

Landform resources for territorial nettle-feeding Nymphalid butterflies: biases at different spatial scales

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Dennis, R. L. H., 2004. Landform resources for territorial nettle-feeding Nymphalid butterflies: biases at different spatial scales. *Animal Biodiversity and Conservation*, 27.2: 37–45.

Abstract

Landform resources for territorial nettle-feeding Nymphalid butterflies: biases at different spatial scales.— Observations of perch sites for three territorial nymphalid butterflies reveals a bias in landform use at two spatial scales: at macro-scale, sunlit wood edges at the top of slopes; at micro-scale, molehills and bare ground compared to vegetation substrates. There is a hierarchy in landform exploitation; slope and edge position outweighs micro-landform feature use. Landforms for territories tend to be prominent landmarks. This is especially the case at macro-scale (e.g., wood edges and corners); though also the case at micro-scale (e.g., molehills, earth bank edge) it is not invariably the case and highly apparent substrates (white boards) entered into territories were ignored. The predominant characteristic of all landforms chosen is that they are all hotspots: warm and sheltered sites. Substrates used for perching change with ambient conditions. In cool spring weather warm sites are essential for territorial defence, acquisition of females and predator evasion. As air temperatures increase there is an increasing propensity for territorial incumbents to use non-apparent, vegetation substrates. Bare earth sites are suggested to be important habitat components for butterfly biology as is their continued renewal through human activity.

Key words: Thermoregulation, Territoriality, Micro-landforms, Molehills, Habitat, Utility-resources.

Resumen

Utilización de las formas del terreno por los ninfálidos que se nutren de ortigas: sesgos en distintas escalas espaciales.— La observación de los lugares donde se posan tres ninfálidos territoriales revela un sesgo en el uso de las formas del terreno en dos escalas espaciales: a macroescala, en los linderos soleados de los bosques, en la parte superior de las laderas; a microescala, en las toperas y terrenos áridos en comparación con sustratos con vegetación. Existe una jerarquía en lo que respecta a la explotación de las formas del terreno; las laderas y los bordes prevalecen sobre el uso de las microcaracterísticas del terreno. Las formas de terreno empleadas para definir los territorios tienden a ser importantes puntos de referencia. Esto es especialmente cierto a macroescala (por ejemplo, los lindares de los bosques y recodos) y, aunque también es válido a microescala (por ejemplo, toperas, franjas de tierra), se dan excepciones; así, los sustratos muy aparentes (tableros blancos) introducidos en los territorios fueron ignorados. La característica predominante que compartían todas las formas de terreno escogidas es que eran puntos calientes: cálidos y resguardados. Los sustratos empleados para posarse cambian con las condiciones ambientales. Con el clima fresco de la primavera, los lugares cálidos resultan esenciales para la defensa territorial, la adquisición de hembras y la evasión de los predadores. Pero a medida que la temperatura del aire aumenta, quienes han ocupado el territorio tienden a utilizar sustratos con vegetación no aparente. Se ha sugerido que los lugares de terreno árido son importantes componentes del hábitat para la biología de las mariposas, como también lo es su continua renovación a través de la actividad humana.

Palabras clave: Termorregulación, Comportamiento territorial, Microcaracterísticas de las formas del terreno, Toperas, Hábitat, Recursos funcionales.

(Received: 6 VIII 03; Conditional acceptance: 16 X 03; Final acceptance: 10 XI 03)

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Introduction

Males of nettle-feeding Nymphalid butterfly species *Inachis io* (Linnaeus), *Aglais urticae* (Linnaeus) and *Polygonia c-album* (Linnaeus) are known to defend territories, limited areas, to acquire females (Baker, 1972; Dennis & Shreeve, 1988; Rutowski, 1991). Baker (1969) argues that territorial behaviour seems likely to evolve when some requirement, in this case females, is obtained in greater quantity as a result of staying a certain length of time in one suitable area rather than spending some of that time in voluntary displacement from area to area and when the quantity of this requirement is further increased by defending the area against competing individuals. He also argues that male territories are likely to be found in species in which some requirement of the female (e.g., feeding or oviposition sites) occurs in relatively concentrated areas and less likely to be found in species in which female requirements are diffusely scattered through the environment (Baker, 1972).

Baker (1972) has explored various aspects of territories, including territory size and territorial behaviour, in the two nymphalids, *Inachis io* and *Aglais urticae* (e.g., territory: male ratio; territorial decisions, timing of territorial behaviour; territorial interactions). From this research, we know that these territories are found in distinctive areas; many of the features are shared by the two species. Both select territories on the ground in direct sunlight and both prefer to have some vertical edge on the side away from the sun, typically a line of trees in *Inachis io* and a wall or hedge in *Aglais urticae*. The advantage of an edge site is suggested to be that migrating females, searching for oviposition sites, tend to fly along edges for some distance in their search. Corners seem most advantageous to *Inachis io*. Male *A. urticae* more typically establish territories in areas with hostplant patches (e.g., nettle patches). Nectar source availability in the territory is not important.

However, we have limited information about the nature of the ground occupied by territorial males, the physical features used for perching. The use of different terrain micro-features at the current study site by territorial *Inachis io* was first noticed in April 1999; male territories were established on earth mounds (molehills) created by moles (*Talpa europaea*), a burrowing animal, rather than the cut grass surfaces. These observations were repeated in early May 2000 (Dennis, unpublished observations) for *Inachis io* and *Aglais urticae*, including the use of an abandoned concrete seat base in the same area. Here I explore several issues associated with territorial perches. Are there consistent patterns in choice of landforms for territorial perches? Is landform choice taking place at several scales, at meso/macro-scale (e.g., hillslopes, edge structures, corner sites) and micro-scale (e.g., molehills)? Which spatial scale is dominant in perch choice? Is there differential use of micro landforms

by different Nymphalid species? If so, what is this related to? Also, does micro-terrain use relate primarily to thermal conditions, to feature prominence (i.e., visual stimuli) (Dennis & Williams, 1987) or to areas where consumable resources (viz., host plants, nectar) occur? The latter finding has relevance for the integration of resources comprising habitats (Dennis et al., 2003).

Methods

The study has been undertaken in part of a public park, The Carrs, Wilmslow, Cheshire UK (fig. 1). The area chosen (grid reference: SJ8481), 340 m long by 110 m wide (12,538 m²), comprises a south-west facing slope above the river Bollin, bounded by the river's north bank at the foot of the slope and by a narrow woodland separating the Carrs from housing at the top of the slope. The south-eastern extremity of the study area effectively forms a large sloping clearing with woodland on three sides. The north west end terminates in an abrupt reflex angle in the wood edge, the corner distinguished by a low bank of rough grass (*Dactylis glomerata* Linnaeus) centred on a hollow (> 50 cm deep), the previous site of a tree trunk. Most of the study area comprises short mown grass divided up by small copses of trees, though a very narrow strip of uncut grass and scrub borders the wood upslope and a wider (2 to 3 m wide) strip of vegetation including trees, scrub and tall herbs forms the river levée. The host plant for all three nymphalids, *Urtica dioica* Linnaeus, is restricted to these borders and is substantially more abundant along the river bank (incidence 163 m, 13 m overtopped by vegetation) than along the wood edge at the top of the slope (incidence 58 m, 27 m overtopped). A single path traverses the length of the study area but other, unofficial paths of movement—evident in the flattening of the grass and bare earth patches from foot wear and scuffing—run along the wood edge and riverside.

Molehills are concentrated in seven zones, two at the top of the slope (127 molehills) and five at the base of it (835 molehills); The clearing also comprises a concrete rectangle (116 x 167 cm), a disused seat base, 5m from the top of the slope and cut horizontally into it. The mean diameter of molehills is 50.1 ± 1.3 cm and their total area 193.7 m², occupying 1.54% of the study area. Owing to differences in age and compaction, molehills in the distinct zones contrast in dimensions ($F_{(6,92)} = 10.6$, $P < 0.0001$) and their respective total dimensions have been calculated for each zone separately.

Uniform transects ($N = 36$) were conducted over the entire area ($N = 12$) and the clearing ($N = 24$) afternoon BST between March 18 and 31, 2003 during dry conditions, in sunshine and when shade air temperatures > 14°C. Wind, varying in strength between 1.5 to 8 m/s, was predominantly from the south (mean $182^\circ \pm \sigma 42^\circ$, minimum 134° and maximum 322°) during the survey. Territories at the study location were identified from fidelity to

sites following voluntary patrols and interactions with intruders (Baker, 1972). Distinct zones of the study area were used repeatedly for perching (fig. 1); territorial interactions (Baker, 1972), between the three species as well as between conspecifics, were observed to occur within each of these zones with one exception at the base of the slope. Records were noted for six classes of perch sites for males in established territories: concrete seat base, molehill, bare earth scuff, vegetation debris (dried leaves and twigs), dead grass and live grass. Observations were also made of behaviour on perches. As it was not possible to establish a secure control site in the park, temperature contrasts for the valley slope and perch sites were taken using repeated (> 10 times) alternate paired measurements with a fast-response thermistor (accuracy $\pm 0.5^\circ\text{C}$) between transects. Two white boards (each 25 cm²) were used to test the response of butterflies to enhanced stimuli in the clearing; these presented a cool, glossed white exposed surface. Observations were carried out on two further dry, sunny days (April 15 and 16) when shade air temperatures > 23°C to test perch site use in much hotter conditions. To avoid influencing behaviour, individuals were not marked but identified by distinctive markings.

Comparisons of perching sites have been processed for two sets of data, for all records (observations) of perching and separately for all individuals. In the second case, only the first observation of perching has been used. Individual results are coined in terms of null hypotheses. Micro-scale refers to features of < 1 m and macroscale to features at least an order of magnitude greater (> 10 m).

Results

Selection of large scale landforms. A comparison of slope base and top

Hypothesis: no distinctions exist in territorial perching between the top and base of slope. Five territorial sites were identified at the top of the slope compared to three at the base (fig. 1). However territorial occupancy was substantially greater at the top of the slope for all three nymphalid species. Altogether, almost 10 times more individuals used the top of the slope by the wood edge than the base of it near the river (all records: $N = 126$ and 11; $\chi^2_{(1)} = 31.7$, $P < 0.0001$, single records for individuals: $N = 87$ and 9; $\chi^2_{(1)} = 19.6$, $P < 0.0001$ tests standardised for number of territories). A similar frequency of *Inachis io* and *Polygonia c-album* were found at the base and top of the slope; however, significantly more *Aglais urticae* were found at the base of the slope than for the other two species (all records: *I. io* versus *A. urticae*: Fisher exact test, $P = 0.0003$; *P. c-album* versus *A. urticae*: Fisher $P = 0.002$; Single records for individuals: *I. io* versus *A. urticae*, Fisher $P = 0.008$, *P. c-album* versus *A. urticae*, Fisher $P = 0.019$).

Selection of micro landforms. Biased use of molehills

Hypothesis: no bias occurs in the use of molehills as territorial perches. The three species use molehills significantly and substantially more often than expected by chance based on the area of surfaces available to them (all species lumped together and all records: $\chi^2_{(1)} = 85.4$, $P < 0.0001$; all species lumped together and one record per individual, $\chi^2_{(1)} = 59.3$, $P < 0.0001$; for the three species separately (all records and one record per individual), χ^2 tests and Fisher Exact tests, $P < 0.001$). These results were obtained applying a conservative test, based on the area of molehills as perch sites compared to the area of other sites potentially available to territorial butterflies. This is a conservative test as perches are included for territorial areas at the top of the slope lacking molehills altogether.

Comparison of large scale and micro land forms

Hypothesis: numbers of perch sites corresponds with the number of molehills. Dominance of the use of molehills over slope position should produce a distribution of perch sites equating with the abundance of molehills. However, perch sites dominated the slope top compared to the slope base despite the fact that favoured perch sites (i.e., molehills) were far more abundant (6.6 times) at the bottom of the slope than at the top of it (all species lumped together and all records: $\chi^2_{(1)} = 167.6$, $P < 0.0001$; all species lumped together and one record per individual, $\chi^2_{(1)} = 111.2$, $P < 0.0001$).

Comparison of perch sites used by the three nymphalid species

Hypothesis: there are no distinctions in perch sites among species. Direct comparisons have been made of perch sites by the three nymphalid species. These were found to differ in their exploitation of the six available perch site categories (table 1). They differ significantly in a comparison of bare ground sites versus vegetated sites (all records: $\chi^2_{(2)} = 9.12$, $P < 0.02$; one record per individual: $\chi^2_{(2)} = 6.13$, $P < 0.05$). However, this distinction may be caused by the dominant use of the concrete seat base by *Inachis io* (see below). Comparisons with data adjusted for removal of the concrete base showed homogeneity among species in perch type use for molehills (all records and single records per individual, $P > 0.10$) and bare earth sites (all records and single records for individuals, $P > 0.05$).

Comparisons of the thermal environment and other resources within the study site

Hypothesis: the distribution of resources (nectar, host plants and warm areas) does not influence the distribution of perches. At the time of the survey very few nectar sources were available in the study area

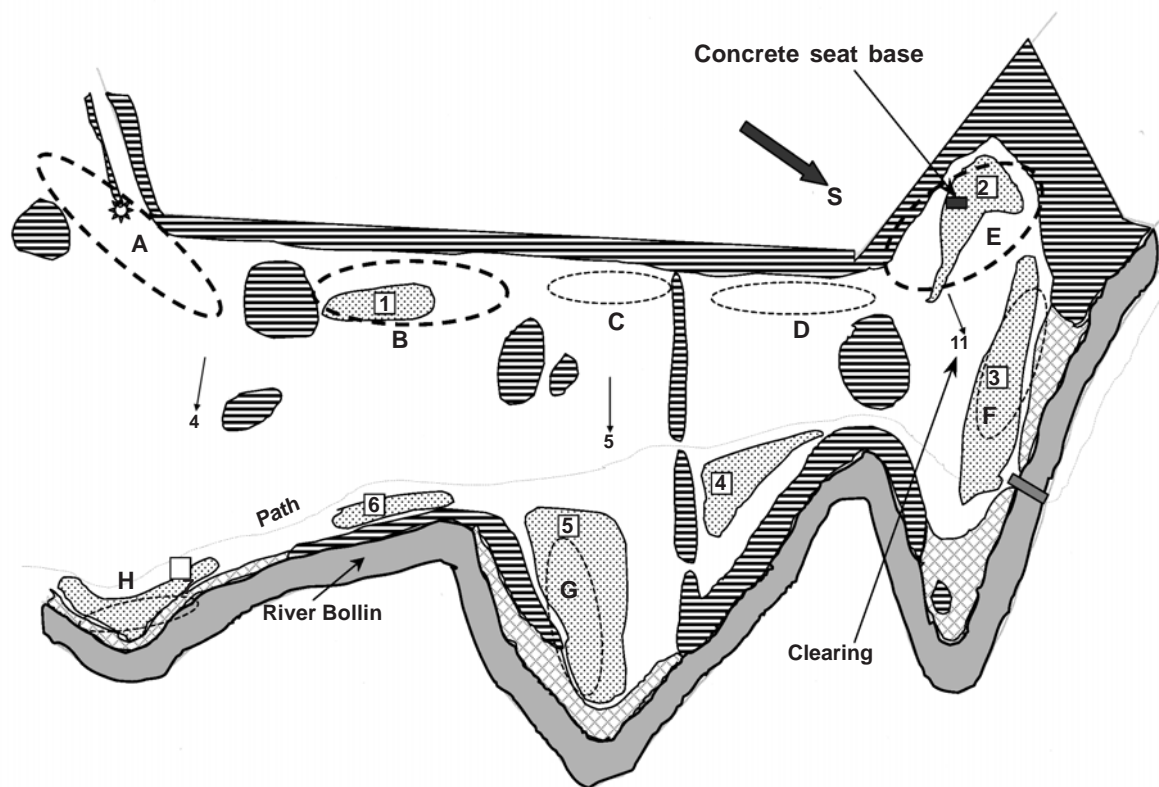


Fig. 1. Schematic map of the Carrs study site: Horizontal shading. Woodland and copse; Unshaded areas. Cut grass; Cross hatching. Rough ground dominated by rank herbs and willow carr; Stippled areas. Molehill zones in 2003 (boxes 1 to 7 indicating number of molehills: 1, 66; 2, 61; 3, 209; 4, 128; 5, 250; 6, 62; 7, 186); Pecked lines. Territories for nymphalids labelled A to H (bold, occupancy in > 50% surveys); Star in territory A. Hollowed out tree trunk; Fine arrows. Slope gradient (degrees). Probability of territory occupancy during surveys (multiple occupancy by one or more species): A, 0.75 (0.33); B, 0.83 (0.17); C, 0.08 (0); D, 0.5 (0); E, 0.96 (0.69); F, 0.04 (0); G, 0.33 (0); H, 0.25 (0.08).

Fig. 1. Mapa esquemático del lugar de estudio situado en Carrs: Sombreado horizontal. Bosque y soto; Áreas sin sombreado. Forraje; Entramado. Terreno agreste dominado por maleza y zona pantanosa con sauces; Áreas punteadas. Zonas de toperas en 2003 (los recuadros 1–7 indican el número de toperas: 1, 66; 2, 61; 3, 209; 4, 128; 5, 250; 6, 62; 7, 186); Líneas discontinuas. Territorios para los ninfalidos etiquetados A–H (en negrita: ocupación en > 50% de los estudios); Estrella en el territorio A. Tronco de árbol hueco; Flechas delgadas. Pendiente (grados). Probabilidad de ocupación del territorio durante los estudios (ocupación múltiple por una o más especies): A, 0,75 (0,33); B, 0,83 (0,17); C, 0,08 (0); D, 0,5 (0); E, 0,96 (0,69); F, 0,04 (0); G, 0,33 (0); H, 0,25 (0,08).

and none in the vicinity of territories. The host plant for all three nymphalids, *Urtica dioica* Linnaeus, is substantially more abundant (2.8 times) along the river bank than along the wood edge at the top of the slope. Nettles occurred in the vicinity (but not in) of only two territories (fig. 1, labelled G and H) largely occupied by *A. urticae*.

Macro-site thermal contrasts exist within the study site. In the clearing, air temperatures recorded at the top of the slope, 5 m from the wood edge, are slightly higher than those at the base of the slope (exposed bulb: mean difference = 1.25°C, $t = 4.8$,

$P < 0.002$; shaded bulb: mean difference = 0.89°C, $t = 2.99$, $P = 0.02$). The difference is greater for ground temperatures, taken from the summit of molehills (mean difference = 3.15°C, $t = 5.2$, $P = 0.0006$). The bias in warmth corresponds with the selection of slope position by nymphalids.

Micro-site thermal contrasts also exist within the site. Ground temperatures are substantially warmer than air temperatures (mean 22.0°C versus 16.1°C, difference 5.9°C, $t = 8.8$, $P = 0.00001$). Temperatures of the boundary air immediately above the surface of molehills is similar to that of grass sur-

faces ($t = -0.87$, $P = 0.40$) as is that of molehills and the concrete seat base in the clearing ($t = 1.05$, $P = 0.32$). However, probe measurements of ground surfaces reveals that the substrates of molehills are significantly warmer than the surrounding grass surfaces and their underlying soil substrates (mean difference = 2.83°C , $t = 10.29$, $P < 0.00001$) or the concrete seat base (mean difference = 1.65°C , $t = -4.34$, $P = 0.002$) during the period of the survey. In the former case, the difference in surface probe temperatures decreases as ground temperatures rise ($r = -0.56$, $P = 0.011$). Temperature contrasts favour bare earth areas, including molehills, on which biased perching occurs.

Thermoregulatory behaviour of nymphalids at the study site

Hypothesis: the species show no thermoregulatory (warmth enhancing) behaviour on perches. Individuals of all three nymphalid species display clear thermoregulatory behaviour on perch sites (see Dennis, 1993). Almost invariably males align themselves to the sun's azimuth when taking up perch stations; one exception was observed for a single event when the sun became obscured. In this position, the wings are generally held open or closed and the body tilted to be orthogonal to the sun's rays (see Shreeve, 1992). Often the hindwing inner margins and abdomen, referred to as hindwing appression, are in contact with the substrate. Full wing appression to the substrate was witnessed in all species on a number ($N = 14$) of occasions with the wings wrapped around the cone of the molehill (Shreeve, 1992; Dennis, 1970, 1993). One individual was observed shivering on the day with highest wind speeds and ambient air temperature at 16°C . Some form of shelter from the wind was observed on 70 occasions (51.5%); this took the form of exploiting hollows in the substrate and/or locating on slopes (e.g., of molehills) away from the wind direction. There was no significant difference among species in the use of shelter ($\chi^2_{(2)} = 2.8$, $P = 0.24$). Although, together, the two forms of wing appression to substrates were more commonly observed on exposed perches, this was not quite significant ($\chi^2_{(1)} = 3.54$, $P = 0.06$). However, hindwing appression also tends to occur, if only inadvertently, when individuals orient towards (body tilt) the sun's azimuth and hollows were often shallow and may have given inadequate shelter.

Landforms as visual landmarks

Hypothesis: perch sites are not distinctive landmarks. At macro-scale, all perch sites were in the vicinity of prominent structures: edges or corners; none were located in the centre of the study site in open grassland. At micro-scale, territories were not invariably sited where prominent landforms such as molehills were available (see above). Molehills were not exclusively used when they were present nor was the concrete seat base used exclusively in the clearing (table 1). Nevertheless,

biased use was made of the concrete seat base in the clearing by *I. io* compared to *A. urticae* and *P. c-album* (all records: $\chi^2_{(2)} = 13.7$, $P < 0.001$; single records per individual: $\chi^2_{(2)} = 11.6$, $P \approx 0.001$). White boards variously placed, singly and together, near and on the concrete base at the top of the clearing within the permanently occupied territories there during one afternoon session of survey were ignored by incumbent territorial *Inachis io*.

Change of perch sites in relation to changing ambient conditions

Hypothesis: no changes in type of perch sites used occur with changes in ambient temperatures. Perch usage is influenced by ambient temperature conditions. During two days of much warmer conditions in mid April ($> 23^{\circ}\text{C}$), when shade air temperatures matched ground temperatures of the main survey period in March, *I. io* was found to use vegetated surfaces significantly more frequently in the clearing (all surfaces: vegetation use rises from 16% to 45%, $\chi^2_{(1)} = 12.9$, $P = 0.0003$; exclusion of concrete base: vegetation use rises from 19% to 61%, $\chi^2_{(1)} = 18.3$, $P < 0.0001$).

Discussion

Landform bias for territories at different spatial scales

The current findings demonstrate that the three nymphalid species, *I. io*, *A. urticae* and *P. c-album* are biased, for the purposes of territorial activity and perching, in their use of landscape features at two different scales. At the macro scale they clearly prefer a wood edge or corner at the top of a south-facing slope compared to the base of it along the riverbank. This confirms Baker's (1972) observations of a bias for sunlit wood edges, a common cue in nymphalids (Watanabe, 2002).

At a micro-terrain scale, the species show a substantial bias in using molehills compared to other features. In the case of *I. io* preference is also shown for a concrete slab though not in *A. urticae* nor *P. c-album* but this may be a feature of their being out-competed by *I. io* for this unique site and substrate. At a higher resolution still, observations revealed finer adjustments to positions on micro-terrain features, for instance to hollows on molehills and molehill slopes (aspect). So, terrain exploitation extends to the infra-molehill level.

Hierarchy in landform selection across spatial scales

A hierarchy in landscape exploitation exists; decisions at a macro-scale outweigh those at a micro scale, slope position dominating micro-landform (molehill) choice. Some large molehill zones at the foot of the slope were ignored whereas territories were established where no molehills and little bare ground occurred.

Table 1 Perch sites adopted by three nymphalid species in the study site during spring 2003: Cs. Concrete seat base; M. Molehills; B. Bare earth; Vd. Vegetation debris; Dg. Dead grass; Lg. Live grass. Mean number of territorial males encountered per survey: *Inachis io*, 1.42; *Aglais urticae*, 0.78; *Polygonia c-album*, 0.53; all species, 2.72.

Tabla 1. Lugares escogidos para posarse por tres especies de ninfálidos en el lugar del estudio durante la primavera de 2003: Cs. Base de cemento; M. Toperas; B. Terreno árido; Vd. Restos vegetales; Dg. Hierba muerta; LG. Hierba viva. Promedio de machos territoriales encontrados en cada estudio: *Inachis io*, 1,42; *Aglais urticae*, 0,78; *Polygonia c-album*, 0,53; todas las especies, 2,72.

Perch sites							
All records							
Species	Cs	M	B	Vd	Dg	Lg	Total
<i>I. io</i>	13	41	10	4	7	1	76
<i>A. urticae</i>	1	16	4	5	7	0	33
<i>P. c-album</i>	0	14	3	7	0	4	28
All groups	14	71	17	16	14	5	137
Single record for each individual							
Species	Cs	M	B	Vd	Dg	Lg	Total
<i>I. io</i>	11	27	6	0	6	1	51
<i>A. urticae</i>	1	13	4	3	6	0	27
<i>P. c-album</i>	0	10	2	5	0	1	18
All groups	12	50	12	8	12	2	96

Consumer resource distributions and territories

Territories (perch sites) were not associated with nectar sources and the host plant occurred near only two of the (weaker) eight territories. Compared to the other two nymphalids, the significantly greater propensity of *Aglais urticae* for riverbank sites (as opposed to the wood edge) tends to support Baker's (1972) finding of a greater tendency for territories in *Aglais urticae* to occur near host plants. The incidence of nettle along the river bank is nearly three times that along the wood edge.

Are landforms used for perching landmarks or look-out posts?

Territorial sites often provide visual cues for resident males (Dennis & Shreeve, 1988; Rutowski, 1991). However, a distinction necessarily has to be made between sites providing visual cues to enhance conspecific contacts and sites enhancing visibility for resident males (Dennis & Williams, 1987). The findings in this study support Baker's (1972) observations that macro-scale sites (woodland edges, hedge lines and field corners) provide visual landmarks, locations where females are likely to pass in movement across the countryside. Other species (pierids such as *Pieris napi* L., *Anthocharis*

cardamines L. and *Gonepteryx rhamni* L.) were using the same features (i.e., wood edges in sunshine) as flyways during the survey.

At a micro-scale, features such as molehills, the earth bank in territory A and the concrete seat base are clearly distinctive landmarks, in the sense of being visually apparent structures. Yet, by no means were all micro-scale sites prominent from the surrounding matrix (e.g., cut grass, dead leaves) and enhanced visual stimuli (e.g., white boards; discarded magazines by the public, Dennis, personal observation) in territories were ignored. Yet, such stimuli are highly effective in other species (e.g., *Ochlodes venata* Bremer & Grey; Dennis & Williams, 1987). Although some micro-scale sites may provide prominent look-out posts (e.g., molehill summits) for passing females and intruders, again many do not. Many molehills chosen were flattened and depressed below the grass surroundings. An example of an important site presenting poor visibility was the deep hollow on the earth bank at the apex of territory A. During the strong breeze on March 31 the resident male *I. io* perched deep inside (> 30cm) this hollow; although still in sunshine, its arc of detection was very restricted. As is frequently the case anyway from perches, this male undertook voluntary patrols to search its

territory returning to this hollow. Such observations suggest that visibility is compromised by ambient conditions and requires an experimental approach to determining which factors dominate under specific conditions.

Are landforms used for perching hot spots?

Perch biases for the landscape features at different scales all have a common climatic component. They are warmer areas or more sheltered, which amounts to the same thing. It is likely that there are no terrain features that do not have climatic implications, and thus fitness consequences for butterflies as regards mate location. Warmer sites ensure greater motility and mobility, particularly important in the scramble for mates and defence of sites as well as evasion of predators (Shreeve, 1992; Stutt & Willmer, 1998). At the macro-scale, it is not possible to distinguish the impact of the wood edge as a potential visual cue for mate location from its influence as a warmer area enhancing flight and mobility. Light and warmth are inextricably linked, shaded wood edges at one and the same time lack the contrast and warmth of wood edges in sunshine.

At the micro-scale, molehills and bare ground substrates are warmer (or provide more shelter) than vegetation surfaces and the bias for bare soil sites supports the notion that they are chosen as hot spots. It was noticeable that sunlight to two of the molehill areas (fig. 1, zones 4 and 6) ignored by perching nymphalids was filtered by trees. Although the concrete base presented a cooler surface than molehills, it provided more shelter from prevailing winds up the slope. Two further observations corroborate this suggestion for hot spots. First, there is a substantial and significant increase in the use of vegetation substrates by *I. io* in warmer conditions (shade temperature 7°C increase). This observation can be coupled with another for the difference in temperature between ground surfaces for bare soil and grass-covered soil that diminishes as air temperatures increase. In effect, as overall air temperatures rise, the area of ground with minimum suitable temperatures for perching increases and the difference between soil (molehills) and vegetation becomes less critical for perching males.

Second, warmth is critical for butterfly activity. For sustained flight, butterfly species with moderate to fast wings beat frequencies typically require thorax temperatures in the range of 28–40°C and for vigorous flight 33–38°C (Kingsolver, 1985), temperatures well above those experienced in the study area during March and early April. Nymphalid males show a range of thermoregulatory behaviour on the micro-scale perch sites: wing and body adjustments to sun azimuth, hindwing, full wing and abdomen appression to substrates, shivering and seeking shelter (i.e., hollows and lee slopes of molehills) in relation to wind (Shreeve, 1992; Maier & Shreeve, 1996; Dennis, 1993; Kemp & Krockenberger, 2002). It was noticeable that wing

and body appression could not be achieved, and difficulties were experienced in wing orientation to the sun, when vegetation surfaces were used instead of the soil substrates.

Butterflies are known to change their mate location behaviour with changing air temperatures (Fischer & Fiedler, 2001; Ide, 2002); this finding now confirms that they may also change their perching sites as temperatures change (Rutowski, 2000). Although just what perch sites they use is affected by what is available, these need to be warm enough for individuals to function efficiently (Maier & Shreeve, 1996).

Nymphalids are known to use taller vegetation for territorial perching (e.g., *Polygonia comma*, *P. c-album*, *Vanessa atalanta*) (Bitzer & Shaw, 1979, 1983; Hardy, personal observations), especially during the summer emergence in the UK (Wiltshire, 1997; Dennis, personal observation), further suggesting that access to bare ground in suitable locations becomes less critical as ambient conditions become warmer.

Macro- and micro-scale landforms are important resources for butterflies

Macro-terrain cues for mate location are common to a number of butterfly species. Both Pieridae (e.g., *Pieris napi* L., *Pieris brassicae* L., *Anthocharis cardamines* L., *Gonepteryx rhamni* L.) and Nymphalinae share the physical cue of the south-facing wood edge for mate location, but the former invariably patrol along its length whereas the latter perch as well as patrol (Dennis & Shreeve, 1988). At the micro-scale, other Nymphalids are known to use bare ground for territorial perches (e.g., *Vanessa atalanta* L. and *V. cardui* L.) (Bitzer & Shaw, 1979; Dennis, personal observations). Nevertheless, bare ground is an important utility resource for a range of activities by butterflies in cool temperate regions; it is part of the habitat (Dennis et al., 2003) and is a component of the hostplant biotopes of at least 24 British butterflies (Shreeve et al., 2001). Because of rapid vegetation succession it is a short-lived resource and needs to be continuously created by disturbance.

The use of molehills for mate location forms one of several examples of butterflies using micro-terrain created by animals for its activities (e.g., egg-laying by *Lasiommata megera* L. Satyrinae in recesses caused by rabbits and cattle hoof marks) (Dennis, 1983). However, by far the greatest number of relief features used by butterflies, as currently known, is created by human activity. These range from "hills" and "hollows" at the macro-scale (e.g., Neolithic burial tombs, hill fort ramparts and ditches, spoil heaps, quarries and bomb craters) to similar features at a micro-scale (e.g., field ridge and furrow, drainage lines, piles of gravel) associated with agriculture and construction, including elements of landscape furniture (e.g., fences, walls) all of which are known to be used by butterflies for different activities. Bearing in mind how important,

but short-lived, a resource bare ground is for butterfly biology, the creation of bare ground is one area where human activity is clearly beneficial to butterfly persistence, especially as it triggers early seral vegetation for butterflies dependent on pioneer host plants.

Acknowledgements

My thanks to Peter Hardy for his comments on the paper and observations on perching nymphalids and to two referees and Dr. Adolfo Cordero Rivera for their helpful comments on an earlier draft.

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