model positioned parallel to the sun's rays (wings vertical). The temperature of an animal maximizing  $T_b$  was the mean of the two measurements with the model positioned perpendicular to the sun's rays (wing-plane perpendicular to rays).  $T_0$  was the mean of the four measurements with the model positioned at  $45^\circ$  to the left or right of the sun (wings vertical).

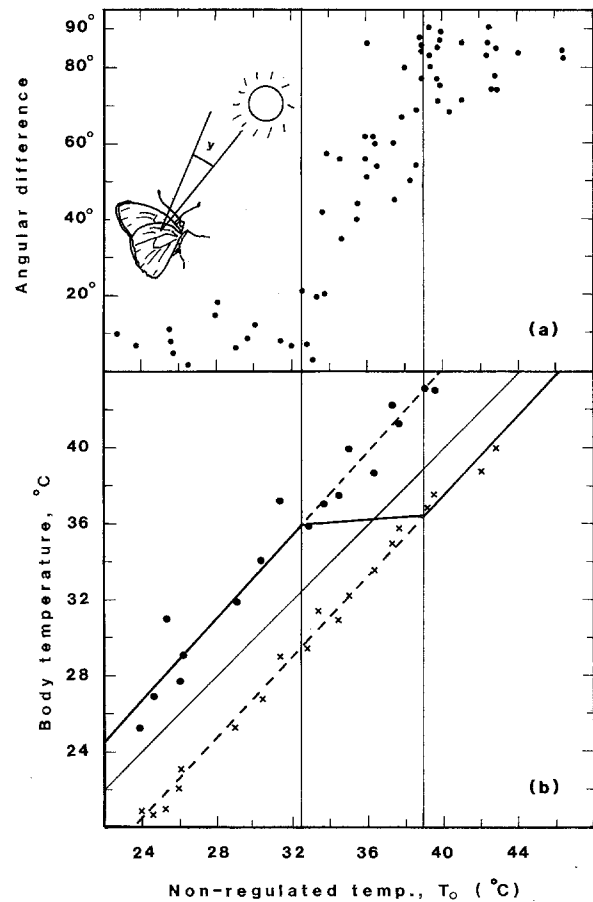
The skipper model was provided with an implanted thermistor and mounted on a stick as described for the grayling. The stick was fastened to a tripod and the model positioned on one of the plants 30–40 cm above the ground.  $T_0$  was estimated by placing the model in a horizontal position with closed wings and oriented  $45^\circ$  to the left or right of the sun. In order to estimate  $T_b$ s of a basking animal, a model with its wings positioned as described above was oriented and tilted so that the body axis along the wing-plane (hindwings) was perpendicular to the direction to the sun.

Time budgets were determined by observing 21 males of both species for up to 1 h each, and timing the sequence of sitting, flying and feeding (recorded on a dictaphone and later timed by means of a stop-watch).  $T_0$  was recorded for 2–3 min before and after each observation.

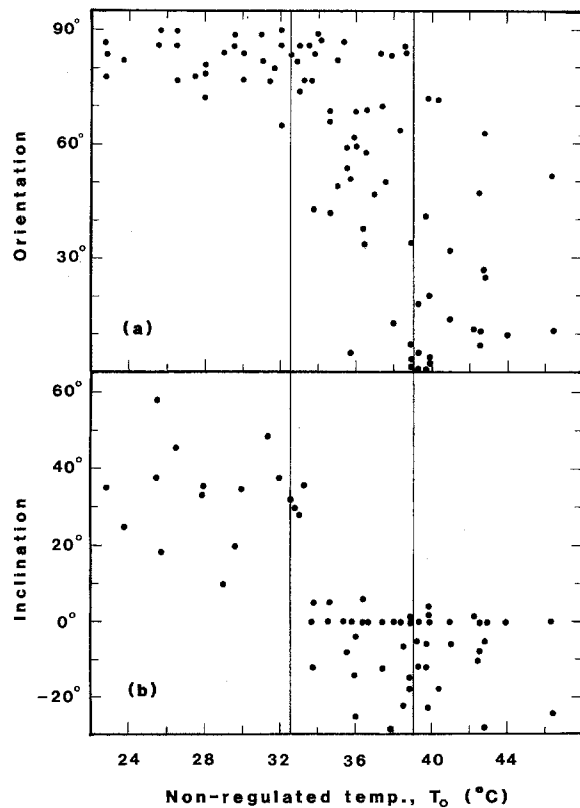
## Results

### Observations on grayling males

Tinbergen et al. (1942) showed that grayling males defend patches of open sand which function as mating territories. They spend their time perching on the sand, making short dashing flights towards passing females and other insects, and engaging in aerial fights with other males. Courting and copulations also occur, but are rarely seen. A perching male practically always orients the body and tilts its wings in a predictable way in relation



**Fig. 2a, b** Thermoregulatory behaviour and resulting body temperatures in territorial *Hipparchia semele* males in relation to the body temperature of a hypothetical non-regulating animal ( $T_0$ ). **a** The angle ( $y$ ) between the perpendicular to the wing-plane and the direction to the sun. **b** Operative  $T_b$ s of animals maximizing (●) and minimizing (x) the heat load (regression lines are highly significant). The thin oblique line is the line of equality (no regulation). The three thermoregulatory phases (see Fig. 1) are separated by vertical lines for ease of interpretation. The estimated daily course of the regulated  $T_b$  is indicated by the three heavy connected lines in **b**



**Fig. 3** The two components of thermoregulation in *H. semele*: **a** body orientation (angular difference between the longitudinal body axis and the sun's azimuth), and **b** wing tilting ( $0^\circ$ =wing plane vertical). The two components are combined in Fig. 2a. Vertical lines separate the three thermoregulatory phases (see Fig. 1)

to the sun. Figure 2 a shows the angle ( $\gamma$ ) between the normal to the wing-plane and the direction to the sun during the daily increase of temperatures. Three stages corresponding to the three phases of the model can be recognized:

1. At low  $T_0$ s, the wing-plane was kept perpendicular to the direction to the sun ( $\gamma=0^\circ$ ), thereby maximizing the projected body area (the basking phase).
2. At an intermediate range of  $T_0$ s, the angle increased, and thereby gradually reduced the projected body area (the graded phase).
3. At high  $T_0$ s, the wing-plane was parallel to the sun's rays ( $\gamma=90^\circ$ ), which minimized the projected body area (the heat avoidance phase).

The temperatures separating the phases can not be determined precisely. However,  $32.5^\circ\text{C}$  and  $39^\circ\text{C}$  are believed to be realistic estimates of  $T_0$  at the onset and termination of the graded phase, respectively (thin vertical lines in Fig. 2).

In order to estimate the resulting  $T_b$ s, operative temperatures were measured in animals maximizing and minimizing the solar heat load (Fig. 2b). The temperature excess achieved by basking was practically constant (mean:  $3.1^\circ$ ). The temperature deficit achieved by minimizing the projected body area decreased slightly with an increase of  $T_0$ . The mean was  $2.5^\circ\text{C}$  during the heat avoidance phase. If the estimated  $T_0$ s defining the graded

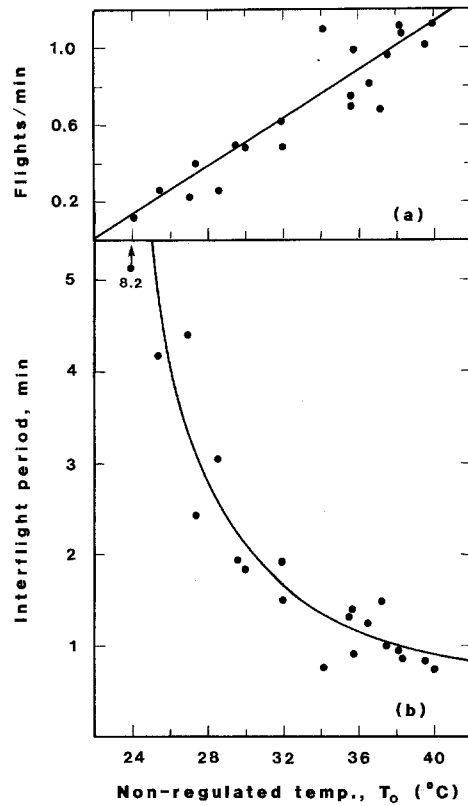
phase are accepted (see above),  $T_b$  only increased from c.  $36^\circ\text{C}$  at the onset of the phase to c.  $36.6^\circ\text{C}$  at its termination, i.e.  $T_b$  is kept practically constant during this phase. According to the model, this  $T_b$  corresponds to the preferred temperature. In accordance with the model (Fig. 1), the daily course of the estimated  $T_b$ s is shown as the fully drawn stepped function in Fig. 2b. It should be noted that these estimates are equilibrium temperatures, and do not include a possible effect of the short flights (see Discussion). It should also be noted that the temperature deficit during the heat avoidance phase may have been larger in live butterflies than the estimate shown in Fig. 2b, because the animals were sometimes observed to stilt during this phase. No butterflies were seen on the open sand at  $T_0 > c. 46.5^\circ\text{C}$ .

Orienting and wing-tilting are shown separately in Fig. 3a and b. During the basking phase, all animals oriented perpendicular to the direction to the sun and tilted at an angle away from the sun. The tilting angle, of course, depended on the altitude of the sun, i.e. on the time of day. During the graded and heat avoidance phases, most animals adopted an upright position and used orientation for keeping  $T_b$  constant or minimized. However, during both phases, a number of animals tilted towards the sun (negative values) and oriented at a larger angle than in those sitting upright.

The flights of territorial males could be categorized as shown in Table 1. Almost half occurred spontaneously without any apparent external cause. The rest were mostly short dashing flights towards passing heterospecifics. Both types lasted only a few seconds, and their durations were not significantly different (although flights in response to the similar speckled wood butterfly lasted significantly longer). Only 14% of the flights were in response to conspecifics, mostly to other males. Flights in response to the approach of other males lasted significantly longer than other flights, because they usually escalated into contests, during which the pair engaged in a spiral flight (see also Lederhouse et al. 1992; Ravenscroft 1994).

**Table 1** Mean duration (s) and relative frequency distribution of different flight categories in territorial grayling and large skipper males (SDs in parentheses). Flights were either spontaneous or elicited by the approach of other insects belonging to the same or different species. Since the sex of an approaching conspecific could not always be determined in the skipper, the mean flight duration for the "males" and "females" categories in this species only includes cases where the sex determination was certain (16 males and 7 females)

Category	Grayling		Large skipper	
	Rel. freq.	Duration	Rel. freq.	Duration
Spontaneous	0.45	4.2 (2.7)	0.25	7.1 (5.4)
Conspecifics	0.14		0.52	
Males	0.12	24.1 (17.6)		17.5 (19.6)
Females	0.02			6.6 (3.2)
Other butterflies	0.32	5.5 (3.0)	0.17	6.6 (5.9)
Other insects	0.09	4.0 (2.3)	0.05	7.7 (6.9)
No. of flights	126		92	



**Fig. 4** **a** Frequency of flights and **b** the duration of perching bouts in *H. semele*. The regression line in **a** is:  $y = -1.35 + 0.062 T_0$  ( $r = 0.92$ ;  $P < 0.001$ ). The hyperbola in **b** is:  $y = 970 / (T_0 - T')$ , where  $T' = 22^\circ \text{C}$

The duration of the flights did not depend on the temperature ( $r = 0.14$ ;  $0.50 < P < 0.60$ ), but the number of flights per time increased significantly with the temperature (Fig. 4a). This was true for both spontaneous and elicited flights. Flights were not observed below  $T_0 = c. 23^\circ \text{C}$ , corresponding to  $T_b = 26^\circ \text{C}$ , which is believed to be the lower limit for flight. Since the relation between flight frequency and temperature is linear, the relation between the inter-flight interval (=duration of perching bouts) and temperature is a hyperbola (Fig. 4b). The shortest mean perching bout lasted about 50 s, and the longest over 8 min.  $T_0$  has been used as the independent variable, because most flights were elicited by external events.

If the flights occur randomly, the coefficient of variation ( $CV = SD/\text{mean}$ ) of the inter-flight interval is equal to 1. However, in practically all individuals, CV was below 1, the average being 0.63, i.e. the flights tended to have a regular distribution. The reason for this was that fewer short sitting bouts ( $< 1$  min) occurred than expected from a random distribution.

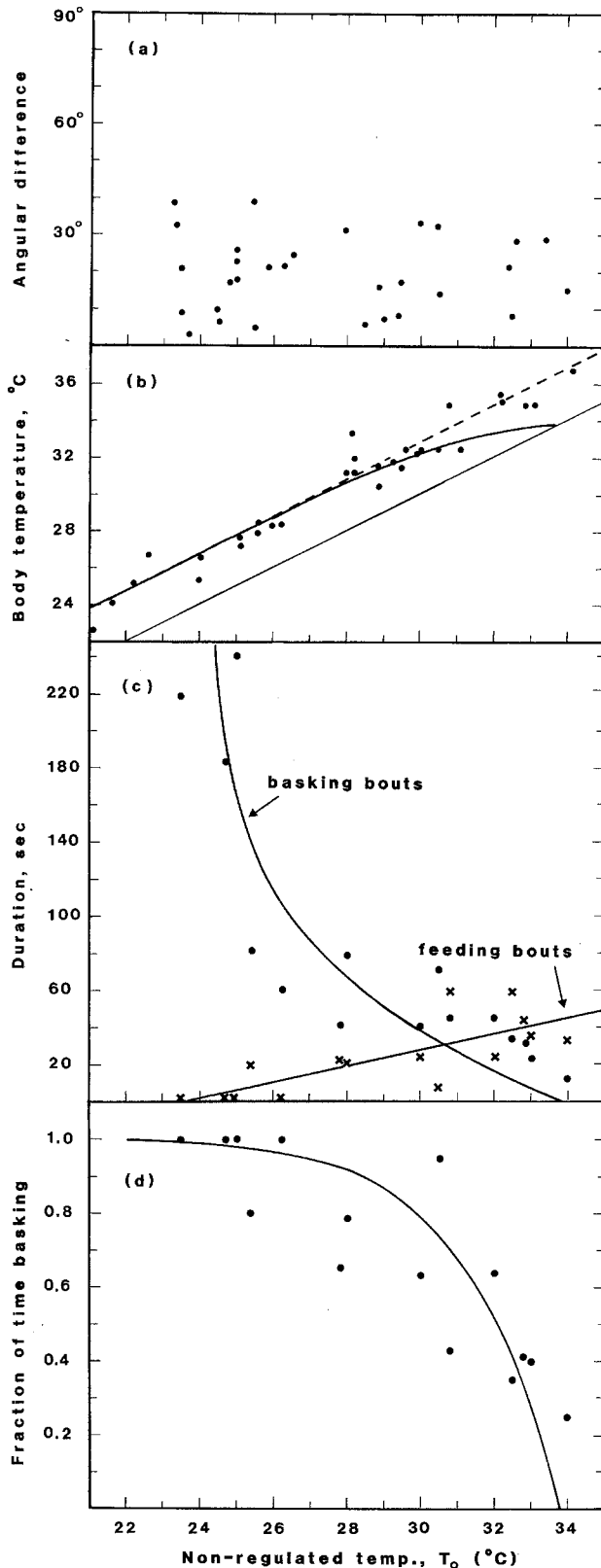
#### Observations on large skipper males

Territorial skipper males alternated between basking, feeding at flowers, and making short flights like those described in the grayling. Males with open wings always

maximized the solar heat load (Fig. 5a). A gradual change of orientation or tilting in relation to the sun was not observed. A gradual closing of the wings, which occurs in some species (Vielmetter 1958; Heinrich 1986), was not observed. In other words, the skippers only reached the basking phase, and had no graded and heat avoidance phases. Fig. 5a shows that basking occurred at  $T_0$ s between  $23^\circ \text{C}$  and  $34^\circ \text{C}$  (higher temperatures were not recorded). Basking was less precise than in the grayling, perhaps because orienting and posturing is more constrained on a plant than on the ground. Estimated  $T_b$ s of basking animals were constantly  $2.7^\circ \text{C}$  above that of a randomly oriented animal with closed wings (stippled line in Fig. 5b). No males were seen on the plants at  $T_0 < 23.5^\circ \text{C}$ , i.e. the lower limit for flight is about the same as in the grayling.

Flights could be categorized as in the grayling (Table 1). A comparison shows that elicited flights were relatively more common and spontaneous flights rarer than in the grayling. This was due to a higher population density in the skippers, and to the foraging of the females at the plants guarded by the males (for these reasons, there was also a higher number of flights per time at a given  $T_0$  than in the graylings). These flights lasted slightly longer than in the grayling. Male interactions lasted significantly longer than other flights, but shorter than the same flights in the grayling. As in the grayling, flight duration was independent of the temperature. Mean CV of inter-flight intervals was 0.77, i.e. their temporal distribution tended to be regular, although less so than in the grayling.

The skippers differed from the graylings by having an additional behavioural category: feeding at the flowers of the plants on which they perched. When feeding, a male moved about on the plant with closed wings and oriented randomly, i.e. it did not thermoregulate while feeding. The duration of the basking bouts, of course, is determined by the frequencies of the flying and feeding bouts. The duration of the feeding bouts increased significantly with the temperature (Fig. 5c), and their frequency decreased. The flight frequency, on the other hand, increased with temperature (as in the grayling, cf. Fig. 4a, but with a higher slope). The overall result was an exponential decrease of the duration of basking bouts with an increase of  $T_0$  (Fig. 5c). The function which has been fitted to the data intercepts the abscissa at about  $T_0 = 34^\circ \text{C}$ , which according to the model corresponds to the preferred temperature (when basking ceases). These data thus indicate that when the skippers reach the preferred temperature, they cease basking and then feed almost all the time. The mean body temperature of a perching male at a given  $T_0$  can be found as the mean of the temperature of a basking male (stippled line in Fig. 5b) weighted by the fraction of time spent basking (Fig. 5d) and the temperature ( $T_0$ ) of a feeding male weighted by the fraction of time spent feeding (1 - fraction spent basking). This is shown as the fully drawn curve in Fig. 5b, and shows that the mean perching temperature is practically equal to the equilibrium basking temperature at most  $T_0$ s, except at the highest where the duration of feeding bouts



exceeds that of the basking bouts. These calculations do not include an effect of the flight activity of the males (see Discussion).

## Discussion

The function of thermoregulation in territorial male butterflies is probably to maximize flight efficiency, which could be important in male-male contests and/or predator avoidance. The flights in response to the approach by conspecific males are contests for the ownership of the territory (e.g. Wickman and Wiklund 1983; Wickman 1986; Rutowski 1991). Baker (1972) showed that during the initial spiral flight each male tries to get and stay above and behind the other, and when this position is achieved by one of them, they go into a series of dives and climbs during which spiralling may or may not be resumed. The uppermost male was the one which eventually settled in the territory. Wickman (1992) suggested that flight speed, fast acceleration and high manoeuvrability are important for territorial males. In accordance with this, muscle ratios and wing disc loadings are higher in territorial species than in patrolling species. Other studies have suggested that sexual selection in butterflies has been important for the evolution of the physiology of the flight muscles (Watt et al. 1986) and the ability to generate heat endogenously (Srygley 1994). Thus, if sexual selection has acted on flight physiology and morphology, it has probably also acted on the ability to regulate  $T_b$  at or near the physiological optimum for flight. The present study implies that a body temperature only a few degrees closer to the preferred level than a non-regulated temperature is advantageous (Figs. 2b and 5b). A male approaching another male's territory by flight may have  $T_b < T_0$ , which means that the advantage of regulating in a territory could be larger than indicated by the measured temperature excess. Approaching males sometimes settled near the territory without being detected, which could provide an opportunity to warm up. On the other hand, a stationary male in a territory could be at a disadvantage at very high temperatures compared with a flying male, which may partly explain why the males of some species give up territoriality at high temperatures.

A female may choose a territorial male because the territory contains some resource she requires, e.g. nectar (skippers) or an oviposition site (graylings). This mating system is called resource defence polygyny (Thornhill

**Fig. 5a-d** Thermoregulation and time budget of territorial male skippers, *Ochlodes venata* in relation to a non-regulated body temperature. **a** The angular difference ( $y$ ) between the perpendicular to the wing-plane and the direction to the sun in perching animals with open wings. **b** Operative  $T_b$ s of basking animals maximizing the heat load (stippled line is the regression line). The lower line is the line of equality (no regulation). The curve shows the weighted mean  $T_b$  of animals alternating between feeding and basking. **c** Duration of feeding ( $x$ ) and basking ( $\bullet$ ) bouts. **d** Fraction of time spent basking (excluding flights); an accelerated function has been fitted to the data ( $r=0.88$ )

and Alcock 1983). However, the system studied here is probably not resource defence polygyny because numerous undefended plants or sandy patches occurred in the area (flowers of defended plants contained no more nectar than those of undefended plants) (see also Ravenscroft 1994). Alternatively, females may choose the males which hold the most contested territories because their offspring then inherit the ability to defend a territory attractive to females, which includes good flight and thermoregulatory abilities, and perhaps a general good fitness. This corresponds to a lek system.

The short flights elicited by other flying insects have been termed inspection or assessment flights, because a male may not be able to distinguish between its own species and other species unless at close range. However, there is reason to doubt this explanation, because the flights are very conspicuous, and may, therefore, expose the males to a considerable risk of predation. The frequent spontaneous flights do not fit this explanation either. Alternatively, the flights function as a sexual signal. This could explain their regular occurrence: if the male signals its presence to females moving about in the area, a flight should not occur too soon after the male has settled, because the probability that a female has already moved into the area is too small, nor should it be delayed too long because of the competition with other males in the area. Flight frequency should increase with the temperature and the activity of the females, as was observed.

If these flights expose the males to an increased risk of predation, thermoregulation may increase the probability of escape if a predator should attack (Kingsolver 1987; Srygley and Chai 1990). The two functions, of course, are not mutually exclusive.

This study supports the idea that a thermoregulating ectothermic animal passes through three temporally successive phases during the day, and thereby keeps  $T_b$  close to a preferred level (Fig. 1). The graylings went through all three phases (Fig. 2a), but the skippers did not go beyond the first (Fig. 5a) because they perched in a more moderate microclimate. Both species seem to be shuttling ectotherms (see Model section), because the males alternate between basking and flying, and because the duration of basking bouts decreases with an increase of  $T_0$  (Figs. 4b and 5c). However, I believe this is not true in a strict sense. In the original model, a shuttling ectotherm maximizes its food intake rate during the basking phase by means of an optimal trade-off between the efficiency of searching for and capturing prey, which increases with the time spent basking, and the time available for foraging, which increases with a decrease of the time spent basking. This trade-off is realized by switching from basking to activity, and vice versa, when certain temperatures during basking (heating) and activity (cooling), respectively, are reached (Dreisig 1984). As  $T_b$  increases towards the preferred level during the basking phase, foraging efficiency increases, which means that the duration of the basking bouts can decrease, and the duration of activity bouts increase (i.e. the fraction of time spent basking decreases). In other words, tempera-

ture is a constraint on efficiency, which necessitates basking, and basking is a constraint on searching time. These constraints are reduced with an increase of ambient temperatures, and become zero when  $T_b = T_p$ , i.e. with the end of the basking phase.

For a number of reasons, the behaviour of the butterflies does not fit this description, probably because the males only maximize flight efficiency, not flying time.

1. Flight duration did not increase with  $T_0$ . Although data are limited, this also includes the contest flights.

2. Most flights were elicited by external random events, and, therefore, not caused by the attainment of a threshold temperature.

3. The time course of heating and cooling shows that most onsets of flight occurred after the equilibrium body temperature was attained. Unpublished experiments show that the heating constant is 1.0 in *H. semele* and 1.24 in *O. venata*, while the cooling constants are 1.44 and 1.85, respectively. Unfortunately, only little is known about the effect of flight on  $T_b$  of butterflies, but available data either show no effect or a heat loss. Most flights lasted only a few seconds (Table 1), and if heat loss occurs during this time, it can be regained in almost the same time after the animal has settled on the sand or on the plant. Mean perching bouts always lasted considerably longer than the mean flight bouts (Figs. 4b and 5c), which implies that most flights were undertaken after the equilibrium  $T_b$  had been attained.

The observed decrease of the duration of the basking bouts with an increase of  $T_0$  in *H. semele* is qualitatively in accordance with the predictions of the behaviour of a shuttling ectotherm. However, it is not caused by an increase of the duration of the activity bouts, as in a true shuttling ectotherm, but by the increase of the frequency of the flights. The latter is either caused by the function of the flights as a signal (see above) or by a general increase of the activity with temperature. The same applies to the skippers, although in this species the decrease of the duration of basking bouts and the fraction of time spent basking was also caused by an increase of the duration of the feeding bouts (Fig. 5c). The skippers might, therefore, bask in order to increase the efficiency of nectar foraging, but this seems unlikely for the same reasons as explained above.

A more likely explanation is that the butterflies only maximize flight efficiency, not flying time. This would be the case if the function of thermoregulation is to prepare the animal for some random event which requires efficient flight. Thus, a perching butterfly regulates at an equilibrium body temperature in order to be ready to function most efficiently in case another male should attempt to take over the territory, a female appear, or a predator attack. This type of regulation probably also occurs in many sit-and-wait predators, where its function is to maximize the prey capture efficiency. It should be noted that non-territorial butterflies (patrollers) are probably true shuttling ectotherms if they must maximize both flight efficiency and the time searching for females.

In conclusion, I suggest that there are three categories of thermoregulation in ectothermic animals:

1. Some animals remain stationary during all three phases in order to maximize the rate of some physiological function, like egg maturation or growth. Their  $T_b$  is an equilibrium temperature, and they use body orientation and posture in order to respectively maximize, regulate, and minimize the heat load during the three phases.

2. A number of animals likewise regulate at the equilibrium  $T_b$  during all three phases; the means used are the same as in the first category, but the function is to maximize the efficiency in case of some randomly occurring event.

3. Some animals trade off efficiency and activity time by shuttling between basking and being active during the basking phase. During the following two phases they are active all the time, and regulate at the equilibrium  $T_b$  by means of posture (stilting). During the heat avoidance phase, some may shuttle again, but this time between sun and shade.

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