Chapter 1

WHAT IS A HABITAT? AN AWKWARD QUESTION

A collector who is a careful observer is often able to examine a terrain and to decide, intuitively as it were, whether a given butterfly will be found there, and that rare being the really accomplished naturalist will nearly always be right. Of course he reaches his conclusion by a synthesis, subconscious as well as conscious, of the varied characteristics of the spot weighed up with great experience; but this is a work of art rather than science, and we would gladly know the components which make such predictions possible.
(Ford, 1945, p. 123, courtesy of HarperCollins Publishers)

It cannot be over-emphasized just how important the concept of a habitat is in butterfly ecology and for biology generally. The habitat has long been regarded as the basic unit around which both theoretical advances and practical applications have been generated in animal ecology and population biology (Watt, 1947; Elton, 1966; Southwood, 1977; Knight and Morris, 1996). More important today is its role in conservation; to conserve organisms we need to know what we mean when we talk about protecting or conserving a species' habitat (Dennis *et al.*, 2007). It is no good vaguely pointing to a wood, as say 'a silver-washed fritillary *Argynnis paphia* habitat', and declaring that 'it needs to be conserved'. It is usually obvious that something does need to be done, but just what about the wood needs to be managed or conserved: the wood as it is, the wood as it was, elements and sections of the wood, or specific resources used by the butterfly in parts of the wood? We have long understood that simply to preserve the bounds of vegetation units will almost certainly not adequately conserve a specific organism in them. The vegetation unit may often be a distinct land unit and therefore the legal or ownership unit for management; that does not mean that some management practice should be applied broadcast across the entire unit in one sweep. As the memorable quotation above from Ford (1945) illustrates, the concept of habitat is elusive when transferred to the ground. Difficulties in producing a functional definition of habitat are not surprising; different organisms, including butterflies, vary enormously in their environmental associations and in their responses to environmental gradients (Thomas, 1994). Furthermore, among butterflies the different sexes and stages require different conditions for existence and are therefore not necessarily found in identical locations (Wiklund, 1977; Dennis *et al.*, 2003).

DEFINITIONS OF HABITAT

Developments in understanding habitats have been frustrated by inconsistencies in the definition and treatment of an organism's habitat and in the lack of precision over terms (Table 1.1; Hall *et al.*, 1997). Typically, but variably, a habitat refers to an identifiable locality (viz., site, place, situation, residence) or to the environment (viz., topography, soils, vegetation types, environmental conditions) and its subdivisions (i.e., microhabitats) occupied by an organism; but practical guidance is noticeably lacking. In *The Concise Oxford Dictionary* (Thompson, 1995), habitat is: (i) the natural home of an organism, and (ii) a habitation (Latin = it dwells). The emphasis is on a place where an organism lives, and it lives there because it has the requirements for existence. In this book, we do not move away from this basic understanding of habitat. But, there is a need to know how to identify the space and what is essential to it.

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Table 1.1 Definitions of habitat.

- Place, living space, where an organism lives (Odum, 1963)
- The place where an organism lives, characterized by its biotic or physical characteristics (Whittow, 1984)
- Type of environment in which an organism lives (Collin, 1988).
- The locality, site and particular type of local environment occupied by an organism; *ece*, local environment; *oike*, oikos (Lincoln *et al.*, 1982)
- Place where a species normally lives, often described in terms of physical factors such as topography and soil moisture and by associated dominant forms (e.g., intertidal rock pools or mesquite woodland). Definitions in ecological literature vary widely but consensus for the following: key environment features related to a species; habitat and vegetation classifications may be concordant, but not always so; subdivisions occur – microhabitats (Calow, 1999)
- Habitat is a suite of resources and environmental conditions that determine the presence, survival and reproduction of a population (Caughley and Sinclair, 1994; Weddell, 2002)
- Habitat is a zone (area) comprising a set of resources, consumables and utilities, for the maintenance of an organism. The resources occur in union and/or intersect and may also be equivalent; links between resource outlets are established by individual searching movements of the organism (Dennis and Shreeve, 1996)
- Habitat [as] the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism. Habitat is organism-specific; . . . it is the sum of the specific resources that are needed by organisms (Hall *et al.*, 1997)
- Habitat is 'the sum of the abiotic and biotic factors essential to the life and reproduction of the species within its natural geographic range' (Haslett, 2007)

DISTINGUISHING HABITAT FROM BIOTOPE AND VEGETATION UNITS

Habitat is most frequently, and it is emphasized *wrongly*, treated as being synonymous with a particular vegetation category or alternatively with a **biotope** (Webb, 1993). Biotope, as in the case of a habitat, has also been described in different ways; some definitions of biotope relate it to a habitat (e.g., Lincoln *et al.*, 1982) but, to avoid confusion, it is sensible to define it in stand-alone terms. Collin (1988) defines biotope as a small area with uniform biological conditions (climate, soil, altitude, etc.). This is sound if biological conditions are understood by the reader to have variance. For those who adopt a literal interpretation of 'uniform', but then no space is entirely uniform, **biotope is understood to mean a region (area, space; e.g., woodland, heath, cliff, dune complex) that is distinguished by particular environmental conditions; therefore, it will tend to contain a characteristic assemblage of organisms** (Calow, 1999). The treatment of habitat as a vegetation unit or a biotope belies reality, as Ford well understood, and this is most unfortunate if only because vegetation associations, and biotopes, are capable of being described at a hierarchy of levels, the bounds between which are often arbitrary. For example, woods and meadows are distinct biotopes but share many plant species, and meadows may well have emerged as a minority integral part of the ancient Holocene forests, grassland that was initially maintained by large herbivores (Vera, 2000; Peterken, 2009). Moreover, and more importantly, vegetation and biotope both typically describe a space that is either insufficient or surplus to that occupied by a specific organism but rarely neatly demarcating it. A vegetation hierarchy is clearly illustrated in the five-volume classification of British vegetation types (Rodwell, 1991–2000). A monumental work, it describes the natural vegetation units as 'communities', and their descending tiers in the hierarchy as 'sub-communities' and exceptional cases as 'variants', within the following major vegetation types: aquatic vegetation, swamps and tall-herb fens; grasslands and montane vegetation; heaths and mires; woodlands and scrub; salt-marsh, sand dune and sea-cliff communities; and weed vegetation.

The key to understanding the relationship between an organism's habitat and vegetation is to appreciate that vegetation is infinitely variable, even to the extent, as Rodwell explains, of having to allocate a field sample of vegetation to a community even though one or more of the marker plant species for the unit is missing. Variability inevitably suggests hierarchy in inclusiveness of plant species; thus, by way of example, in the general introduction to Rodwell's volumes is tabulated details for one category of mesotrophic grasslands, *Centaurea-Cynosurus* grassland (knapweed/crested dogs-tail grass, coded MG5) and the table illustrates the sub-communities, one of which is the *Galium verum* (lady's bedstraw) sub-community. This approach is not unique; the classification technique has close affinities with the Braun-Blanquet method (see Box 5.2) and Braun-Blanquet and Tuxen (1952) identified a similar unit on the European mainland called *Centaureo-Cynosuretum cristati*. Butterflies are faced, then, with a variety of major vegetation structures and substrates and infinitely varied vegetation and therefore plant associations. From this five principles become immediately apparent about butterfly–vegetation associations to those studying butterflies in the field.

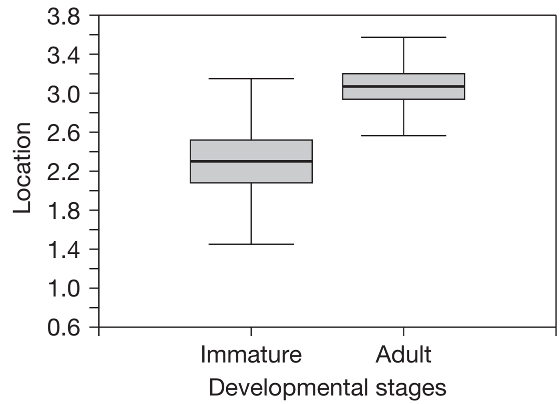

Fig. 1.1 Vegetation types and substrates occupied by early developmental stages and adults of British butterflies. Immature and adult stages occupy distinct vegetation. Means (lines), standard errors (2 standard errors, grey boxes) and 1 standard deviation (whiskers) are shown for 60 British butterfly species. Distinct resource uses, $N > 5$–19 for each stage of each species ($t_{(59)} = -10.04$, $P < 0.0001$). Locations for resource uses are scored as: 0, underground; 1, soil surface; 2, short turf; 3, tall herbs; 4, shrubs and shrub edge; 5, climbers, trees and wood edge. (From Dennis *et al.*, 2003, courtesy of Blackwell Publishing.)

Principles relating to butterfly–vegetation associations

- **P1.1: Different butterfly stages often occupy different vegetation types and substrates.**
- **P1.2: Different individuals of the same species and developmental stage often occupy different vegetation types.**
- **P1.3: Individuals (a population) of a butterfly species rarely occupy the entire zone of a vegetation unit.**
- **P1.4: A key resource for a butterfly (larval hostplant, nectar flower) is rarely restricted to a single vegetation unit or community.**
- **P1.5: Resources for a butterfly will tend to be distributed differently over a vegetation unit(s).**

Different butterfly stages are typically observed to occupy distinctly different vegetation types and substrates (e.g., surfaces such as rock types, walls, soils); the statistical pattern is a significant one over all British butterflies (Fig. 1.1; **P1.1**). Though undoubted examples of species exist where all stages are found in one vegetation type (e.g., purple hairstreak *Favonius quercus* on or under an oak tree), inevitably, because of the contrasting needs of eggs, larvae, pupae and adults, distinctions in vegetation associations among butterfly stages are invariably found in a butterfly community. Larvae, but particularly adults, often occupy very different vegetation types in relation to their behaviour (e.g., searching for mates and nectar feeding), and eggs and pupae of some species can be distributed over different vegetation types and on different substrates (**P1.2**). Thus, silver-studded blue *Plebejus argus* adults actively use areas of scrub as well as different categories of calcareous heath on the Great Ormes Head, North Wales (Dennis, 2004b; Dennis and Sparks, 2006) and the peacock *Inachis io* seeks out mates on a variety of vegetation types including bare ground but lays eggs on tall herbs (nettles) (Baker, 1972; Dennis and Sparks, 2005).

A butterfly is rarely found to occupy the entire area of an apparently homogeneous vegetation unit, nor the entire area of hostplant zone in a locality (**P1.3**). This fact is well known from Professor Jeremy Thomas's detailed research on the Adonis blue *Polyommatus bellargus*, the eggs being distributed in relationship to turf height and microfeatures (thus microclimate), the surfaces chosen varying between the two broods (Thomas, 1983a; Roy and Thomas, 2003). Thus, the speckled wood *Pararge aegeria*, which is regarded as a typical woodland butterfly, is not expected to occur evenly throughout woodland and can be abundant or absent from different but similar-looking parts of the same wood. This is a distinctly noticeable feature of densely packed conifer woods, such as the Macclesfield Forest in east Cheshire, UK; here, the butterfly is found along the forest edge and tracks, but is absent a few metres into the deep, dark, litter-strewn interior which is deficient of ground vegetation (R. L. H. Dennis, personal observation); it is also a feature of deciduous woods, though to a lesser extent (P. B. Hardy, unpublished data). When it is realized that key butterfly resources can occur, and are used, in very different vegetation types (**P1.4**), even nettle patches for common nymphalids (see Fig. 4.1) (Dennis, 2008a), the mismatch between butterfly species and vegetation units is something that has to be expected and not treated as an exception. Not even a single resource, such as a hostplant for a locally monophagous butterfly – nor then, potentially, butterfly eggs and larvae – is invariably restricted to a single vegetation unit. For example, cow wheat *Melampyrum pratense* for the heath fritillary *Melitaea athalia* is found in woodland clearings in Kent and on heathland associated with bilberry *Vaccinium myrtillus* in Exmoor combes (Kemp *et al.*, 2008). It then follows that different resources supporting a butterfly (e.g., larval hostplant and nectar flower species) will tend to occupy different parts of the same vegetation unit or different vegetation units altogether (**P1.5**). The same *apparent* resource will also vary significantly in quality throughout the same biotope. Thus honeysuckle (*Lonicera* sp.) in full sunlight may be used by the white admiral *Limenitis camilla* for nectar feeding but is unsuitable for oviposition and larval development (Fig. 1.2) (Fox, 1996). A simple exercise that the reader can undertake to appreciate this point would be to map the local distribution of cuckoo flower *Cardamine pratensis* and hedge garlic *Alliaria petiolata*, both larval hostplants for orange-tip *Anthocharis cardamines* and green-veined white *Pieris napi*, and the occurrence of eggs on these plants. The distributions of the plants will be found to overlap but differ significantly for landform and vegetation types (Dennis, 1982a).

The habit, therefore, of referring to vegetation units (e.g., grassland, heath, woodland) as habitats is at best unhelpful and at worse misleading and ultimately results in poor ecological science and bad conservation practice (Dennis *et al.*, 2006b) – they are either vegetation or biotope. To make the point clear, some schematic examples are illustrated in Boxes 1.1 and 1.2. In Box 1.1, an assumption is made that we can identify the bounds of a butterfly's habitat, at this stage simply defined as the place where the butterfly lives out its existence. Three situations are illustrated: where the habitat is something less than the vegetation unit within which it occurs, where it almost exactly equals the bounds of the vegetation unit, and finally where it crosses different vegetation units. Of course, the habitat comprises different needs (resources) for different stages of development and the sexes; the most obvious are the hostplants that larvae eat and nectar flowers used by adults. The plants (nectar plants, larval hostplants) that form part of the habitats in these cases are components of the vegetation units. Without mapping these particular resources we do not know their relationship to the area used as a habitat within which butterflies are largely restricted. But, different situations may be envisaged. For example, in Fig. B1.1b the hostplants and nectar plants are perhaps expected to occur throughout the triangular field, in Fig. B1.1a they probably have a distribution limited to the zone marked as a habitat; whereas in Fig. B1.1c they are more likely to occur in different vegetation zones, if only because in this last case the habitat does so too, and indeed outside the zone marked as habitat where conditions may not be suitable for egg laying. The point is: we do *not* know any of this until the resources are mapped or at least inspected. The implication, discussed at length in the following chapter, is that hostplant presence does not necessarily mean existence of a habitat for a butterfly; it has to be in suitable condition, as do other items making up the habitat. To drive the point home, in Box 1.2 two other schematic diagrams illustrate the break up of the habitat zone, which we accept here as the place a butterfly lives and is found, into distinct resources. Just two possible combinations out of many are illustrated. Just how many combinations exist when more resources are considered can be appreciated by glancing briefly at Box 6.3.

A start along these lines of identifying habitat was made many years ago by Wiklund (1981), to whom the credit for this approach should go, but butterfly biologists were deflected from following the path taken in this book by a shift in focus from single to multiple populations and the need to have simple mechanisms to delimit habitat patches rapidly during field surveys. The pattern of study being followed by Christer Wiklund (1977, 1981) and Jeremy Thomas (1984) was effectively abandoned with the burgeoning of multiple

Fig. 1.2 White admiral resources in woodland biotopes. (a) Shade woodland biotope for honeysuckle *Lonicera periclymenum* drapes, at Bentley Wood (Hampshire/Wiltshire border, UK), required by female white admiral *Limenitis camilla* for egg laying and for larval development. Inset is *L. camilla* feeding on honeysuckle. (b) Contrasting biotope of woodland clearing at Bentley Wood that is inappropriate for white admiral *L. camilla* egg laying and larval development, but suitable for adult feeding and for broad-bordered bee hawk-moth *Hemaris fuciformis* L. (Sphingidae) development. (a, b, courtesy of Barry Fox.)

Box 1.1 **Relationship between habitat, vegetation units and biotope**

The habitat of an organism does not have to equate with the area of vegetation or land units (i.e., fields). It may occupy an area less than the land or vegetation unit, match it almost exactly or extend over several vegetation and land units. The schematic diagrams illustrate these alternatives. It is assumed that the habitat can be identified based on the locations of individuals belonging to different stages.

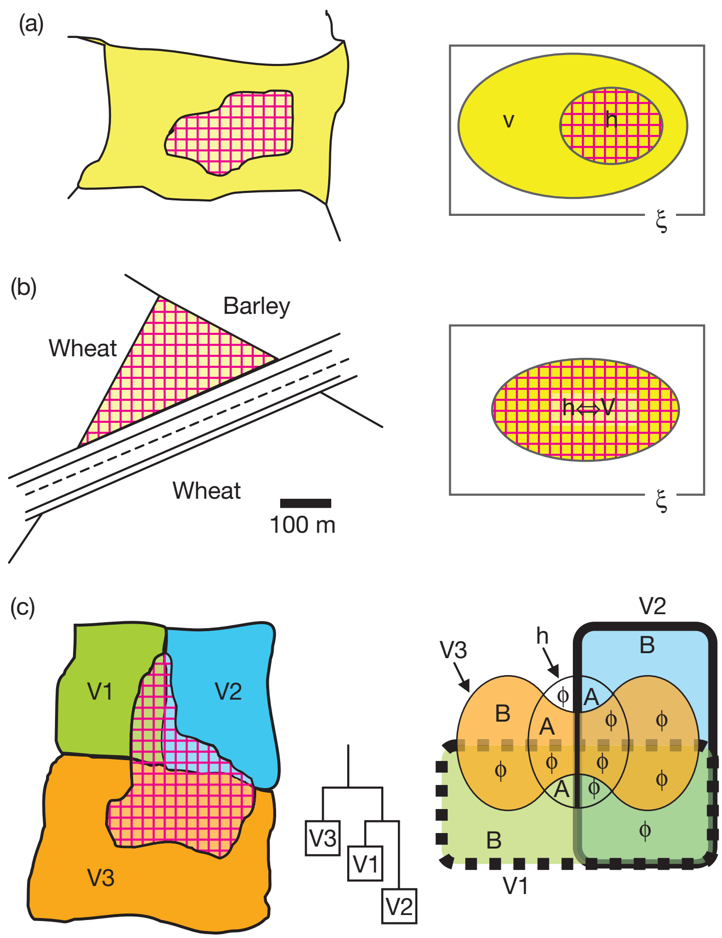

Fig. B1.1 (a) Habitat area is smaller than a vegetation unit and this is a subset of the vegetation unit (e.g., marsh fritillary *Euphydryas aurinia* habitat based on an area of devil's-bit scabious *Succisa pratensis* in lowland purple moor-grass *Molinia caerulea* pasture, called 'rhos' in Wales). (b) Habitat area is the same as the vegetation unit; there is one to one correspondence between them (e.g., remnant tall-herb grass and scrub in field corner abandoned with dual carriageway development and occupied by meadow brown *Maniola jurtina*). (c) Habitat area overlaps a single biotope made up of the vegetation units in which V1 and V2 have more similarities in plants than have either V1 and V2 with V3. In the Venn diagram, 'A' indicates habitat as a subset of one of the vegetation types, 'B' is the complementary set (a vegetation unit but not habitat) and ϕ the empty set (the combination does not exist in this example) (e.g., wet (V1) and dry (V2) heathland and wooded (birch) (V3) heath all with *Molinia caerulea* and used by large skipper *Ochlodes sylvanus* on Lindow Common, Cheshire (Dennis and Williams, 1987)).

Yellow, gold, lime and pale blue are vegetation types (v); pink cross hatching, supposed habitat area within vegetation zones (h); pink cross hatching over yellow, overlap of vegetation and habitat in Venn diagrams for (a) and (b).

Box 1.2 **Schematic maps to illustrate the variable relationships among some resources, habitat and vegetation patchworks**

Habitat is not a uniform homogeneous entity or spatial unit. It comprises various resources used by a species and there is no reason why these should overlap let alone exactly coincide. Instead of illustrating what is understood to be a habitat in vegetation or land units, the schematic diagrams 'map' three resources that necessarily form a part of habitats for butterflies within field boundaries to illustrate two situations. First, where all these occur within a single field and, second, where these variably cross field boundaries. The diagrams also qualify a key resource used by butterflies, the larval hostplant, identifying a zone within the hostplant patch where oviposition is restricted, to impress that a resource may not be all that it seems to be. Immediately, it becomes obvious that the bounds of a habitat are not that clear.

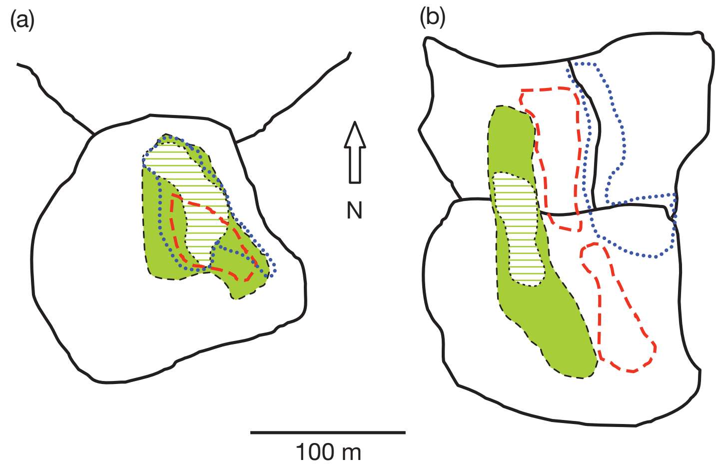

Fig. B1.2 (a) Complementary resources (e.g., mate location, nectar) coincide with the hostplant area (but not entirely with the hostplant area that is suitable for egg laying) and within a single vegetation unit. (b) Complementary resources do not coincide with the hostplant area and both hostplants and complementary resources cross vegetation units. Typically, the area over which a hostplant is exploited by a butterfly will generally be a fraction of the total hostplant area and resource zones are not expected to coincide with vegetation units. Thick continuous lines, vegetation unit boundaries; green areas, hostplants; shaded areas, hostplants suitable for oviposition and breeding; red dashed lines, nectar zones; blue dotted lines, mate location zones.

population (metapopulation) studies, though Thomas in his continued study of *Maculinea* ecology has constantly impressed on us the crucial part played by intrahabitat quality (Thomas *et al.*, 1998a, 1998b). What did Wiklund envisage? He understood that the 'Essential requirements for the survival of most butterfly populations are that (1) males and females can find each other and mate, (2) adult females can deposit the eggs in such a way that the larvae can find their hostplants and (3) adults can find food in order to live long enough to perform both activities mentioned above'. Thus, the area occupied by any given butterfly population should include a 'mating habitat', a 'breeding habitat' and a 'foraging habitat'. 'This being a functional classification of habitats, means that these habitat types can be spatially separate or identical' (Wiklund, 1981:164). Wiklund distinguished primary from secondary, and from novel and unsuitable 'breeding habitats' based on the larval hostplants used (Wiklund, 1981). What in this book are called 'resources' (Dennis *et al.*, 2003), Wiklund referred to as a specific habitat type. The question is: how do they integrate to form a complete butterfly habitat? Is there anything missing? Is it possible to map this habitat identified by Wiklund?

The crux of the matter is as follows. Because reference is habitually made to butterfly habitats, a clear definition of habitat becomes axiomatic. Just what definition of habitat is applied can have serious consequences for developments in butterfly biology and particularly for butterfly conservation (Dennis *et al.*, 2003, 2006b, 2007; Shreeve *et al.*, 2004); for this reason alone the topic deserves careful thought and detailed consideration. In all empirical and theoretical population work, habitat is implicitly or explicitly a bounded space (e.g., Southwood, 1977; Baker, 1978; den Boer and Reddingius, 1996; Hanski and Gilpin, 1997; Ehrlich and Hanski, 2004); butterfly biologists draw boundaries on maps purported to enclose habitat patches. The fundamental problem is that it is rarely evident what, in detail, this space comprises and there is typically implicit, even explicit, treatment of an organism's habitat as a particulate, homogeneous and invariant unit – and inevitably this is a vegetation type, biotope or even the area occupied by a single plant species. But it is none of these things and examples in this book attempt to illustrate just what is involved in the notion of a butterfly habitat. Habitat is necessarily the location where an organism lives out its life cycle. As such, it follows that it should be possible to map the bounds of a habitat in terms of life history requirements. The next chapter begins to outline a suitable procedure to this end.