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Activity in *Heodes virgaureae* (Lep., Lycaenidae) in Relation to Air Temperature, Solar Radiation, and Time of Day

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Summary. The degree of activity of *H. virgaureae* in the field is largely dependent on air temperature, solar radiation, and wind velocity. Solar radiation increases body temperature above ambient. The butterfly orientates its back towards the sun and exposes the dorsal surface of the wings. At high temperatures they close the wings thereby minimizing the surface exposed to the sun. The optimal body temperature lies around 35° C as was indicated by laboratory experiments. In cloudy and cool to fairly warm conditions the butterfly is inactive. In sunshine the butterfly basks at low radiation intensities or low air temperatures while feeding (in males also flying) predominates at full sunshine or very high air temperatures (around 30° C). Males fly 5–10 times as much as females. A change from unfavourable to favourable weather is followed by an immediate increase in activity of the butterfly, which enables the butterfly to utilize short periods of sunshine.

Introduction

Ambient temperature largely determines the body temperature of insects and hence their activity. A number of forms have evolved mechanisms to raise the body temperature above ambient. This is particularly the case in butterflies which absorb heat from the sun by means of their wings (*e.g.* Clench, 1966; Kevan and Shorthouse, 1970; Leigh and Smith, 1959; Vielmetter, 1958; Watt, 1968). In these studies flight activity and thermoregulating behaviour has been investigated whereas other activities *e.g.* feeding have received little attention.

The present study means to elucidate the entire activity pattern of a butterfly in relation to temperature and solar radiation during the course of the day.

The species studied, *Heodes virgaureae* L., is easy to observe in the field and the sexes are easily recognised. The wings of the male are dorsally shiny orange with black marginal borders. The female is less bright and has extensive dark markings. The species is common in northern Europe and occurs in open flower-rich places in woodland. It feeds on nectar as do most temperate species (particularly from Compositae and Dipsacaceae flowers). It is on the wing during the warmest part of the year (early July to mid or late August).

Methods

Observations of the behaviour of *H. virgaureae* were carried out in 1963–1966 in a small area (3.4 ha) in southern Sweden (Douwes, 1970) referred to as the study area. The main investigations were made in 1966 (13–27 July) and were restricted to a small area within the study area. This area (10 × 50 m) was a partly arbitrarily delimited part of a formerly cultivated field with a uniform vegetation of tall grasses (up to 1.5 m), abundant flowers (the dominating nectar source for *H. virgaureae* being *Achillea ptarmica* L.), and planted spruce (1–1.5 m high). In the west the area bordered on a forest. At the edge of this there were a patch of ferns and a stand of small trees which were used as a perch site of territorial males (Douwes, 1975). The area was sheltered from wind, particularly the western part where most of the observations were made.

In 1966 air temperature and solar radiation were measured. For the latter a similar radiometer to that shown in Vielmetter (1958) was used which measures the temperature excess of a thin blackened metal foil due to the direct radiation from the sun. The sensor was kept perpendicular to the sun by means of a clockwork mechanism. The radiometer was calibrated against a thermopile (Kipp & Zonen, Type E 3). The response of the radiometer was sufficiently rapid for this investigation; the radiation being recorded every 30 sec. Radiation was measured 2 m above the ground in the middle of the area. The values from this level were used despite that the radiation intensity was slightly lower at flower-level. Measurements with a luxmeter showed a 0–15% (at noon) and 10–40% (at 17 hrs) reduction in intensity.

The temperature was measured by thermocouples. These were constructed from copper and constantan wires and had a junction diameter of max. 0.1 mm (length 0.5–1 mm). The thermocouples were placed freely in the air without radiation shields. Due to the small size of the sensor radiation error is negligible (Mattsson, 1965). The location of the thermocouples was: No. 1 50 cm above the ground (flower level) in the middle of the area. No. 2. As No. 1 but in the middle of the western part of the area. No. 3. 150 cm above the ground (upper limit of normal flight) between No. 1 and 2. No. 4. In the morning (until 12–14 hrs) 150 cm above the ground (at approx. perching level) in the patch of ferns and small trees in the westernmost part (the territory). In the afternoon in the middle of the eastern part 50 cm above the ground.

The thermocouples and the radiometer were connected to a 6-point potentiometer recorder (Withoff, Transocomp TEU 72 o). Each measurement point was registered after 6×5 sec; in special situations after 6×2 sec.

When sitting, *H. virgaureae* has its body 2–3 mm above the substrate (flower or leaf) where temperature conditions could be suspected to be different than those where the temperature was measured (10 cm from nearest plant). To check this the temperature around two different flowers and a leaf were measured.

Wind was regularly measured with an anemometer 150 cm above the ground and when wind speed exceeded 1 m/sec (which rarely occurred) no investigations were made.

Observations on the behaviour of *H. virgaureae* were recorded on a tape recorder and were performed on one individual at a time. This one was continuously observed for 10 min or less if it left the area, except at times when the butterflies were inactive (earlier than 08 hrs and when very cloudy). Then the same individual was observed all the time. When observations of one individual were completed I looked for a new one and the first one found was observed. The individual to be observed early in the morning was selected the evening before. By doing so a large and fairly random sample of individuals was observed. The males presented a special problem. They either occurred in the territory and did not feed, or they occurred in the rest of the area mainly feeding. For this reason the behaviour of the territorial and the non-territorial males was described separately.

The behaviour was noted as follows: flying—sitting (including walking), part of vegetation visited (species of flower, other part of vegetation), feeding—not feeding, directed towards the sun—not directed towards the sun (see below), and angle between the wings (estimated by inspection as 0, 10, 30, 60, 90 or 120°). The exposure to the sun was assumed to have thermoregulatory significance. Also noted were egg-laying and interactions (including mating) where *H. virgaureae* was involved, partly described in Douwes (1975).

To simplify the analysis only observations at constant radiation were treated (sunny or cloudy during at least 3 min). For each period of observation (3–13 min) the mean temperature, the percentage of time flying, sitting on flower or other part of the vegetation, feeding, and sitting with the dorsal surface of the body perpendicular to the direction of the sunlight (directed towards the sun) were calculated. Moreover the mean angle between the wings when directed towards the sun and when not were estimated. Longer periods of observation (> 13 min) were equally divided in two or more parts and for each the percentages and means were calculated. For instance, a period of observation of 25 min yielded three periods each being 8 min 20 sec long.

The calculated percentages and means were lumped into 10 temperature and 11 radiation classes (10×11 combinations) and for each temperature-radiation combination the mean was calculated (Figs. 1–6). The reliability of the figure so obtained depends on the number of periods of observation it is calculated from and on the total time of observation for that combination. The total time (= area of the circles in the figures) is used here to indicate the reliability. Similarly the data from observations during sunlight were divided up according to hours and temperature.

The significance of radiation for the body temperature of *H. virgaureae* was tested in the laboratory. Body temperature and ambient temperature were measured with the instrumentation described above (p. 288) except that the body temperature was continuously recorded on a Servogor S potentiometer recorder. The thermocouple was implanted laterally into the thorax. After an hour the wound had healed and the thermocouple was firmly attached. The flight of the butterfly was then checked and only individuals that behaved normally were used. The butterfly was placed on a small stand in a wind-tunnel where the temperature was kept constant ($\pm$ 0.5° C) by a slow air current (0.2 m/sec) and was exposed to the radiation from a 500 W photolamp through an opening in the black wall. Individuals that started to fly immediately or that did not manage to orientate to the light source were excluded. The course of the tests is shown in Fig. 10. Each individual was exposed to 76 $mW \cdot cm^{-2}$ (full sunlight) during 10–15 min (or shorter when it started to fly; 2 females). For 7 of the 12 individuals the radiation intensity was then changed to 34 $mW \cdot cm^{-2}$ (10 min). The angle between the wings was estimated as in the field investigations.

Results

From the observations in 1963–1965 the following picture of the behaviour of *H. virgaureae* was obtained. In the morning from shortly after sunrise to about 07 hrs when the rays of the sun strike the butterfly it starts basking. The dorsal surface of the body is directed towards the sun and the wings are opened to an angle of 90–120° between them. On warm days the first individuals are seen flying at 07–08 hrs. Later in the morning all individuals are active, mainly feeding on flowers. Also during feeding the back is mostly directed towards the sun, the angle between the wings being 0 to 90°. The butterfly also visits leaves and other parts of the vegetation but hardly ever settles on the bare ground. Males fly more than females, the latter visiting each flower for a longer time and flying shorter distances. When laying eggs, however, the female flies more frequently. She then flies short distances in the upper part of the vegetation visiting for short moments different plants. When landing on a *Rumex acetosa* or *acetosella* (the larval food plant) she climbs down to the ground and deposits one or two eggs. Females apparently do not spend much time egg-laying as compared to feeding which is the predominating behaviour of both sexes in sunshine. Males often approach feeding females for copulation. In such situations the female flutters and almost invariably tries to escape and the male usually soon leaves her. Late in the afternoon the butterflies go to roost. Common roosting sites are the surrounding trees and the higher parts of the meadow vegetation *e.g.* the top of a tall stem of grass. The head is turned downwards and the wings are closed with the fore-wings almost entirely covered by the hind-wings.

Cloudy weather and wind inhibits flight and feeding activity. If *H. virgaureae* flies in cloudy weather it is in search of shelter, and the flight is slow.

The results of the investigation in 1966 shown in Figs. 1–8 are based on 30 and 16 hrs observation (302 and 119 periods of observation) of males and females, respectively.

The weather during the period of investigation was normal for the area. It started cold and predominately cloudy the temperature 150 cm above the ground at noon being 17–19° C (13–17 July). From the 18th (23° C) the weather became warmer and sunnier reaching a maximum on the 23rd (28° C). The last four days were mainly sunny and moderately warm (21–24° C). Males were with a few exceptions studied on 13–22 July and females on 21–27 July. Relative humidity which was regularly measured varied between 35 and 70% at noon. At least males were investigated in all kinds of weather occurring during the flight season of *H. virgaureae* except in very high temperatures.

Owing to the uniform vegetation the horizontal variation in temperature in the area was assumed to be small. This was the reason why so few measuring points were used. Three of the thermocouples measured the temperature at flower-level (Nos. 1, 2, 4). Their values were similar rarely diverging more than 2° C. Such a difference is insignificant compared with the rapid fluctuations that the butterfly was exposed to also during constant intensity of the sunshine and calm weather. The standard deviation of 10 succesive values (5 min) from each of these thermocouples was $\pm$ 1–$\pm$ 1.5° C (full sunshine, no wind).

This means that the values from thermocouple No. 1 can be considered as being representative for the flower-level of the whole area. Also vertical variations in temperature were small (between 50 and 150 cm), the values from thermocouple No. 1 being on average 1.5° C higher than those from thermocouple No. 3 when the sun was shining (8–15 hrs).

Thus, since *H. virgaureae* spends most of the time at flower-level or flying slightly above it the behaviour of the butterflies was compared with the values from thermocouple No. 1 irrespective of where in the area the butterfly was observed except after 15 hrs or when observed in the territory. Then the values from No. 4 were used.

The results of the temperature measurements around the flowers and the leaf given in Table 1 show that the temperature 2–3 mm above the surface of the flower/leaf was 1–2° C higher than 10 cm beside. However, the sitting butterfly shades the spot where it is sitting and so the difference is probably smaller than the one measured.

Table 1. Temperature around two different flowers and a leaf measured with thermocouples. Mean and 1 standard deviation of 20 successive recordings (4 min). Each measuring point was registered after 6 $\times$ 2 sec. Sunshine (71–77 $mW \cdot cm^{-2}$) and no wind during the recordings which were made at 13.00–14.40 hrs

Flower (F)/leaf (L) 60 cm above the ground	Temperature (°C)			
	0.2–0.3 cm above F/L	2 cm above F/L	10 cm beside F/L	90 cm above F/L
Achillea ptarmica F	23.7 $\pm$ 1.2	22.8 $\pm$ 1.1	22.6 $\pm$ 1.0	21.6 $\pm$ 1.0
Cirsium arvense F	22.8 $\pm$ 1.6	21.5 $\pm$ 1.0	21.1 $\pm$ 1.1	20.1 $\pm$ 0.6
Salix sp. L	24.6 $\pm$ 1.5	22.2 $\pm$ 0.9	22.6 $\pm$ 0.8	21.6 $\pm$ 0.8

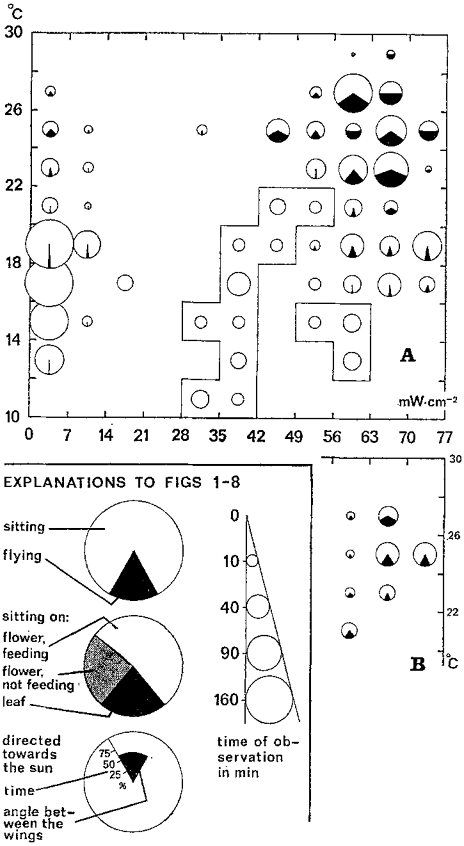

Fig. 1

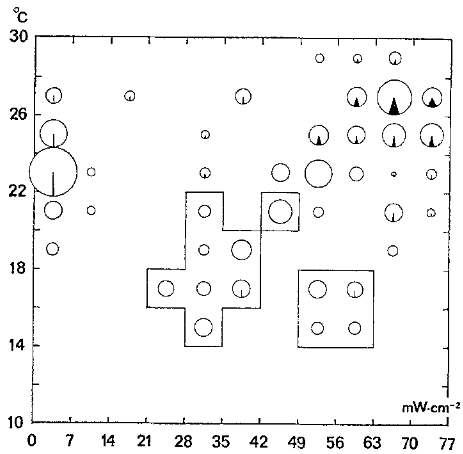

Fig. 2

Fig. 1A and B. The fractions of time spent in flying expressed as % of total time observed in non-territorial (A) and territorial (B) *H. virgaureae* males in relation to air temperature (°C) and solar radiation (mW·cm^{-2}). The area of the circles is proportional to the time of observation. The circles within the thin line are to more than 50% based on observations made before 07 hrs

Fig. 2. The fractions of time spent in flying expressed as % of total time observed in *H. virgaureae* females in relation to air temperature (°C) and solar radiation (mW·cm^{-2}). For explanations see Fig. 1

Flight activity was 5–10 times higher in males than in females (Figs. 1 and 2). Since males fly up at passing butterflies flight activity in that sex depends on the number of butterflies in the area. This is particularly true for territorial males (Douwes, 1975). The influence of other butterflies on flight activity is hard to quantify. All flights that were initiated by another butterfly amounted to 5 and 25% of the flight activity of non-territorial and territorial males respectively.

Figs. 1 and 2 show a more or less gradual increase in flight activity with both air temperature and radiation intensity, the flight activity being highest at the maximum values of these factors. However, the high flight activity of the males at high temperatures during cloudy weather is mainly based on a few persistent flights (15–20 sec). In sunshine most flights were shorter than 2 sec. From Figs. 7 and 8 showing activity at different times of the day (in sunshine) it is also evident that flight activity followed temperature and radiation except in the morning (06–08 hrs) when activity was lower than could be expected from these factors.

Feeding activity, expressed as the percentage of the sitting time that was spent feeding (*i.e.* time used for flying excluded), shows the same relationship

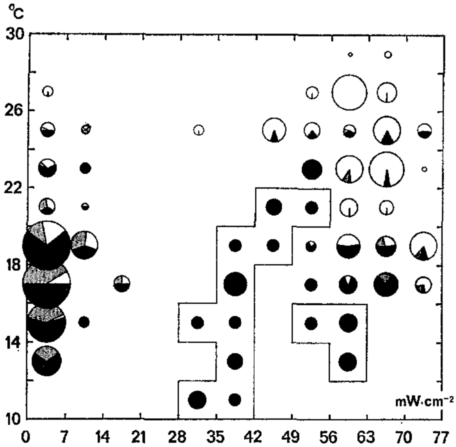

Fig. 3

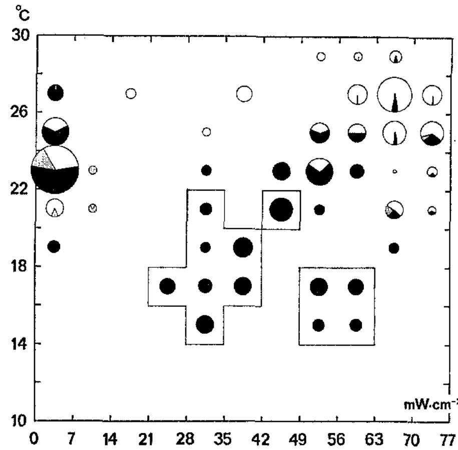

Fig. 4

Fig. 3. The fractions of time spent visiting leaves/flowers (feeding and not feeding) expressed as % of total non-flying time in non-territorial *H. virgaureae* males in relation to air temperature (° C) and solar radiation (mW · cm^{-2}). For explanations see Fig. 1

Fig. 4. The fractions of time spent visiting leaves/flowers (feeding and not feeding) expressed as % of total non-flying time in *H. virgaureae* females in relation to air temperature (° C) and solar radiation (mW · cm^{-2}). For explanations see Fig. 1

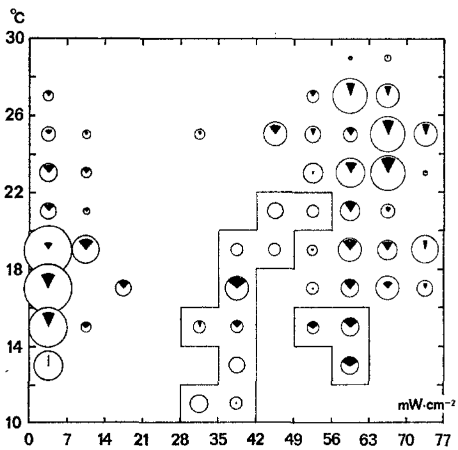

Fig. 5

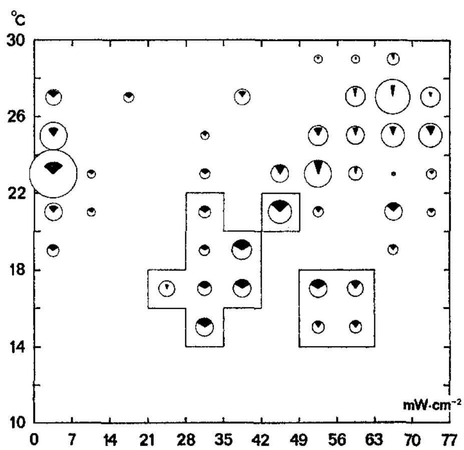

Fig. 6

Fig. 5. The fractions of time sitting with the dorsal surface of the body directed towards the sun expressed as % of total non-flying time and the mean angle between the wings when directed towards the sun in *H. virgaureae*-males. For explanations see Fig. 1

Fig. 6. The fractions of time sitting with the dorsal surface of the body directed towards the sun expressed as % of total non-flying time and the mean angle between the wings when directed towards the sun in *H. virgaureae* females. For explanations see Fig. 1

Table 2. Body temperature, time of warming-up and angle between the wings of 5 males and 7 females of *H. virgaureae* at different radiation intensities produced by a Philips Photolamp (500 W, type PF 218 E/49). A = 0 $mW \cdot cm^{-2}$; B and C = 76 $mW \cdot cm^{-2}$; D = 34 $mW \cdot cm^{-2}$. A to D refer to Fig. 10. Females Nos. 3 and 5 started to fly after 8 and 6 min, respectively

Ex. No.	A temp. °C	B time sec	C angle	C temp. (°C) max	C temp. (°C) min	D angle	D temp. (°C)	D angle
♂ 1	20.7	50	90	33.2	28.9	50	28.0	90
2	21.3	30	90	36.4	35.4	30	28.5	90
3	21.5	35	90	35.4	33.8	60	28.7	90
4	21.5	40	90	36.5	34.6	60	—	—
5	21.2	30	90	34.7	33.7	60	—	—
♀ 1	20.1	50	70	37.7	34.9	25	—	—
2	21.2	45	90	33.7	33.7	30	26.4	90
3	21.2	45	90	34.0	33.2	30	—	—
4	21.4	40	90	33.5	32.7	30	26.8	90
4	21.4	40	90	33.5	32.7	30	26.8	90
5	21.6	40	90	33.4	32.1	30	—	—
6	21.5	35	90	35.4	35.4	30	26.7	30
7	21.6	40	90	33.1	31.5	53	26.8	90
Mean	21.2	40	88	34.8	33.3	41		

to temperature, radiation and time of day as flight activity (Figs. 3 and 4, and 7 and 8). There was an increase in visits to flowers as well as in feeding when sitting on a flower with temperature and radiation intensity. No significant differences between the sexes were obtained.

So far activity has been compared with the simultaneously prevailing temperature and radiation. The conditions that prevailed before might be of importance. Fig. 9 shows the activity in males when weather changed from cloudy to sunny (data were insufficient to elucidate the corresponding situation for females). Comparing Fig. 9 with Figs. 1 and 3 it is obvious that the preceding cloudy weather did not significantly influence the activity in sunshine.

In more or less sunny weather (> 21 $mW \cdot cm^{-2}$) the upper surface of the body was usually directed towards the sun and the angel between the wings was inversely related to air temperature and radiation intensity (Figs. 5 and 6). (When not directed towards the sun the angle was almost invariably zero). This picture suggests that the butterflies regulated their heat absorption by increasing the surface exposured to sun when ambient temperature or radiation intensity decreased. The situation in cloudy conditions is difficult to determine, owing to difficulties in estimating the orientation of the butterflies. For this, the figures presented here are uncertain. Figs. 1 and 7 show that there was a large variation in the early morning as to the orientation of the males towards the sun. This was due to one individual that happened to be in the shade until 07 hrs and therefore did not become active until very late.

From the experimental studies on the body temperature of *H. virgaureae* the thermoregulatory significance of the orientation towards the sun is obvious.

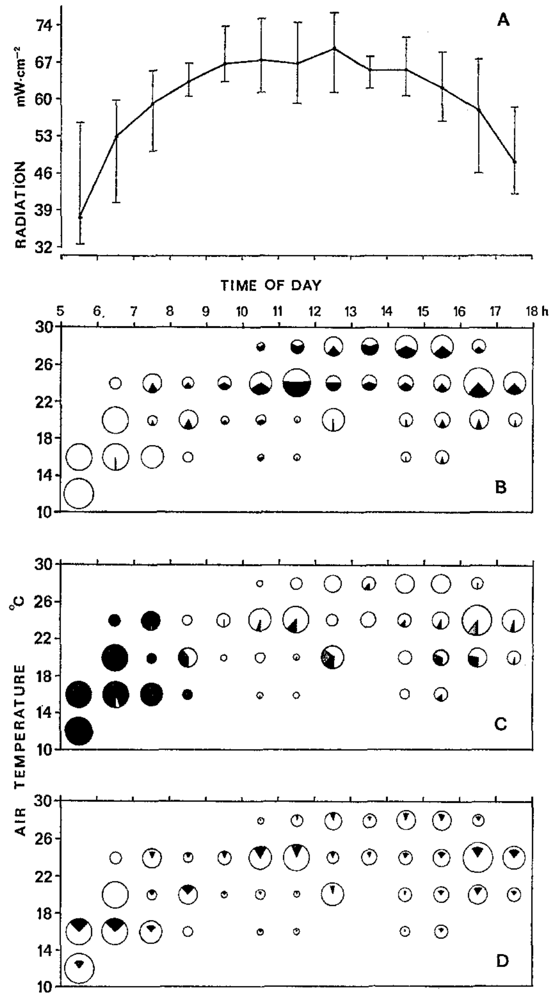

Fig. 7 A—D. The fractions of time flying (B), visiting flowers and leaves and feeding (C), and sitting with the dorsal surface of the body towards the sun and the mean angle when sitting so (D) (expressed as % as in Figs. 1, 3, and 5) in non-territorial *H. virgaureae* males in relation to air temperature and time of day in sunny weather. The solar radiation during the observations, mean and range, is shown (A). For explanations see Fig. 1

When exposed to a radiation of 76 mW·cm^{-2}, which corresponds to full sunlight, body temperature raised 10–15°C above ambient (21°C) (Fig. 10, Table 2). During the warming-up period the angle between the wings was around 90°. This angle decreased when a body temperature of 30–35°C was reached and a fairly constant body temperature of 33–35°C was kept at an average angle of 50° (males) and 30° (females). As a measure of the rate of warming-up the time used for half of the increase rather than the whole increase in body temperature was used owing to difficulties in estimating the point where a steady level was reached. Half of the increase took place in 30–50 sec. At a radiation intensity

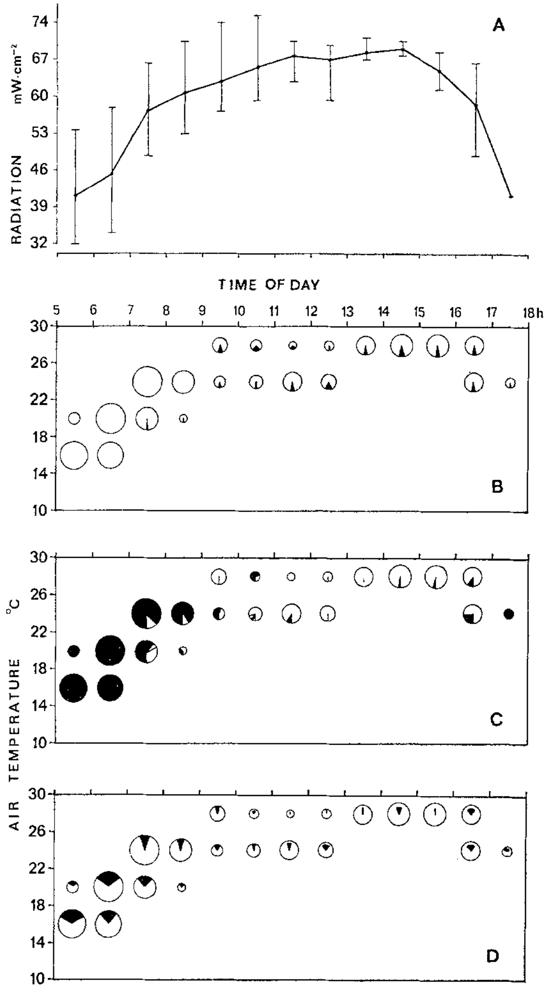

Fig. 8 A—D. The fractions of time flying (B), visiting flowers and leaves and feeding (C), and sitting with the dorsal surface of the body towards the sun and the mean angle when sitting so (D) (expressed as % as in Figs. 2, 4, and 6) in *H. virgaureae* females in relation to air temperature and time of day at sunny weather. The solar radiation during the observations, mean and range, is shown (A). For explanations see Fig. 1

of 34 $mW \cdot cm^{-2}$ body temperature was raised only 7° C (males) and 5° C (females) above ambient.

Discussion

Air temperature and solar radiation was found to be of paramount importance for the activity of *H. virgaureae*, as has been reported from previous studies on butterfly activity (Leigh and Smith, 1959; Vielmetter, 1958; Watt, 1968). The activity in *H. virgaureae* depends on a combination of air temperature and solar radiation, a low temperature being compensated by a high radiation intensity

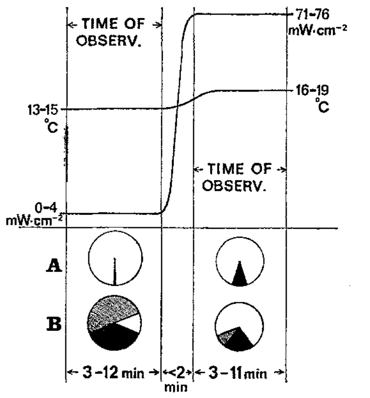

Fig. 9

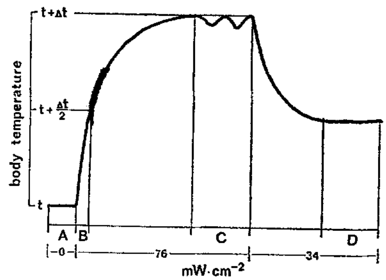

Fig. 10

Fig. 9. Behaviour of *H. virgaureae* males when weather changed from cloudy to sunny (means of 11 occasions). Total time of observation was 54 min (cloudy) and 48 min (sunny). *A* Flight activity. *B* Flower visiting and feeding. For explanations of white, grey, and black section see Fig. 1

Fig. 10. Change in body temperature (diagrammatically) during the experiments with *H. virgaureae* exposed to different radiation intensities (mW $\cdot$ cm^{-2}) from a lamp under constant air temperature (20–22° C). *A*–*D* refer to Table 2

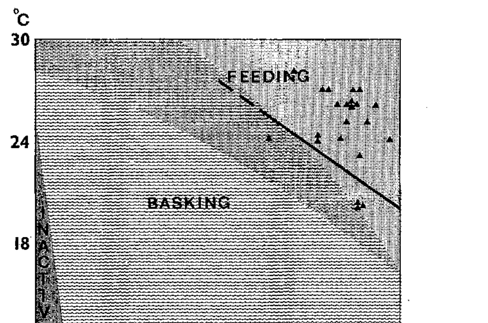

Fig. 11. Activity in *H. virgaureae* in relation to air temperature and solar radiation (diagrammatically). Compiled from Figs. 1–6. Basking = sitting > 50% of the time with the dorsal surface towards the sun and with > 60° between the wings > 50% of the time. Feeding = feeding > 50% of the time spent sitting. Above thick line flight activity is > 25% (males) or > 5% (females). Black triangle = 1 observation of a male courting a female

and vice versa. This is shown diagrammatically in Fig. 11. No upper limit of feeding and flight activity was found, but few observations were made above 28° C and no observations above 30° C. Similar conditions were shown by Vielmetter (1958) for *Argynnis paphia* (Nymphalidae).

It is obvious both from field observations and experiments that *H. virgaureae* regulates its body temperature by directing the dorsal surface towards the sun and varying the angle between the vings. It also appears that about 35° C is an optimal body temperature which was also found by Watt (1968) for *Colias* spp. (Pieridae) and by Vielmetter (1958) for *Argynnis paphia*. Apparently a fairly high radiation intensity is required for a body temperature of 35° C in *H. virgaureae*. 34 $mW \cdot cm^{-2}$ at 21° C was not sufficient (Fig. 10).

The diurnal flight and feeding activity pattern is largely determined by air temperature and solar radiation. However, both these activities start later in the morning and cease earlier in the afternoon than might be expected in regard to prevailing air temperature and sunshine. On sunny and warm days most *H. virgaureae* go to roost between 16.30 and 17.30 hrs. This means that the figures for the activity at 16–18 hrs (Figs. 7 and 8) are not representative; the figures show the activity of those individuals that have a prolonged activity period. It is also seen that *H. virgaureae* go to roost before air temperature and solar radiation become critically low for their activity, thereby being able to fly around in search of a suitable roosting site. This is situated in the uppermost part of the meadow vegetation or in a bush or tree. By settling there instead of staying on the flower the butterfly is exposed earlier to the sun on the following morning and, hence, becomes active earlier.

As could be shown for males, *H. virgaureae* can utilize short periods of favourable weather. During spells of intermittant sunshine the butterfly becomes active (feeding, flying) almost immediately, provided that the air temperature is not too low. This is important since sunshine is sometimes restricted to short periods for a substantial part of the flying season.

So far mating and egg-laying have not been mentioned. Egg-laying was observed once only in 1966, certainly because the investigations were made too early in the season. Most eggs are laid in the end of July—beginning of August. Since flight is involved, egg-laying activity is certainly correlated with flight activity. This is probably also true for mating activity. At least, this is not contradicted by Fig. 11 where all observations of males attempting to copulate with a female in 1966 are plotted. However, mating is probably more frequent in the morning, since all copulations (4) that I have seen during 10 years of field studies of *H. virgaureae* occurred between 08.30 and 10.00 hrs.

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