

## CHAPTER ONE

# The bird and its habitat: an overview of concepts

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People have been describing habitat associations and asking deeper questions about how birds select their habitat, and the factors that determine their fine-scale distribution, for a long time (e.g. Brock, 1914; Grinnell, 1917a, b). This chapter outlines where concepts relating to habitat selection stand in the early twenty-first century. These concepts embrace a bewildering array of behavioural, ecological and evolutionary ideas. The processes involved in habitat selection have evolved to maximise fitness by ensuring that individuals can recognise and use suitable habitat. The notion of habitat quality (i.e. what constitutes ‘good’ or ‘best’ habitat) is therefore a central concept to which I have devoted a large part of the following chapter. Neither of these introductory chapters reviews the topics comprehensively, but the examples and references will, I hope, serve as useful background to the multi-faceted subject of habitat selection. I acknowledge the existence of some bias in the examples chosen because they lean towards terrestrial birds, especially those of forest and shrubland, reflecting my personal interests.

Not surprisingly, there has been a gradual shift towards more quantitative research and theoretical models. But description remains important, both to document how birds continue to respond to the ever-changing world and to provide crucial information upon which conservation policies can be founded. The literature is voluminous. The review of habitat selection in birds by Olavi Hildén (1965) covers much of the early work and continues to be a highly relevant source of ideas and examples. More recent reviews and discussions of aspects of habitat selection include Partridge (1978), Morse (1980), Cody (1985), Wiens (1989a), Block and Brennan (1993), Jones (2001), Johnson (2007) and Boulinier *et al.* (2008).

### **Habitat differences within and between species**

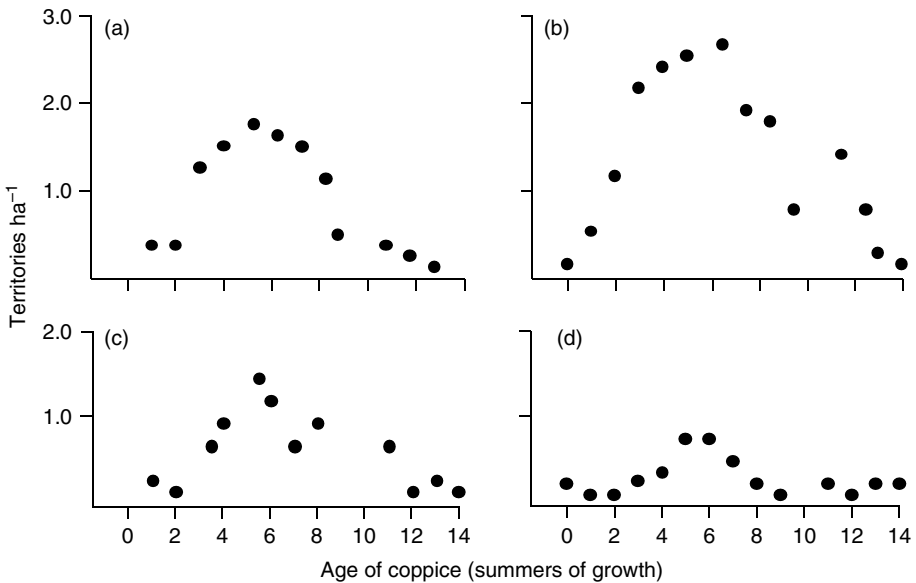
At the simplest level, relationships between birds and habitat are biologically trivial, though they are a source of considerable human pleasure and cultural significance. Landscapes and vegetation types have their typical species. Each species can be readily identified with a set of habitat features such that an

experienced naturalist carries with them a view of what constitutes suitable and unsuitable habitat. This has long been appreciated, as shown in John Clare's poetry, rooted in the English countryside of the early nineteenth century. Habitat relationships become profoundly interesting at the finer scales – the adaptive value of microhabitat selection, for example, is of abiding interest. The spatial and temporal dynamics of habitat use by the individuals that constitute populations are of great importance in the context of population dynamics, lifetime reproductive success, range dynamics, behavioural flexibility and identifying critical habitat needs. Much research centres on elucidating the factors that influence the choices made by birds in their use of space and other resources.

In the 1970s ecologists started to develop quantitative methods of describing how species differ in their fine-scale relationships with vegetation (James, 1971). Detailed studies of particular groups of species have repeatedly demonstrated that sympatric species tend to select different habitats, though frequently the differences are fine-scale ones of microhabitat use (e.g. Kendeigh, 1941, 1945; Snow, 1954; Bond, 1957; Lack, 1971; Collins, 1981; Collins *et al.*, 1982; Glück, 1983; Bairlein, 1983; Martin and Thibault, 1996). Clear separations between closely related species are not universal (Wiens, 1989a; Fig. 1.1). Nonetheless, such observations have underpinned a large amount of theory revolving around 'ecological segregation' and 'niche partitioning'.

Some important points need to be made about habitat differences. Variation in habitat occupancy and use is strongly evident within species, as well as between species. Within species, there can be variation in habitat use between sexes (Marquiss and Newton, 1981; Ebenman and Nilsson, 1982; Lynch *et al.*, 1985; Winkler and Leisler, 1985; Steele, 1993; Parrish and Sherry, 1994; Sunde and Redpath, 2006) and ages of individuals (Marquiss and Newton, 1981; Morse, 1985; Reijnen and Foppen, 1994). Migrant and resident individuals of the same species may differ in habitat use (Adriaensen and Dhondt, 1990; Pérez-Tris and Tellería, 2002). Habitat use may also vary with weather (Petit, 1989), season and phase of the life cycle (Rice, 1980; Alatalo, 1981; Bilcke, 1984a; Moskát *et al.*, 1993; Mills, 2005; Akresh *et al.*, 2009), and time of day (McCaffery, 1998; Gillings *et al.*, 2005). Patterns of habitat occupancy and use may also change spatially and temporally (Chapter 3).

An important and relatively neglected source of variation in habitat use may derive from individual niche specialisation arising from phenotypic differences within populations (Bolnick *et al.*, 2003). Even within apparent habitat specialists there may be considerable variation in habitat use by individuals. The reed warbler *Acrocephalus scirpaceus* is widely regarded in Europe as an extreme habitat specialist, dependent on beds of the reed *Phragmites australis* for breeding. One study found that only 54% of nests were in *Phragmites* and that breeding success was lower there than in other



**Figure 1.1** An example of overlap in breeding habitat use within closely related species. The territory density (territories ha<sup>-1</sup>) of four foliage-feeding insectivorous warbler species in English coppiced woodland is shown in relation to the number of years of coppice regrowth since cutting: (a) garden warbler *Sylvia borin*, (b) willow warbler *Phylloscopus trochilus*, (c) blackcap *Sylvia atricapilla*, (d) chiffchaff *Phylloscopus collybita*. The three photographs show coppice structure at different stages of growth: (A) 1 year of growth, (B) 6 years growth, (C) 10 years growth. Each species reaches maximum density in coppice of about 3 to 7 years of growth when the complexity of low woody vegetation is high (photograph B). Redrawn from Fuller and Henderson (1992).

vegetation types (Catchpole, 1974). Although the species is undoubtedly specialised to use reeds in the way it constructs its nest, it seems to have retained flexibility of habitat use probably because reedbeds can be unstable habitats.

The factors determining how birds use habitat change considerably with time of year; this is especially the case for migratory species and for sedentary birds living in highly seasonal environments. Species may generally show

tighter patterns of habitat association during the breeding season than at other times (Mills, 2005). Breeding can place constraints on habitat selection and use of space that apply more rigidly than at other seasons (Whitaker and Warkentin, 2010). Outside the breeding season, however, individuals only have to be concerned about survival and an entirely different suite of factors may come into play (Chapter 15).

### Definitions and perceptions

The literature contains many studies of species that variously claim to identify habitat use, preferences, selection or choice. Clarity about the meaning of these and other habitat-related terms is essential (Hall *et al.*, 1997; Jones, 2001) so a series of definitions are offered in Box 1.1. Importantly, ‘habitat selection’ and ‘habitat use’ are not interchangeable terms, the former encompassing the processes involved in habitat choice, the latter is the way that birds use their habitat. Concepts of ‘habitat’ are various, but make most sense in terms of the environment in which an individual, rather than a population or a species, lives. The habitat of an individual bird will consist of a complex of biotic and abiotic elements embracing climate and microclimate, soil type, topography, plant species and vegetation structure. Some definitions exclude the social component of the environment (Danchin *et al.*, 2008), but I prefer to include both conspecifics and other species as integral to the habitat, as these can have strong effects on realised habitat quality and habitat use (Chapter 2).

The widespread use of ‘habitat’ as a distinct form of environment is an entirely different but familiar notion based on perceived differences in past and present land use, vegetation, hydrology and even landscape character. Hence, we divide landscapes into units or ‘cover types’ such as woodland, heathland and grassland, often with complex subdivisions based on phytosociology or structural attributes (e.g. Ratcliffe, 1977; Rodwell, 1991; Crick, 1992). Though useful for many purposes, these classifications have limitations. They tend not to describe transitional zones well and typically tell us little, if anything, about the critical resource needs of individuals that are so important in determining where animals live or the cues involved in habitat recognition.

There is a more fundamental limitation to our attempts to delineate the environment of an animal. Humans inevitably sense and perceive the environment in different ways to animals. The variables we choose to measure when attempting to define the habitat of an organism will almost certainly not exactly reflect the perceptions that the animal has of its environment. The concept that animals exist in their individual world (*Umwelt*) was developed by Von Uexküll (1926, cited in Manning *et al.*, 2004). Different organisms in the same location may have entirely differing perceptions (*Umwelten*) of the world about them, depending on their sensory apparatus, their body size, their

**Box 1.1 Some definitions concerning habitat and landscape**

(sources include Johnson, 1980; Dunning *et al.*, 1992; Koford *et al.*, 1994; Jones, 2001; Danchin *et al.*, 2008)

**Habitat:** The environment of the individual bird, including all biotic and abiotic elements. Note that ‘habitat’ is frequently and unhelpfully conflated with ‘land use’ (i.e. human activity) in habitat classifications and definitions.

**Habitat association:** The extent to which an individual or population depends upon, or shows disproportionate use or avoidance of, a defined habitat type. Can be positive, neutral or negative.

**Habitat availability:** The accessibility of a defined habitat type or habitat feature to an individual.

**Habitat occupancy:** The frequency or relative occurrence of individuals in a population within a defined habitat type or patch. See also *habitat use*.

**Habitat patch:** A homogeneous area distinctive from its surroundings due to environmental discontinuities. Habitat patches defined by humans and birds are likely to differ.

**Habitat preference:** A positive association (usually of individuals in a population) with a defined habitat type, i.e. non-random distribution resulting in a disproportionately high number of individuals in certain habitat types relative to their availability. Note that Johnson (1980) defined preference as the likelihood of a habitat being chosen when it is equally available to other habitats.

**Habitat quality (or habitat suitability):** The fitness potential or value of a defined habitat type. *Intrinsic habitat quality* is the fundamental fitness in the habitat taking no account of conspecific individuals and other species. *Realised habitat quality* combines intrinsic habitat quality with Allee effects, competition, predation risk etc. Some authors regard habitat suitability as effectively realised quality.

**Habitat selection (or habitat choice):** The processes by which individuals recognise and choose habitat for different functions resulting in observed patterns of *habitat association*, *habitat use* and *habitat occupancy*. Widely regarded as a hierarchical process.

**Habitat structure (or physiognomy):** A combination of the topography and physical architecture of vegetation constituting a defined patch or habitat type. Where it relates solely to the physical structure or complexity of vegetation (e.g. foliage density and cover), *vegetation structure* is more appropriate.

**Habitat type:** Any defined habitat in terms of vegetation composition and structure, hydrology, topography etc.

**Box 1.1 (cont.)**

**Habitat use:** The way that an individual or population uses habitat. Similar to *habitat occupancy*, but implies a need to specify the type of activity, e.g. nesting, roosting, foraging. Note that Johnson (1980) defined ‘habitat usage’ as the quantity of a habitat component used in a fixed period of time.

**Landscape:** Mosaic of habitat types covering an extensive area larger than the home-range of the study organism, typically for territorial songbirds extending over a scale of several square kilometres.

**Landscape complementation:** Situations where local abundance is affected by availability of different habitat patches providing non-substitutable resources, e.g. for nesting and feeding.

**Landscape composition:** Relative amounts of different habitat types in a landscape.

**Landscape structure:** Landscape pattern defined by a combination of *landscape composition* and the spatial arrangement of habitat types in a landscape.

**Landscape supplementation:** Situations where local abundance is affected by individuals being able to derive additional substitutable resources from different habitat patches.

**Macrohabitat:** Broad-scale attributes of occupied habitat, usually relating to a particular type of vegetation, wetland or landform, e.g. mature conifer forest, saltmarsh.

**Microhabitat:** Fine-scale attributes of used habitat, often relating to specific plants, vegetation structures or soil types. Nest site selection usually occurs at a microhabitat level.

predators, their feeding and mating behaviour and so on. The human ability to capture the essential attributes or characteristics of the *Umwelt* is limited. Not surprisingly, few studies of avian habitats take a deeply considered ‘bird’s eye view’ of the environment as a starting point. We usually attempt to measure features that we perceive as potentially important to the bird in terms of cues, resources and physical structures, without considering how the individual bird might perceive the features around them. This may seem academic, especially in conservation applications, where the usual aim is to identify those habitat elements that require restoration before an endangered species can thrive – provided that the model works, then all is well. However, our inability to view the environment with the same perspective as the focal animal means that our predictors of what constitutes ‘the best habitat’ will always be surrogates or imperfect assessments.

### **Habitat recognition and cues**

Basic ideas underlying modern habitat selection theory are evident in several far-sighted papers from the first half of the last century (Hildén, 1965). The 1930s and 1940s was a period when important advances were made by ecologists undertaking increasingly detailed observations in Fennoscandia, Britain and America. Palmgren's (1930) work in Finnish forests is one such example, soon to be followed by David Lack's influential work on the responses of birds to the creation of extensive conifer plantations in eastern England, supplemented with work on bird-habitat associations in Iceland. Lack (1933, 1937) pointed out that the distribution of birds was determined to some extent by a combination of what he termed 'direct' factors including climate, natural enemies, food and nest sites. However, his work in the plantations led him to state firmly that the distribution of birds was also strongly affected by species-specific habitat selection, such that each species had an innate ability to identify its ancestral habitat. The ability of a species to identify its habitat was vividly described by Svårdson (1949) for migrant warblers prospecting for territories soon after their spring arrival. The process determining where birds settled was anything but passive or random. In Lack's opinion it involved a strong psychological element whereby certain features were critical to how a species recognised suitable habitat. Examples of these features, especially the presence of song posts, are given in Lack (1937, 1939).

### **Ultimate factors and proximate cues**

These early ideas may seem unremarkable now, but they represented a breakthrough in understanding how birds determined their habitat. Moreover, Lack's work pre-figured several important habitat concepts. First, the recognition that multiple factors determine distribution is closely linked with notions of hierarchical habitat selection, discussed below. Second, appreciating that species used recognition markers, such as song posts, was important in developing the idea that stimuli or cues were involved in triggering a settling reaction. Lack realised that these cues were not in themselves of importance to survival or success, but others developed the framework of proximate and ultimate factors in habitat selection (e.g. Klomp, 1954; Hildén, 1965; Morse, 1980; Box 1.2). This distinguishes the underlying factors determining the choice of habitat through its fitness potential (ultimate factors) from the immediate stimuli or cues used in habitat selection, but which in themselves are not necessarily of fitness value (proximate factors). The evolutionary and ecological processes shaping current patterns of habitat use broadly correspond to ultimate and proximate factors, respectively (Wiens, 1989a). To some extent, ultimate factors also equate with critical resource needs, defined as those components of the environment that potentially limit individual fitness or population dynamics (Wiens, 1989a).

**Box 1.2 Ultimate and proximate factors in avian habitat selection**

(This list broadly follows Hildén (1965). See text for further details.)

**Ultimate factors**

1. **Food:** Food-supply can limit bird numbers (Wiens, 1989a; Newton, 1998) so large reliable food supplies will characterise strongly preferred habitats in many species. Food availability may have a relatively strong role in habitat selection outside the breeding season.
2. **Shelter:** This includes factors that reduce the likelihood of predation (or assist early detection of predators by prey). Microhabitat attributes can maintain suitable microclimate at nests and roosts (Walsberg, 1985) and avoid flooding (Wesołowski *et al.*, 2002).
3. **Space:** Species vary in minimum area needs for territory establishment and the acquisition of food, so that spatial pattern and structure of habitat may limit their occurrence.
4. **Structural and functional characteristics:** Through morphology and behaviour birds are adapted to life in particular macrohabitats and microhabitats in obvious and more subtle ways that affect habitat occupancy (Snow, 1954; Winkler and Leisler, 1985).
5. **Other species:** Avoiding habitats where predation risk is high or numbers of major competitors are high may be crucial to survival.

**Proximate factors or cues**

1. **Landscape and macrohabitat features:** Landscapes may be selected with particular general characteristics in terms of topography and composition/pattern of macrohabitats resulting in associations with certain levels of landscape openness, forest cover etc.
2. **Habitat structure:** Occupancy of habitat patches may depend on particular vegetation structures in terms of density or height, or soil properties, e.g. dampness, rockiness.
3. **Microhabitat – functional sites:** Presence of features offering suitable nest sites may be critical; examples include some cavity-nesters and ground-nesting colonial birds. Song posts and watch/foraging perches appear important cues for some birds, e.g. pipits, shrikes.
4. **Other animals (positive effects):** The presence or performance of conspecifics may be used as indicators of suitable habitat – conspecific attraction. Settling close to other aggressive species may confer protection from predators.
5. **Other animals (negative effects):** Presence of predators or competitors (or at least identifying their habitats) may be a cue for habitat



**Box 1.2 (cont.)**

avoidance. High densities of conspecifics may discourage further settlement in a habitat patch.

6. **Other animals (indirect cues):** Potentially competing species may be used as cues in habitat selection – heterospecific attraction.
7. **Food:** Species with specialised diets may use food as a cue in habitat recognition, e.g. some fruit and seed-eaters (waxwings *Bombycilla garrulus* and crossbills *Loxia* spp.) and arctic/boreal skuas, owls and raptors feeding on small mammals. Brambling *Fringilla montifringilla* may use insect abundance as a settling cue (Enemar *et al.*, 2004).

Those features or attributes identified by human observers as characteristic of the habitat of a species are, of course, not necessarily the same as the cues used by birds. Nonetheless, it is convenient to think of the ‘important explanatory variables’ that are derived from species-level habitat-association models as proximate factors. Hildén (1965) reminds us that there must be an element of speculation in identifying the factor or combination of factors used by a species in habitat recognition. Experiments on the cues used by birds are difficult to conduct because of the problems encountered in controlling for habitat quality at the scale of territory or home range (Muller *et al.*, 1997), but increasing numbers of examples exist (Mönkkönen *et al.*, 1990; Doligez *et al.*, 2002).

Proximate factors need to correlate with, or somehow indicate, the ultimate factors. This is especially important where the quality of habitat cannot be determined at the time of settling. This may apply in the case of insectivorous species establishing territory in early spring when spatial variation in insect abundance may not correspond with that during the critical chick-rearing period (Morse, 1980). This was the case in a study of red-eyed vireos *Vireo olivaceus*, where foliage density appeared to provide a fairly reliable cue, being correlated with caterpillar abundance in the nestling period (Marshall and Cooper, 2004). Another example is the selection of nesting habitat by ground-nesting waders, where habitats that are suitable in early spring may be entirely unsuitable later in the breeding season due to vegetation growth (Klomp, 1954; Chapter 11).

**Social information**

Selection of breeding habitat is critical because it is closely linked with reproductive success and will be subject to strong selection pressure. Various strategies or mixtures of strategies can be adopted in which ‘personal information’ or ‘public information’ is used in different ways to assess habitat/patch quality (Doligez *et al.*, 2003; Boulinier *et al.*, 2008). Individuals

may merely select their natal patch or even settle at random. Alternatively they may use their own success as a measure of patch quality. Prospecting breeders may rely on environmental cues such as vegetation structure or the presence of predators. An especially important development is recognition of the importance of strategies involving 'social information' about habitat/patch quality gained through interactions with conspecifics or heterospecifics (Stamps and Krishnan, 2005; Seppänen *et al.*, 2007).

A complex of potential social information strategies exists accompanied by a plethora of hypotheses. It has long been appreciated that territorial animals may be attracted to one another resulting in clusters of territories which cannot be explained by spatial variation in habitat (references in Stamps, 1988; Danchin and Wagner, 1997). In its simplest form this may merely involve using the presence of conspecifics to identify potential habitat (conspecific attraction). The importance of this process is increasingly recognised in managing vulnerable populations. Availability of suitable habitat in the absence of conspecifics may not provide sufficient cues and small populations may have weak persistence due to their inability to provide a sufficiently strong cue to attract recruits (Ahlering and Faaborg, 2006; Laiolo and Tella, 2008). An inability to account for conspecific attraction and other social interactions may cause traditional resource-based models of habitat use to perform poorly (Harrison *et al.*, 2009; Folmer *et al.*, 2010; Nocera and Forbes, 2010). On the other hand, some studies have found that the presence of preferred habitat features is more important in determining site occupancy than presence of conspecifics (Cornell and Donovan, 2010).

Some species can assess habitat quality through the reproductive success of other individuals and use this information in subsequent habitat choice. This is termed 'habitat copying' and has been demonstrated in such diverse species as seabirds, tits, swallows, flycatchers and kingbirds (Doligez *et al.*, 1999; Brown *et al.*, 2000; Wagner and Danchin, 2003; Parejo *et al.*, 2007; Boulinier *et al.*, 2008; Redmond *et al.*, 2009). Pre-requisites for habitat copying are that the environment should be patchy in quality and that it should be predictable, so that evidence obtained in one year will apply in the next year. Habitat copying may even occur between potentially competing species (Parejo *et al.*, 2005). Heterospecific attraction is discussed further in Chapter 2.

### **Flexible and inflexible behaviour**

An implication of habitat copying is that individuals have some flexibility in their choices of habitat for different breeding attempts. An opposite situation might occur where natal experience has such an overwhelming influence on habitat choice that subsequent use of the natal habitat is strongly fixed. Where natal experience does play a role, the effect is to increase preference for the habitat in which the individual is reared (Davis, 2008). Site fidelity