

The influence of temperature on the territorial and mate locating behaviour of the small heath butterfly, *Coenonympha pamphilus* (L.) (Lepidoptera: Satyridae)

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Summary. Individual *Coenonympha pamphilus* males shifted mate locating behaviour depending on temperature. Under low temperature conditions males competed for territories, resulting in a high proportion of potential territories being occupied by stationary males and in long interactions between males in territories. When temperatures became higher, stationary males tended to leave their territories and travel over a wider area, i.e. become vagrant. This resulted in a low proportion of territories being occupied by stationary males and in short territorial interactions. Males could stay longer in flight without perching and hence also search a larger area for females within a given time span with increasing temperatures. This may explain why males adopt vagrant behaviour at higher temperatures. At lower temperatures, on the other hand, when males cannot search effectively for females, waiting for them at a defended territory should be the most successful strategy.

Introduction

Scott (1974) recognized two mate locating behaviours in male butterflies. They were either “perchers”, i.e. stationary males which perch most of their time, or “patrollers”, i.e. vagrant males which spend most of their time flying over large areas searching for females. Stationary males have been supposed to occupy mating stations (see Baker 1983; Thornhill and Alcock 1983) which females search out to become mated. This has been confirmed for the small heath butterfly, *Coenonympha pamphilus* (Wickman, in press).

Although Scott (1974) described the mate locating behaviour as species specific, studies on the butterfly *Pararge aegeria* has shown that both stationary and vagrant males can be found in the same population (Davies 1978; Wickman and Wiklund 1983; Shreeve 1984). These studies also

suggest that the mate locating behaviour adopted by a male is influenced by temperature. However, no data had been collected on individual vagrant or stationary males to show that a male can switch between vagrant and stationary behaviour.

Stationary males frequently engage in aerial interactions with incoming males, usually with the result that one male is excluded. This has caused many authors to describe the behaviour of stationary males as territorial (Shields 1967; Powell 1968; Baker 1972; Douwes 1975a, b; Austin 1977; Davies 1978; Bitzer and Shaw 1979, 1983; Lederhouse 1982; Alcock 1983). This description has, however, been questioned (Scott 1974; Suzuki 1976). As an alternative explanation it has been suggested that the interactions between males are the result of sex-assessment attempts of one male and predator avoidance by the other. A recent study (Wickman and Wiklund 1983) on the behaviour of *Pararge aegeria* corroborates that male butterflies can be territorial although only long interactions seem to be true contests for territory ownership. Short interactions are probably assessment attempts.

This paper reports observations on both vagrant and stationary individual males of the small heath butterfly. It will be shown that individual males do change mate locating behaviour and that temperature is one of the most important factors in deciding what behaviour they will adopt. The length of interactions at different places and times was considered to be directly proportional to the value of the resource to the contestants (cf. Enquist and Leimar 1983). This is used to show that stationary males are territorial and that the value of the resource changes as temperature changes during the day.

Materials and methods

All observations were made in Timmernabben (56°58'N, 16°26'E) on the coast of south-eastern Sweden, 45 km north of Kalmar, on sunny days between 4 and 12 August 1981,

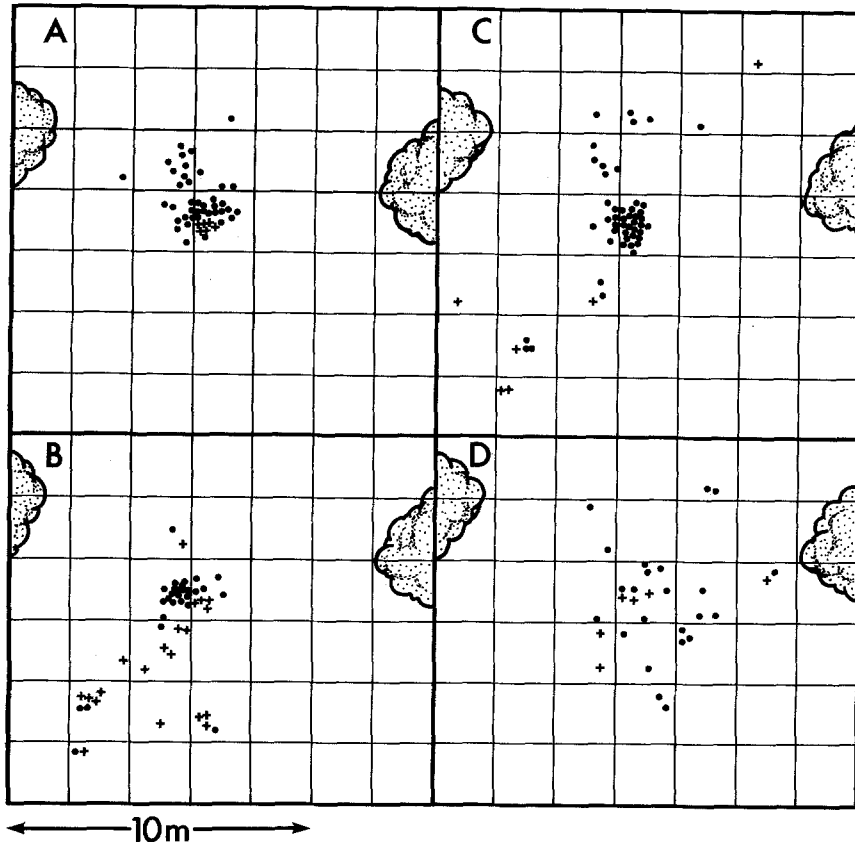


Fig. 1A–D. The perch distribution of male SHI on 1 August 1982 during four observation periods when stationary. The two bushes adjacent to the territory can be used as points of reference. Each dot represents a single perching occasion and a cross a single nectar feeding bout.

A 0907–1007,
 B 1007–1107,
 C 1107–1207,
 D 1705–1736 hours

31 May and 26 June 1982, 24 July and 31 August 1982 and 28 May and 21 August 1983. The small heath adult butterflies were active from late May until early September and were abundant all years observed, especially in heaths dominated by *Festuca ovina* with sparse trees and bushes.

Males were followed and all their activities were timed to the nearest second and registered on a tape recorder. They were individually marked on their wings with permanent ink. Flight paths of vagrant males were drawn on a map of the area and perches of stationary males were marked on a grid representing 2×2 m squares marked with small flags in male territories. By observation of marked individuals in an area of 400×500 m the dispersal abilities of males were documented. Forty-seven males were marked between 31 May and 5 June 1982. The area was searched every sunny day until the last male was resighted on 23 June.

When estimating numbers of stationary and vagrant males at different times of day an 800 m long path was followed every hour on four different days, and occupations of males were recorded. The 1982 path was somewhat extended in 1983 to include more territories. Air temperatures were taken from the Swedish Meteorological and Hydrological Institute reports from their Kalmar station. Time of day is given as Swedish Daylight Saving Time. For mean solar time subtract 55 min.

All means are given with standard errors; 95% confidence limits have been calculated according to Rohlf and Sokal (1981).

Results

Male basic movement patterns

Although individual males could switch between being stationary and being vagrant, these two

behaviours were easily distinguished. Initially the definition of the two activities was based only upon range since such a classification best reflected the two options open to males: to wait for females or to search for them. This also made it possible to relate other parameters such as flight activity and interaction length to mate location behaviour without being tautological.

When stationary, males stayed in a very restricted area, a territory (for reasons that will become obvious later). The maximum distance between two perches of such a male ranged between 1.1 and 14.5 m during 18 one hour observations of 9 different males ($\bar{x} = 7.9 \pm 0.9$ m) (Fig. 1). Territories were always situated near prominent vegetation like bushes and trees and did usually, but not always, contain nectar source plants. They were not always occupied, some being more frequently taken than others (Wickman, in press). The same male could be the resident of a territory for several days or even several weeks (maximum 33 days, $\bar{x} = 7.3 \pm 1.1$ days for 46 males that were observed in the same territory for 2 days or more).

When vagrant, males moved over much larger areas and usually in a more directional fashion (Fig. 2). The distance travelled by vagrant males during a time period varying between 5 and 60 min (vagrant males were often difficult to follow for

as long as 1 h) ranged between 19 m (followed during 7 min) and 160 m (followed during 16 min). The mean distance travelled was 66 ± 8 m (25 observations of 18 different males during a total of 620 min). During their whole lifetime, males could at least become displaced as far as 388 m. However, this was the maximum distance a male was displaced during the 24 day study of 47 marked males. Few males became displaced more than 200 m and on average the longest distance between two recaptures of the same male was 90 ± 13 m.

When all flight and perching durations of stationary and vagrant males are analysed, it becomes obvious that these durations reflect the classification based on range. Stationary males have a mean perching duration of 61.2 ± 3.4 s ($n=788$), three times as long as the 19.1 ± 1.3 s ($n=312$) average perching duration of vagrant males. This difference is highly significant ($P < 0.001$, Mann-Whitney *U*-test, two-tailed). The flight durations are reversed. Vagrant males stay in air almost four times as long ($\bar{x} = 35.1 \pm 2.5$ s, $n=312$) as stationary males ($\bar{x} = 9.5 \pm 0.3$ s, $n=788$) on average. This difference is also highly significant ($P < 0.001$, Mann-Whitney *U*-test, two-tailed). This means that the proportion of time spent flying is 64.8% for vagrant males but only 13.4% for stationary males.

Changes in movement patterns

Twelve marked males were observed to change between stationary behaviour and vagrant behaviour. What movement pattern an individual male adopted was correlated to whether the male was in a territory or not, time of day and temperature. This can be illustrated by the behaviour of male SHI that was the resident of a territory on 1 August 1982 (Figs. 1 and 2). The proportion of time this male spent in flight increased towards noon, and about 1200 hours he became vagrant. During the afternoon the flight activity of this male then declined again, and he eventually became stationary at about 1400 hours. The male was also stationary during shorter periods when vagrant. These stationary interludes always occurred when he passed through his territory and were accompanied by a decrease in the proportion of time he spent in flight.

The pattern of increased male flight activity about noon seemed to be a general phenomenon (Fig. 3), especially in vagrant males. This general trend was also reflected by changes in numbers of stationary and vagrant males during the day, at least on hot days (Fig. 4). On cooler days the decrease in numbers of stationary males at noon was barely discernable. On the hottest day however, this change was very obvious as almost no

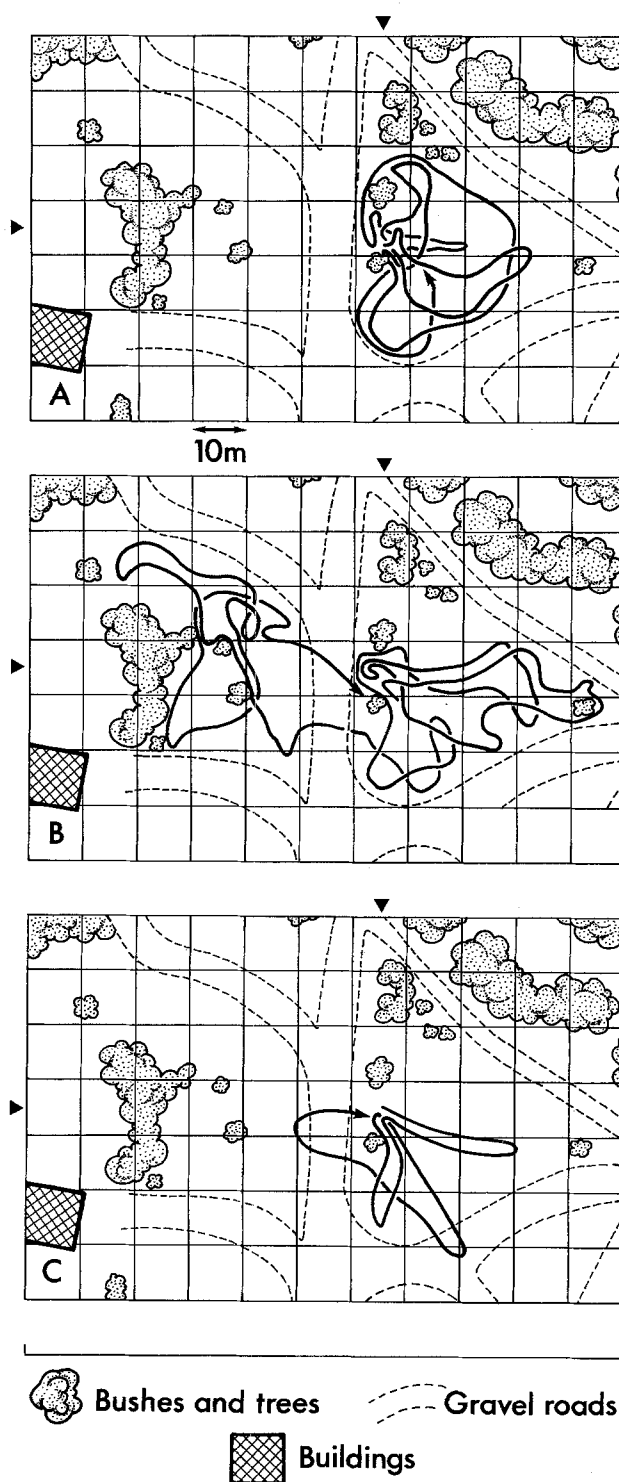


Fig. 2A-C. The flight path of male SHI on 1 August 1982 during three observation periods when showing vagrant behaviour. The location of his territory is indicated by two arrowheads in each map. **A** 1207–1243, **B** 1243–1343, **C** 1343–1442 hours. During the last period the male was mainly stationary and made only three short bouts out of his territory

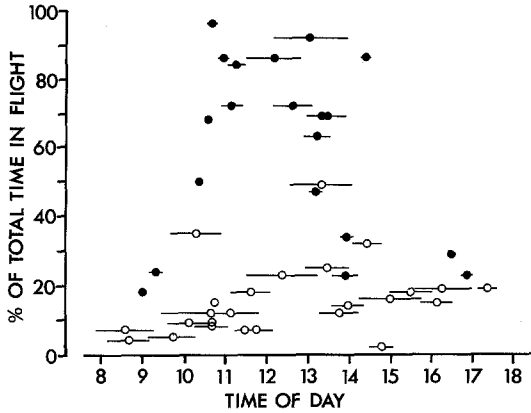


Fig. 3. Flight activity (percentage of total time in flight) of males at different times of day. *Circles* indicate stationary males and *black dots* vagrant males. The *line through each point* is equal to the length of the observation period of that particular male. Time when males were nectar feeding or interacting with other individuals has been omitted

stationary male was seen at midday. Note that vagrant males without territories could always be found, even at low temperatures.

Durations of interactions

When a strange male flew into a territory already occupied by another male, an interaction, where one of the participants was usually expelled, en-

sued on discovery. These interactions were very similar in appearance to those described for *Pararge aegeria* (Wickman and Wiklund 1983) and ranged from “spinning wheel flights” to “horizontal flight pursuits”. Durations of interactions could vary from a second or two to several minutes (Fig. 5).

The mean duration of interactions in territories ($\bar{x} = 12.5 \pm 1.6$ s, $n = 286$), i.e. with a stationary male involved, lasted significantly longer than interactions outside territories ($\bar{x} = 3.1 \pm 0.4$ s, $n = 39$), i.e. between two vagrant males ($0.005 < P < 0.01$, Mann-Whitney *U*-test, two-tailed) (Fig. 5). Outside territories the maximum interaction length was 11 s which is even shorter than the mean duration of interactions in territories.

Interaction length also varied during the day (Fig. 6). The increase in flight activity and the decrease in numbers of stationary males during the middle of the day was accompanied by a decrease in the number of long interactions (> 20 s) in territories.

Discussion

The existence of territorial behaviour in butterflies seems to be well accepted, even if the rigorous definition of a territory as “a fixed area from which

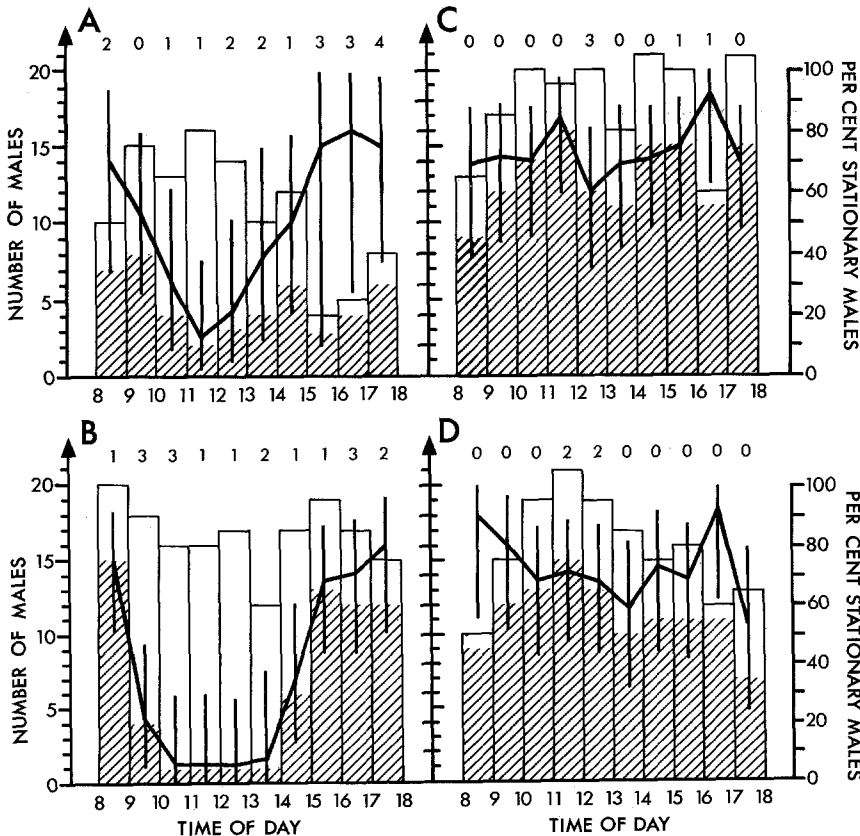


Fig. 4A–D. The change in absolute (*columns*) and relative numbers (*curve*) of stationary (*hatched parts of columns*) and vagrant males (*white parts of columns*) during different days with different maximum temperatures (T_{max}). Relative numbers are given with 95% confidence intervals.
A 5 June 1982, $T_{max} = 30.1$ °C (cloudy between 1500 and 1700 hours);
B 10 July 1983, $T_{max} = 31.3$ °C;
C 8 August 1983, $T_{max} = 26.6$ °C;
D 18 August 1983, $T_{max} = 24.2$ °C.
 The *figures above the columns* denote the number of males that were feeding on nectar during that time period

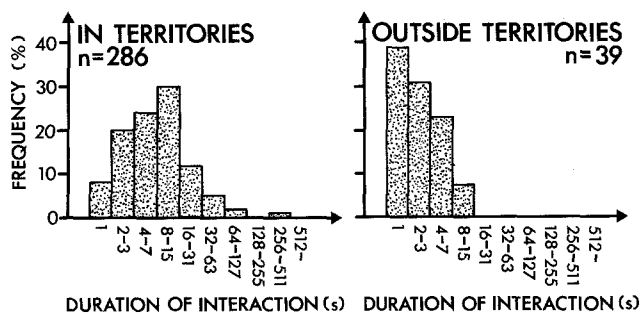


Fig. 5. Durations of interactions in and outside territories. Note the logarithmic scale on the abscissa

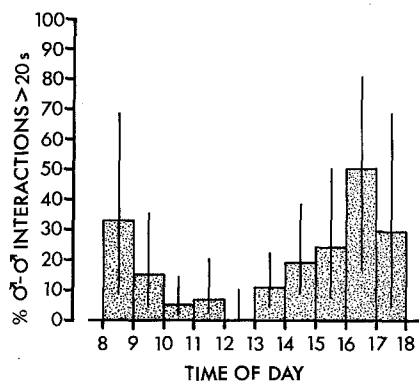


Fig. 6. The proportion of long interactions (>20 s) in territories with 95% confidence intervals at different times of day. Data from all males on different days have been lumped ($n=282$)

intruders are excluded by some combination of advertisement (e.g. scent, song), threat, and attack" proposed by Brown (1975) is applied. This study on *C. pamphilus* and observations on *Pararge aegeria* (Wickman and Wiklund 1983) strongly support the idea that males in these species do compete for territory ownership. The difference in interaction lengths in and outside territories (initially defined in this study as a place occupied by a stationary male, i.e. a fixed area) found in *C. pamphilus* is difficult to account for if interactions are interpreted as the result of sex-assessment attempts of one male and predator avoidance of the other as claimed by Scott (1974) and Suzuki (1976). Since perching male butterflies take off to explore a wide array of objects (from insects to falling leaves) (cf. Tinbergen 1972), they probably have to approach a passing individual to identify it as their own species and to determine its sex. This initial identification phase did not seem to take many seconds, however, as interactions between males outside territories never lasted longer than 11 s, whereas longer interactions, up to several minutes, were restricted to places where stationary males resided. This can best be explained by inferring that longer interactions are true contests for possession of territories in the sense of Brown (1975).

Individual small heath male butterflies changed mate locating behaviour in a manner related to temperature. This can be seen from Fig. 4. The lowest number of stationary males during the different days coincided with what was the hottest period of the day. Moreover, this pattern was most prominent on days with the highest maximum temperatures, showing that movement pattern was ultimately a function of temperature and not of time of day. This suggests that the value of territories to males was influenced by temperature, a notion supported by the daily variation in interaction length. Both in the morning and in the afternoon, i.e. when males showed the greatest tendency to be stationary and territories consequently should be most valuable, interactions also lasted the longest. At midday, on the contrary, most interactions were short, corroborating that the value of territories was low at the time of day when males showed the greatest tendency to leave their territories and become vagrant. A negative correlation between interaction length and temperature has been found in another butterfly, viz. *Pararge aegeria* (Wickman and Wiklund 1983), suggesting that this might be a common phenomenon.

Wickman (in press) has shown that the average mating success, i.e. when not accounting for temperature, was higher for males in territories than for males outside territories. This is explained by the behaviour of virgin females which head for male territories and solicit courtship there (Wickman, in preparation). Thus special conditions, different from the average, must have been prevalent at higher temperatures, or else stationary males would have lowered their fitness by becoming vagrant. At higher temperatures males seemed to have to visit more flowers than otherwise (Fig. 4). Thus it could be argued that stationary males became vagrant to search for nectar. This does not explain, however, why males travelled over large areas which were often abounding in flowers. Neither does it explain why interactions between males in territories were shorter than otherwise. Since females have been observed to mate at any time of day, and also with vagrant males (Wickman, in press), and as the flight activity of males could vary more than tenfold depending on temperature (Fig. 3), it seems more reasonable that stationary males became vagrant because they became more efficient at searching for females at higher temperatures. That butterflies become more mobile with increasing temperatures (albeit only to a certain point) has been shown in repeated studies (e.g. Vielmetter 1958; Leigh and Smith 1959; Kingsolver 1983). Accordingly, at high temperatures few females should ever reach territories be-

fore being intercepted and mated by a vagrant male. Of course female behaviour may also change with increased temperature, making them easier to discover outside territories.

Stationary behaviour and thus territorial behaviour might have evolved in many species as a result of the restrictions set by temperature on the flight activity of males. This is supported by the fact that most species in Scandinavia reported to be territorial fly during spring and early summer when temperatures are usually low (see Wickman and Wiklund 1983). Besides, the few frequently territorial butterfly species flying in summer seem to be small species, viz. *Heodes virgaureae* (Douwes 1975 a, b), *Lycaena phlaeas* (Suzuki 1976), *Polyommatus icarus* (Lundgren 1977) and *Coenonympha pamphilus*, all with wingspans less than 36 mm (Whalley 1981). Small butterflies should generally reach lower equilibrium temperatures than large ones (Parry 1951; Digby 1955; Church 1960) and therefore be more dependent upon high temperatures in sunshine provided that they have the same temperature optimum. As flight activity can be restricted also by high temperatures (Vielmetter 1958; Leigh and Smith 1959), males of many species in hot climates could be expected to be stationary and territorial at the highest temperatures instead.

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