MATE LOCATION BEHAVIOR OF THE LARGE SKIPPER BUTTERFLY *OCHLODES VENATA*: FLEXIBLE STRATEGIES AND SPATIAL COMPONENTS

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ABSTRACT. Male *Ochlodes venata* were studied in lightly wooded heathland at Lindow, Cheshire, U.K., using a combination of transects and more detailed observations of movements and behavior in a woodland clearing. Males locate mates by perching and patrolling but are also opportunists and approach females when feeding. Behavior is flexible, and varies with time of day, weather, season, and location. On clear, sunny days, males show a significant bias for patrolling during mid- and late morning, and for perching during early morning and afternoon. Switches then from one activity to another are not entirely related to temperature and energy levels, and may depend on availability of females, males perching when females are relatively scarce. Scent seems to play a prominent part in the location of females during patrolling. Defended territories are located at topographic vantage points (at habitat edges and path junctions), and have a biased distribution to areas where female resources (nectar, oviposition sites) are also available. Territories and even the same perches (specific locations where the insects alight) within them are used by different individuals in the same and different years.

Additional key words: Hesperiidae, England, territoriality.

In the process of obtaining mates, male butterflies are described by Scott (1974) as adopting one of three strategies: perching or waiting for them, patrolling or actively seeking them in flight, and locating them with the use of long-distance pheromones. The last is regarded as of rare occurrence and understood to be a proximate cue (Scott 1972), vision dominating long-distance communication. But *Heliconius erato* males locate preemergent females using chemicals emitted by the pupae (Bellinger 1954). Perching males select characteristic sites, distinct in surface, height, and situation where they bask in the sun and launch themselves at passing insects (Baker 1972, Davies 1978, Dennis 1982a, Bitzer & Shaw 1979, 1983). Patrolling males typically cover much larger areas but differ in the extent and nature of the areas covered (Courtney 1980, Dennis 1982b, Peachey 1980). Scott (1974) regards these processes as distinct; when perching occurs the females necessarily find males, but patrolling males actively find females. Perching has been likened to territoriality by Baker (1972), since defense of some "resource" is involved, but this is denied by Scott (1974).

Recently, mate location behavior has been shown to be more varied. Perching and patrolling provide alternative strategies in some species depending on demographic trends (distribution of females, male-female

ratio) and environmental conditions (sunshine and temperatures, time of day, habitat topography, physical resources) (Scott 1975, 1983, Dennis 1982a, Shreeve 1984, Rutowski 1983, Wickman 1985a). Moreover, it seems that many butterflies adopt intermediate strategies, involving intermittent flight, basking, and feeding bound only to loose areas and without territories, where males are constantly vigilant for females (Dennis 1982a, Morton 1985).

The various aspects of mate location in butterflies are far from resolved. The present paper on *Ochlodes venata* (Bremer & Grey) responds to the need for comparative data. In particular, it addresses issues of territoriality, switches in mate location activity, and siting and structure of territories. *O. venata* is single-brooded in Britain and flies from the latter half of June into late July (Heath et al. 1984).

METHODS

The study was conducted intermittently over a three-year period (1983 to 1985) at Lindow Common near Wilmslow in Cheshire, U.K. (grid reference SJ834812), a 16-ha site of special scientific interest, comprising patches of dry heath (*Calluna vulgaris* with *Ulex* spp., *Vaccinium myrtillus*, and *Deschampsia flexuosa* over podsol soils on fluvioglacial sands) and wet heath (*Calluna* and *Erica tetralix* on permanently wet peaty soils over boulder clay), encircled by *Betula-Quercus* woodland. The site is intensively used for recreation and is crisscrossed by paths and tracks.

Data were obtained by recording behavior and location of adults along repeated transects over fixed routes (Pollard 1977, 1979). Transects were established at two scales, one covering the variety of vegetation zones on the common, the second limited to a small clearing. The clearing was divided down the center into two zones, and observations made from the wooded margin. Transects were walked at a standard pace 6 times over 20 min in each hour. The clearing comprises an open space some 25 m by 18 m divided into 2 zones of *Molinia caerulea* and *Calluna*, and surrounded by birch canopy and furze. Spatial data were plotted on an Ordnance Survey 1:2,500 base and on a detailed plan of the clearing (Fig. 1). More intensive observations were made using a cassette recorder relating behavior and movements of adults to coded landmarks. Individuals were followed as long as possible (minimum of 3 min), and activities divided into the following categories: resting, basking, feeding, flight, interspecific interaction, conspecific interaction, attempted courtship, and inspection. To these were added locational data and as much interpretation as feasible. Capture of individuals for marking was found to affect their behavior, and for these observations each male required a unique mark. The
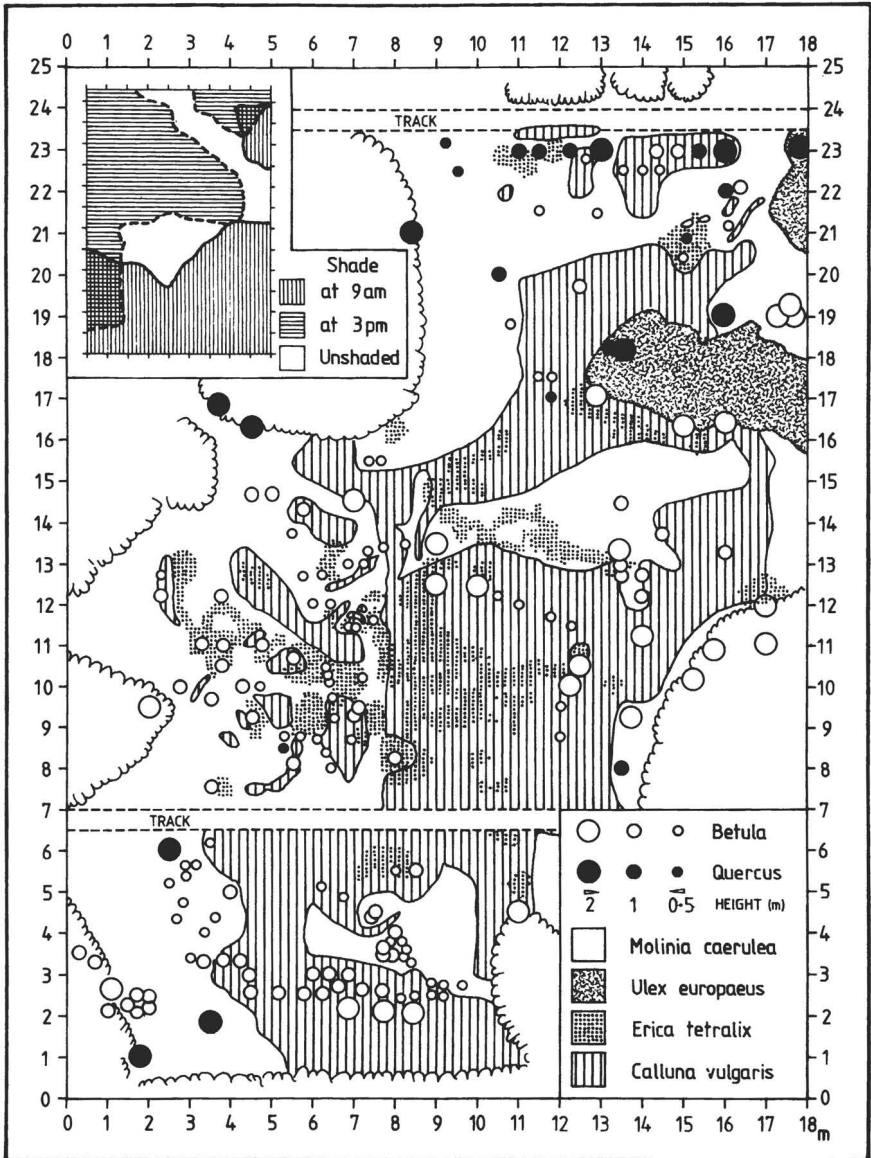
FIG. 1.   Topography, vegetation, and shading of the clearing used for observations on territoriality. The scale around the edge of the map is also used as a coordinate system for Figs. 5, 6, 7 and 8.

TABLE 1. Counts of male *O. venata* for different habitats and associated flora from 9 transects on Lindow Common.

	F	% I	% T
Habitat			
Woodland cover	0	0	26
Woodland glades & fringe	132	68	42
Open sward	43	22	27
Open track	20	10	5
Woodland bramble	0	0	5
Associated flora for open areas			
Calluna	7	4	30
Molinia	156	96	70
Tall-herb grassland	11	5	9
Bramble	97	50	13
Dry heath	10	5	19
Wet heath	11	6	9

F, number of adults; % I, percent of insects recorded on transects; % T, percent of transect associated with the habitat and flora. Based on 195 insects. Length of transect 2.24 km.

marking of individuals varied sufficiently for them to be traced following interactions with other males. Observations on particular individuals ceased if there was doubt as to their identity. All cassette recordings and transect observations were carried out in cloud-free conditions with shade temperatures above 20°C. As part of the program to determine the factors in the selection of perch sites, an artificial landmark (a white plastic bag) was used in the clearing, alternated with the natural background for identical observation periods.

RESULTS

Distribution of Adults on Lindow Common

Males have a clustered distribution on the common. They are not found under woodland shade (Table 1, $\chi^2_{(1)} = 69.1$, P < 0.001) and, in open areas, show a bias for wet heath, *Molinia* grassland, and tall-herb grassland as opposed to *Calluna* and dry heath (Table 1, $\chi^2_{(1)} = 35.5$, P < 0.001). There is no preference for clearings and open spaces surrounded by woodland compared to open areas extending beyond woodland ($\chi^2_{(1)} = 1.78$, P > 0.1). Edge sites are preferred, along tracks in the woodland or out on the open heath, at path junctions, in woodland clearings, and along the woodland fringe, males congregating at boundaries between tall and short vegetation rather than in open expanses of low growth (comparison with bramble areas excluded, $\chi^2_{(1)} = 35.1$, P < 0.001). However, males significantly "clump" on bramble bushes (*Rubus* spp.) most of which are also located by the side of tracks or at path junctions ($\chi^2_{(1)} = 223$, P < 0.0001), but ignore bramble under dense woodland cover ($\chi^2_{(1)} = 47.7$, P < 0.001).
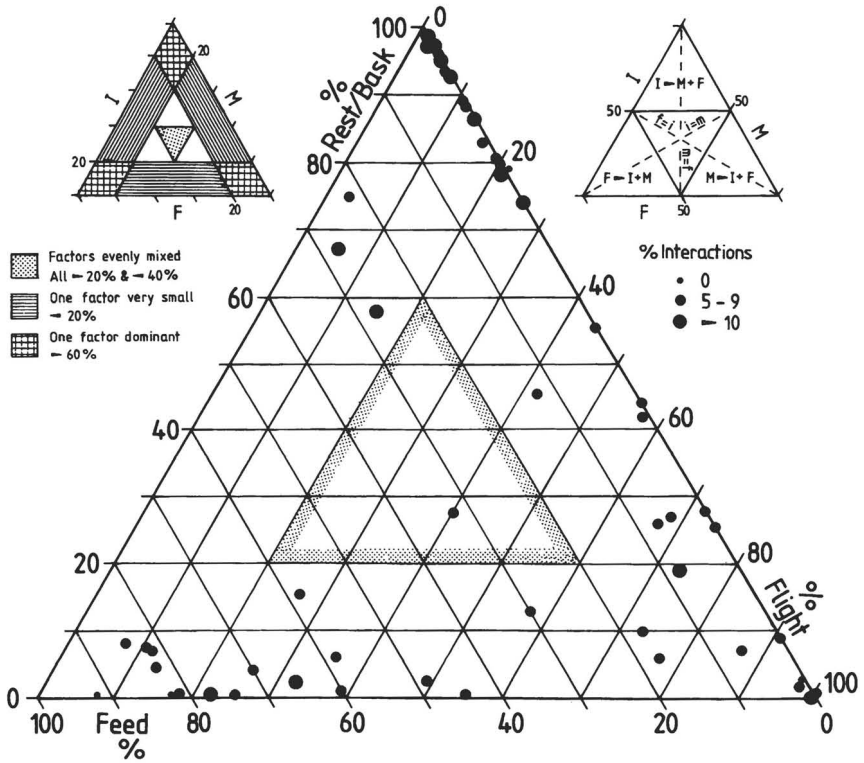
FIG. 2.   Behavior of 54 male *O. venata* observed for at least 3 min each (mean time = 405 sec, standard deviation 249 sec) recorded in triangular co-ordinates for basking, flight and feeding. Percentage interactions are overlaid as proportional symbols. Inset diagrams: I, inactive; M, mobile; F, feeding.

The female distribution is very similar to that of the males. On Lindow, *O. venata* larvae feed mostly on *Molinia*; females regularly oviposit on this grass and have been reared on it (Bink 1985).

Modes of Behavior

Modes or patterns of behavior are made up of individual acts of behavior. This is evident from placing 54 males in triangular coordinates for flight, basking-resting, and feeding. Several distinctive features emerge (Fig. 2). With three exceptions, males are restricted to areas on the graph where one activity is virtually dominant. Males do not behave randomly but bask, fly, or feed for extended periods, although grades of activity occur between flight and feeding and between basking and flight (far less between feeding and basking). Conspecific interactions (skirmishing between males and attempted courtship) occur for

each of these activities, which suggests that the butterfly is opportunistic in mate location. However, interactions are more frequent when males are basking. We argue that three distinctive types of behavior exist in male *O. venata*: perching, patrolling, and feeding. These behaviors are perhaps better visualized in the form of real-time plots of activity (Fig. 3), and become easy to distinguish using the spatial components of each behavior pattern, as will become clear below.

The perch behavior (Fig. 3a) is restricted to small areas, where a vantage point is adopted. Here, male *O. venata* bask in the sun and "sortie" after passing objects. Response to the latter varies dramatically from rapid inspections to violent spirals and chases depending on (i) the insect involved, (ii) the sex of the intruder if conspecific and (iii) prior ownership of the area. Conspecifics induce much greater activity than nonconspecifics, and contested ownership of the space leads to the most violent aerial activity, during which the impact of the males can be heard. Interactions between male *O. venata* are significantly longer when one of the males is territorial than when both are feeding or patrolling ($t = 3.98$, $P < 0.001$) (Table 2) (compare Wickman & Wiklund 1983, Wickman 1985b). Passing females trigger attempted courtship, though males are usually easily put off by fecund females, which flutter their wings and, having landed, on occasion, raise their abdomens. We suggest that some chemical deterrent is released. Males repeatedly return to perches in the same small area, which distinguishes this activity from patrolling. Perches are typically low vegetation, small seedlings of oak or birch, bramble leaves, occasionally herbs or grass stems, which barely overtop the ground vegetation. Only rarely are perches more than 1 m above the ground adopted, but the butterfly will rest (become inactive) on vegetation above this level. Males feed least during perching; apart from interactions, flight is restricted to short investigative patrols (as distinct from continuous patrolling) within and immediately beyond the area occupied.

At perch sites, extended interactions occur that are not simply the result of the resident male investigating the sex of the intruder and the intruder attempting to escape from a would-be predator (Scott 1974). Not only is female response to male approaches very different (many land and engage in mate-refusal posture), but this would not explain why intruding males (recognizable from wing marks) return after what can only be described as extremely violent aerial combat, and why such sorties take place back and forth over the area involved. The relation between the aggression of the incumbent and the inclination of the intruder to leave attests further the defensive role of interactions. Specific tolerance thresholds need to be exceeded before intruders leave an area, and similarly determine whether incumbents stay or abandon
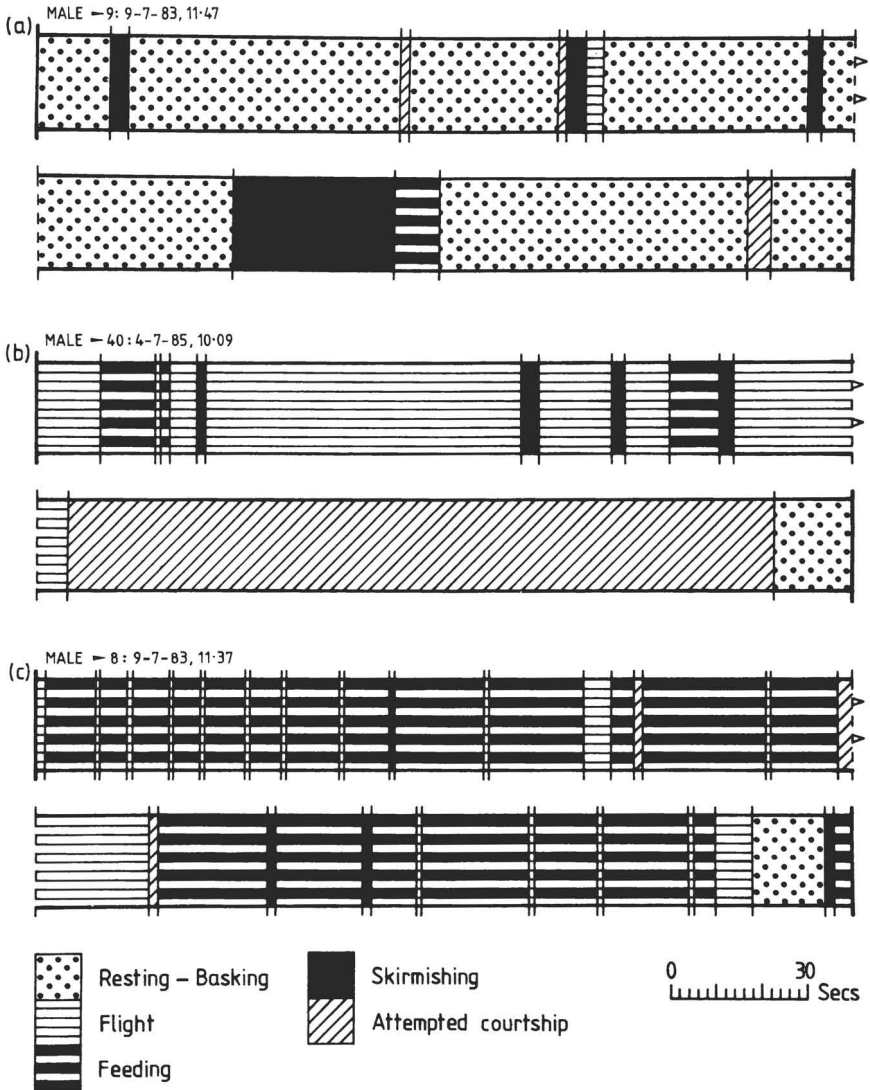
FIG. 3. Real-time plots of changing behavior in three male *O. venata* engaged in (a) territorial activity, #9, 1147 h, 9 July 83, (b) patrolling, #40, 1009 h, 4 July 85, (c) feeding, #8, 1137 h, 9 July 83.

territories. To some extent it was possible to simulate these responses using a net. Perching males that are merely disturbed by passing a closed net over them invariably return to the perch; those caught in the net bag and released in one gentle move usually return or retire to an area nearby, and return within 10 seconds. Males caught in a sweep

TABLE 2. Duration of interactions between male *O. venata* and other insects.

Interaction	Statistics[a]	Perching	Patrolling and feeding
Between males	x̄	7.7	4.3
	SE	0.7	0.4
	n	73	28
With other insects[b]	x̄	2.4	2.5
	SE	0.1	0.3
	n	76	16
Attempted courtship	x̄	3.8	3.8
	SE	0.7	0.3
	n	12	43

[a] x̄, mean time (seconds); SE, standard error; n, sample size.
[b] Other insects include *Maniola jurtina*, bees, and flies (mostly syrphids).

of the net and then released exit in a straight line at high speed never to return (Fisher exact test, $P < 0.001$) (Table 3). This not only has connotations for territoriality but also for mark, release, and recapture work with *O. venata*. Finally, *O. venata* males reveal distinct signs of pugnacity to other insects, such as syrphids, which hover in the area, effecting direct onslaughts rather than gentle investigative flights of which they are capable.

Patrolling (Fig. 3b) is distinguished by extended and spatially unbounded flights. The flight can be very slow, at any height up to 3 m, but is usually very low, where the butterfly engages in weaving, scanning, hovering, often circular inspections interspersed with infrequent halts (physical inspections), but always remaining close to vegetation, skimming over its surface. Flight can also be much faster, several m/second, apparently when the butterfly is changing location, and cues are weak. Patrolling behavior is intensive and seems to be influenced strongly by scent. One male was observed searching a 1 m tall birch seedling systematically for 15 min, weaving in and out of the twigs and leaves, before it found the female. The female left the clearing followed by the male. On other occasions, persistent searches by males of small areas (<0.5 m²) in circuits were witnessed where females were found eclosing.

Males feed while patrolling, but for short sessions. They also bask and rest, especially after extensive flight, although platforms differ from territorial perches (occurring at a greater range of heights up to 3 m; territorial perches are below 1 m), and are used once only. Skirmishes with conspecifics take place; some of these may well be short inspections, but many are sharp interactions which effect spacing of individuals.

Feeding behavior (Fig. 3c) is equally distinctive, involving short feeding sessions interspersed by "hops" or short flights from flower to flower. Short periods of basking and resting occur as do longer flights

TABLE 3. Effect of artificial disturbance on territorial male *O. venata.*

Disturbance level	Direct return	Delayed return	Rapid, linear exit
Closed net swept above insect	10	0	0
Gentle capture	6	3	2
Determined capture	0	0	7

as the butterfly relocates to new resources. Mate location is opportunistic rather than directly sought, non-conspecifics being ignored, and skirmishes with conspecifics being brief but pugnacious or investigative. Attempted courtships also occur frequently, males tending to harrass nonreceptive females feeding on the same resource. The length of each feeding episode depends much on the nectar source, and is longer on *Rubus* spp. and *Hierarchium* than on *Erica tetralix.*

The above three modes of behavior are distinctive and facilitate the classification of the 54 individuals in the ternary graph. Even so, only occasionally was it possible to follow males long enough to note switches from one behavior to another, although a number of males were seen to abandon territories, usually after prolonged periods of inactivity when intruders were lacking.

Switches in Mate Location Activity

Typically, males patrolled in the morning and perched in the afternoon (transect data over heath: $\chi^2_{(1)} = 5.8$, $P < 0.02$; observations in clearings: $\chi^2_{(1)} = 33.8$, $P < 0.001$). The number of males engaging in territoriality increased in the afternoon in areas lacking nectar ($\chi^2_{(1)} = 13$, $P < 0.001$) and in areas having it ($\chi^2_{(1)} = 4.8$, $P < 0.05$). This pattern was influenced by weather. During cloud-free days (Fig. 4), males perch early but switch to patrolling after 1000 h. In the afternoon, there is a reversion to perching, and some new territories are established. However, in favorable locations, territorial males can be found throughout the day, as in the clearing (Fig. 1). Similarly, patrolling males can be found in the afternoon, but there is typically a great reduction in patrollers in the wet heath areas during afternoon. This pattern was much affected by weather; after overcast mornings, males patrolled in the afternoons. The marked diurnal pattern may also break down during the season. Preliminary observations point to a bias towards perching at the outset of the flight season and at the very end when unmated females are scarce. On 23 July, an equal number of perching males were recorded in the morning and afternoon. Other factors can lead to a breakdown of the typical model. During 1985, emergence was delayed by cloudy and cool weather during the last week of June. When conditions changed on 1 July, an abundance of fresh males and females
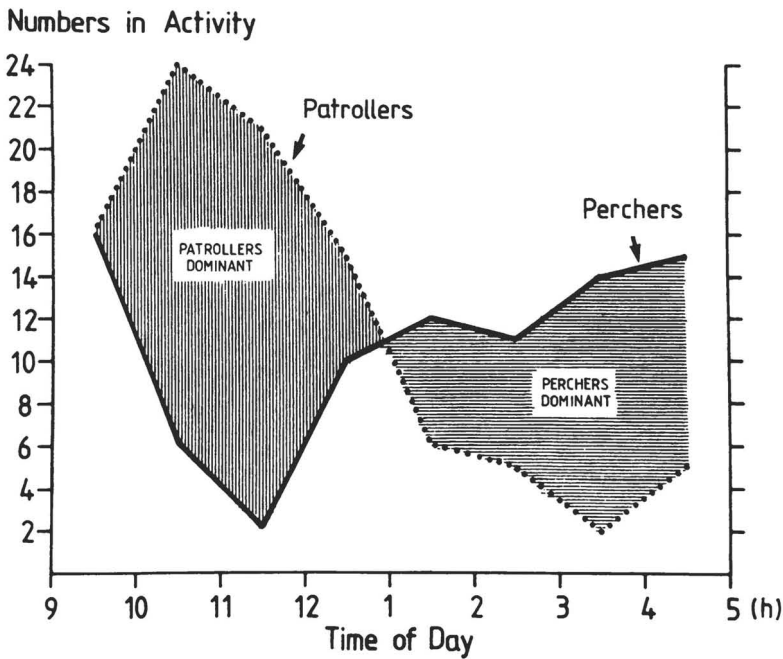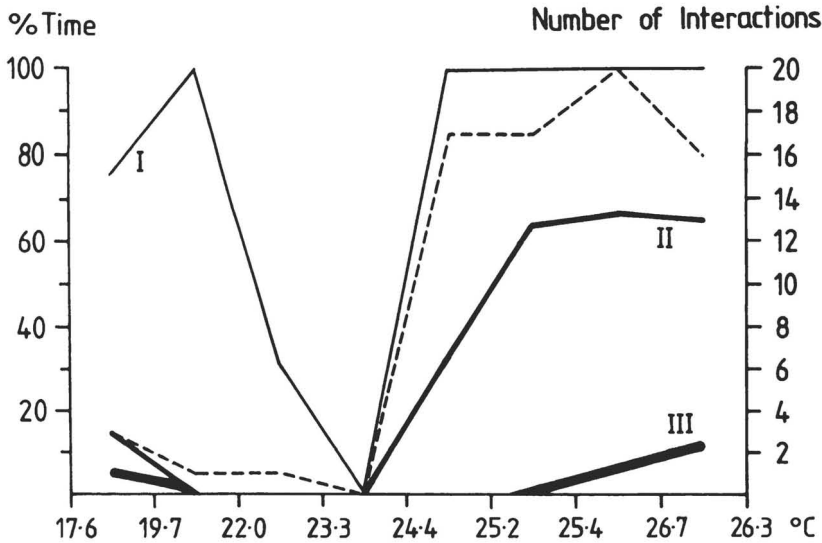
FIG. 4. Diurnal changes in male *O. venata* behavior in the clearing for clear sky conditions on 7 July 1984. Top: Percentages of territorial males and number of interactions between conspecific males (for 20 min in each h) in the main territory centering on map coordinates 070100. Intermittent line, number of interactions. Number of males in territory: line I, 1; line II, 2; line III, 3. Bottom: Frequency of territorial males and patrollers

appeared, and males patrolled as much in the afternoon as in the morning (perch : patrol, 1:2.75 to 1:2; $\chi^2_{(1)} = 0$).

Territories

Location of territories. Transect data over the common revealed that males establish territories at edge or junction sites mainly at woodland margins. Sites without nectar are less favorable as males establish territories in these areas only in the afternoon. A comparison of two groups each comprising four woodland margins equal in size and similar in aspect differed in the number of territories they contained on the basis of a nectar source, bramble ($\chi^2_{(1)} = 6.72$, P < 0.01).

Repeated transects (6/h) in the clearing throughout the day for several days revealed that territories were established in two main areas (Fig. 5): in the middle of the clearing (map grid reference 070100) and in the NW part of the site (map grid reference 1222). The canopy edge facing direct sunlight, the tall birch seedlings in the center of the clearing and the main body of heather and furze were all generally ignored. Crowding of the clearing by males led to a number of subsidiary territories being established in the afternoon, but the main territories occupied edge sites, exposed to sunshine, between the hostplant and some other vegetation type. The central territory was not affected by shade at any time of the day and included an extensive area of *E. tetralix*, a major nectar source. By comparison, the NW territory was abandoned in the late afternoon when it became shaded and nectar sources were limited.

Except for the central territory, the pattern of perches was noticeably affected by the diurnal changes in shade, a significant shift in territories occurring from W to E as the day progressed ($\chi^2_{(1)} = 16.38$, P < 0.001). None of the perch sites below vertical coordinate 07 was occupied before 1200 h. Apart from this diurnal shift, the pattern of territories remained virtually stable from year to year. There is, however, clear indication of a seasonal shift in perches in the central territory, a significant movement northwards in perches between 3 and 7 July 1984 ($\chi^2_{(1)} = 7.41$, P < 0.01) and between 7 and 23 July 1984 ($\chi^2_{(1)} = 6.38$, P < 0.02). This coincided with a shift in flowering of *E. tetralix*, from the shorter *Molinia* zone to the *Calluna* sward where it is partially overtopped. Males were perching 10 cm higher on 23 July and therefore in a cooler microclimate during cooler conditions (maximum temperatures: 7 July, 27°C; 23 July, 24°C; windspeed: 7 July, 3.4 knots; 23 July, 5.9 knots).

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from 48 transects covering clearing. Mean hourly number is obtained by dividing numbers in activity by 6. The few males feeding have been omitted. Shade temperatures are given for each hour (°C).
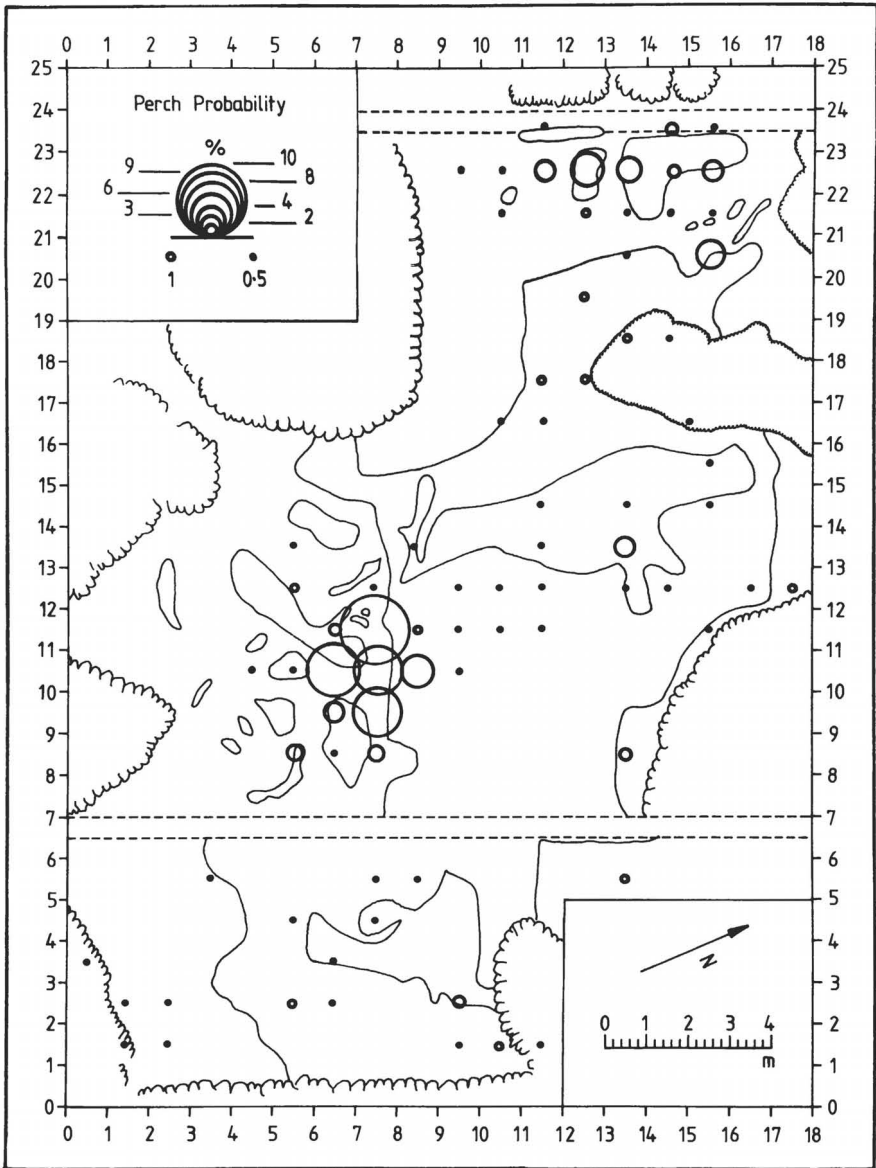
FIG. 5. Probability distribution map for territorial male *O. venata*, based on 162 transects in clear conditions evenly spaced over 4 days, 30 June, 3, 7, and 23 July 1984 (6 transects/h). Two well established territories occur; the most important centers on map coordinate 0710, the second around 1422.
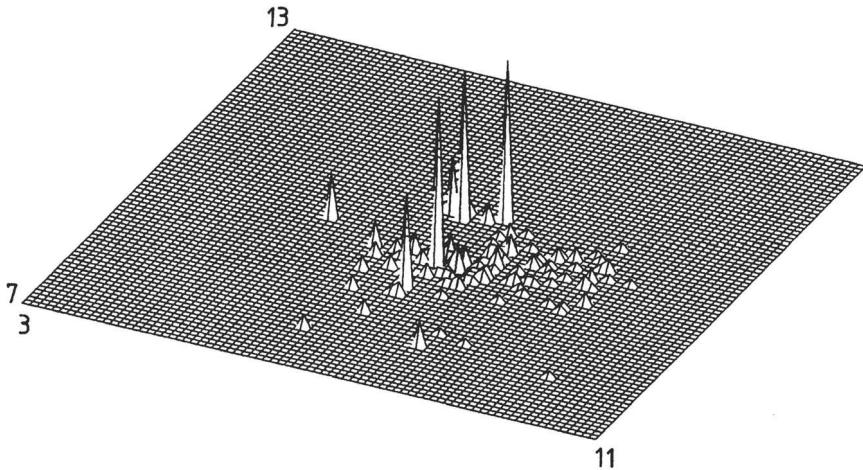
FIG. 6.   Fish-net plot illustrating relative frequency of different perch sites by territorial male *O. venata* in main territory of clearing (map grid reference 070100) based on 38 insects and 364 records (resolution 10 cm). The figures at the corners are map coordinates for Fig. 1.

Inside territories. There is a distinction between what can be labelled a territory (the area defended by each male) and perches within a territory (the platforms or sites used by males after each sortie or voluntary patrol in the area defended). Dominant among perches in the main territory of the clearing are tiny birch seedlings under 15 cm tall (the same height or lower than surrounding heather), corresponding to the six substantial peaks in the plot (Fig. 6). The multiplicity of residual "relief" relates to sprigs of heather or cross-leaved heath, even grass blades, casually used during voluntary patrols or after interactions.

The actual size and shape of the territory varies from individual to individual (Fig. 7) despite the fidelity of different insects from day to day and year to year to the main perches illustrated in Fig. 6. Many males are restricted to some smaller portion of the two territories in the clearing; in the central territory, to the E or W half separated by the bank of *Calluna*. Nevertheless, others use a wider array of perches, and the unified structure of the main territory is evident in the links joining the main perches in Fig. 7. Interactions between males lead to the discovery and use by incumbents of a wider array of perches. Thus, both the main territories in the clearing are too large for one *O. venata*; intruders can pass over a portion of the territory and temporarily settle in another part of it unnoticed. However, each territory is also too small for two or more *O. venata*. A sortie after intruders by one occupant usually triggers activity in the other. Once this happens, violent interactions occur, often repeatedly triggered by a third party, until one of
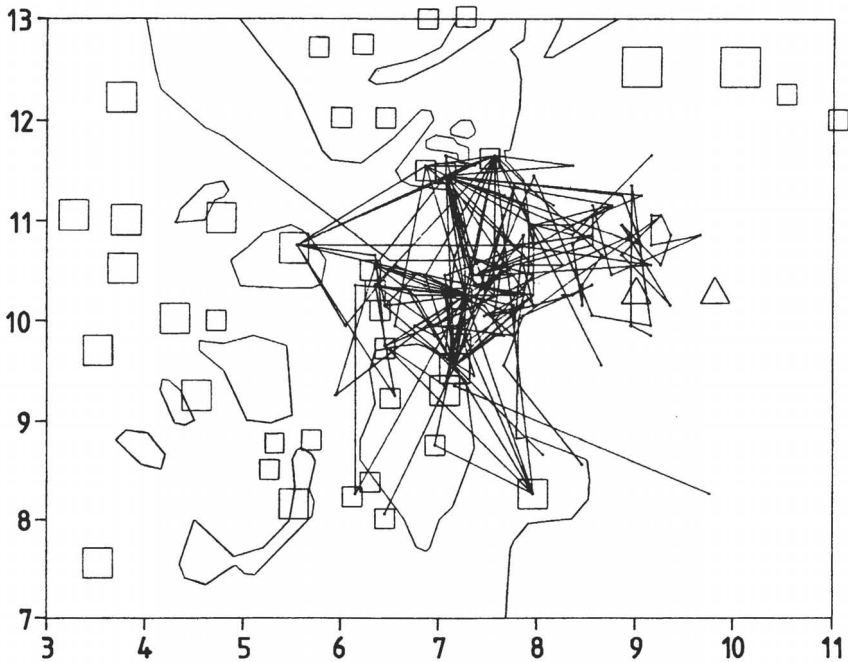
FIG. 7. Linkage diagram illustrating consecutive moves by male *O. venata* between perch sites in main territory of clearing around grid coordinate 0710. Zone covered by peaks in Fig. 6 represents a single territorial unit. Frequency of moves between perches is not illustrated. Data as in Fig. 6. Base map includes location of vegetation boundaries and tree seedlings (squares) shown in Fig. 1.

the two prior occupants leaves. Occasionally such premium is placed on the central territory that fourth and fifth males were noticed to enter while three contesting the zone are immersed in dispute. They, in turn, become incorporated in the next "dog fight".

The siting of territories has priority over perches, although shape and size of a territory can be distorted by altering the nature of perches within it. Males occasionally perched on artificial objects on the common, and used these repeatedly even if these "perches" were moved about. This effect is shown for the clearing where Fig. 8 illustrates perch sites adopted with and without a white plastic bag, alternated 4 times over 10 min periods. Clearly, the plastic bag disrupts the pattern of activity (Fig. 8, $\chi^2_{(1)} = 51.6$, P < 0.001) and acts as an overoptimal

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FIG. 8. Linkage diagrams illustrating consecutive moves by male *O. venata* between perch sites in main territory of clearing; Top: in the presence of an artificial object (white plastic shopping bag). Bottom: in its absence. Triangles show two locations used for the artificial perch.
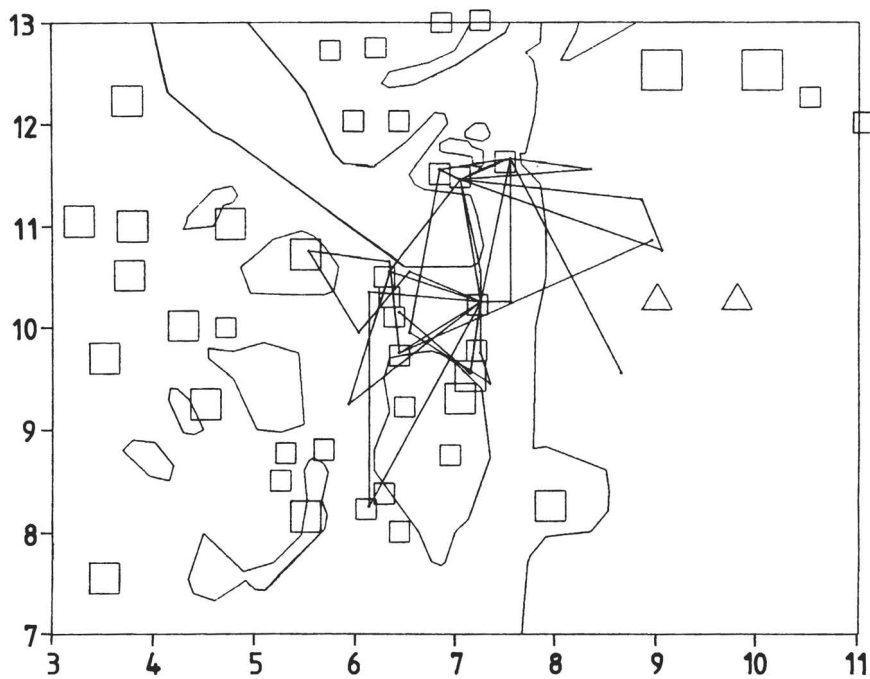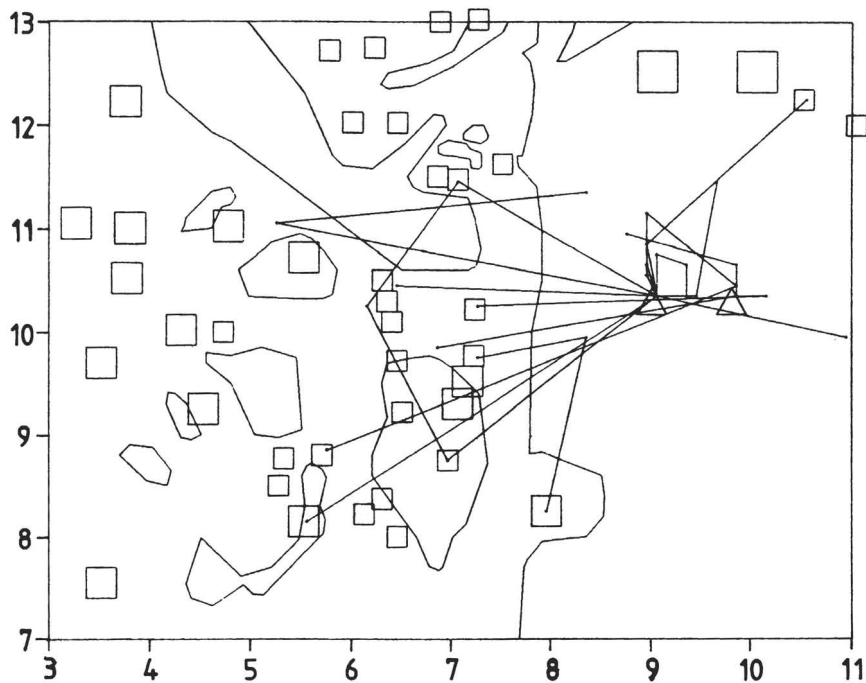
stimulus compared to the territory. There is, however, a limit to which territorial sites can be distorted. Artificial perches are used in the vicinity of sites where territories would normally be established, but apparently not in open areas usually ignored by the butterfly. At the woodland edge, the plastic bag was occupied continuously over 17 min of observation and contested for 13 times. In an adjacent wet heath area, it was visited twice by male *O. venata* during 11 min who inspected it while in flight and moved on.

DISCUSSION

O. venata males reveal similarities and some differences with other butterflies that should complement the discussion on mate location behavior. Pertinent questions are: What determines the distribution of males? Why do they both perch and patrol? Why do they change their activities through the day, and how do they know when to change? Does the butterfly engage in territorial defense and, if it does, what factors induce the butterfly to defend one area more vigorously than another? How does it recognize good territorial sites and suitable perches in them?

Males are absent from the woodland cover and the dry heath. The woodland cover is dense, little light reaches the ground, and the butterflies would not be able to thermoregulate under it. The other negative zone, the dry heath, is void of nectar sources and lacks larval hostplants. Males are found in *Molinia* areas where there are eclosion sites, the most predictable locations for females. The enormous bias for bramble bushes points to a combination of factors: bramble is a major nectar source, and *Molinia* occurs in the immediate vicinity. Moreover bramble is typically associated with edge and junction sites.

O. venata perches and establishes territories in the early morning when air temperatures are low, and during the afternoon when they are highest. However, the insect treats afternoon as morning if the early part of the day has been cloudy and cool. In this respect, it is similar to vanessids in behavior, which also establish territories in the afternoon (Baker 1972, Bitzer & Shaw 1979, 1983), but differ from three satyrids, *L. meqera, P. aeqeria,* and *C. pamphilus,* which patrol more when air temperatures are highest (Dennis 1982a, Shreeve 1984, Wickman 1985a). Adoption of perching implies that a particular resource is more difficult to obtain. For one or more of several reasons, scrambling for the resource over a wider area becomes ineffective, and it is then necessary to wait for females at vantage points. The reasons are: (i) males have insufficient energy supplies to remain patrolling; more specifically, energy used in patrolling begins to exceed that used in defense (Baker 1972). (ii) Ambient conditions are inadequate for sustained flight, which lowers body

temperatures (Shreeve 1984). (iii) The ratio of available females is substantially reduced, and patrolling becomes less effective than perching at vantage points, regardless of energy resources. Energy losses during perching may match those of patrolling as skirmishing in territories can often be continuous and more violent than patrolling flights. Some territories are also occupied in the mornings, during the early and late flying season and in prime locations, presumably when energy levels are high.

Early morning perching may well relate, in part, to the need for both sexes to warm up and become fully active, but does not explain afternoon perching and mid-morning patrolling. On clear days, temperatures are higher after 1300 h than before. Perching as opposed to patrolling is more likely to relate to the unavailability of unmated females. It is possible that most unpaired females may be found by patrolling in the early part of the day, but that a switch to perching is effected in the afternoon as patrolling for a dwindling resource becomes unsuccessful. Whatever the explanation for switches in behavior, the reason is closely tied to the cue used by males to determine when switches are made. As neither energy nor ambient conditions (heat and sunshine) seem sufficient to explain the timing of switches in behavior, contacts (or lack of them) and scent may form prominent cues. The way males are arrested in flight to scan small areas for several minutes where nothing is to be seen suggests this. Clearly, more needs to be known about the influence of scent, particularly the distances over which behavior can be influenced by it.

Perching (and in some cases patrolling [Shields 1967]) has been likened to territoriality by Baker (1972) since defense of some "resource" is involved. This is denied by Scott (1974) for three reasons: (i) Males are incapable of learning topographic details of sites, and move on to new areas. (ii) As obvious resources are missing, there can be no territories for feeding, roosting, or oviposition. (iii) Interactions involve investigation of sex and not defense. Baker (1972), Davies (1978) and Dennis (1982a) have shown that males return to the same area repeatedly, even to the same perches, and that butterflies are capable of a spatial learning process (Baker 1978). We agree that species are genetically imprinted for characteristic topographic sites in which to establish territories (Scott 1974:107), but not for the precise details of sites, as insinuated by Scott. Scott's insistence that males should occupy the same area during several days does not hold in any case, since occupancy should be gauged against the time required to fulfill a particular function. Some perches are clearly established where there are female resources (hostplant sites in *A. urticae* [Baker 1972]; possible thermoregulation sites in *P. aeqeria* [Parker 1978]; oviposition, therefore emergence, sites in *L. meqera* [Den-

nis 1982a, 1986]). In *O. venata*, males have a bias for establishing territories where there is nectar in addition to the hostplant. Even where fundamental resources for females are missing, researchers have in every case shown that perches correspond to strong linear features or prominent visual markers, which have the capacity for concentrating resources. For virgin females, the most essential resource is males. Such strong visual lines dictate movement in insects and determine predictable locations for both sexes (Baker 1972, Dennis 1982a, Dennis & Bramley 1985, Shields 1967, Bitzer & Shaw 1979, 1983). Scott's own research has shown this to be the case in hilltopping males (Scott 1968) and for perching skippers (Scott 1973).

Finally, Baker (1972, 1983) has indeed shown that defense can be involved, and his observations are substantiated by others (Davies 1978, Dennis 1982a, Bitzer & Shaw 1979, 1983, Wickman & Wiklund 1983). In *O. venata*, perch sites are undoubtedly defended and are thus territories. Baker's (1972, 1983) observations are confirmed in that, usually, intruders failed to settle in an area unless the area was vacated, and unless escalated contests occurred when ownership was disputed. Two issues point away from Scott's insistence that territoriality in butterflies is no more than the investigation of the sex of the intruder by the incumbent and avoidance by the intruder of a would-be predator. First, interactions are significantly shorter between patrolling males; clearly it does not take long for males to determine the sex of individuals. Interactions between males at perch sites involve escalated contests back and forth over the perch site. Secondly, if the intruder is attempting to escape from a predator, it is then difficult to explain why it returns, often repeatedly, to the site to invite further strikes from the "predator". Despite these criticisms, it would be a mistake to regard the territorial defense (Baker 1983) and investigation (Scott 1974) models as mutually incompatible, although Scott's reasons for denying territorial defense are wrong. We suspect that the scale of defense is as variable as mate location behavior is flexible. At least three features point to an ability in *O. venata* to assess costs and benefits in defense: (i) the degree to which occupancy and defense varied between different territories in the clearing (corresponding to the premium placed on sites by males measured in numbers of intruders, length and violence of interactions); (ii) the varying degrees of pugnacity between contacting males when engaged in different activities (feeding, patrolling, and perching); and (iii) the voluntary abandonment of territories after unsuccessful periods.

Territories are typically established along distinct linear features, visual markers such as edges and junctions, but there is some indication that female resources may also be a factor in the location (as well as degrees of defense) of territories. Some sites, such as those in the clearing

(Fig. 5) associated with nectar sources, had territories throughout the morning on many days, but other sites along the woodland fringe associated with hostplant but without nectar were established only in the afternoon. Moreover, there was a distinct shift in location of the main territory in the clearing (Fig. 5) which coincided with changes in nectar apparency but not with temperatures. The varying frequency of perches in different parts of this clearing is in itself evidence of the varying quality of sites. However, not all hostplant locations and emergence sites become territories. Open areas, where females were found eclosing, were ignored. Visual rather than scent cues seem to be prominent in setting up territories.

Perching spots in territories are repeatedly used after interactions, but the fidelity to particular perches depended on the array of opportunities (number of potential perches) and the degree of disturbance by intruders, which usually led incumbents to cover a wider area and take up different posts. Typical perches were low, robust launching platforms providing effective observation posts. Taller seedlings over 1 m high were avoided, presumably because incumbents would then not be able to pick out intruders against the background vegetation beneath them. *O. venata* learns the spatial configuration of its territory quickly. Searches for artificial objects used as perches, removed during interactions, are first made where they occurred, the insects thereafter increasing the area searched. Voluntary patrols within the area of the territory probably contribute to gaining familiarity with territory landmarks. Several features then combine to demonstrate the adaptability of this hesperiid: opportunist behavior, spatial memory, ability to recognize resource-generating landmarks, and perhaps location of mates using scent—a developing theme in butterflies demonstrating degrees of "intelligence" in short-lived temperate species as well as tropical relatives with long-lived adults.

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