Integrated ecomorphology – challenges and solutions

From right to left. Three different modes of clinging on vertical stalks. Bearded Reedlings straddle, Eurasian Reed Warblers grasp the vertical stem with a supporting leg and a pulling leg held far apart, and Penduline Tits climb actively and energetically.
Whilst on board his ship, moored off the island of Sulawesi (then called Celebes) during an expedition to the South Seas in 1900-1901, Oskar Heinroth (1871-1945), one of the founders of ethology, was given two newly-fledged birds. Although he was unable to identify them, he was experienced bird breeder enough to be able to feed them up and restore them to health. He soon suspected that they must be some kind of reed-dwelling warblers, although at that time no *Acrocephalus* species was known from the island. He decided to try a little experiment and built a cage with both horizontal and vertical perches. As soon as he placed the birds in the cage they clambered with ease up and down the vertical perches. Based on this observation, and an examination of the anatomy of the fully grown individuals, he concluded that the birds could only be reed warblers, and proceeded to name them as a new species (Heinroth 1903). Today they are classed as a subspecies (*celebensis*) of Clamorous Reed Warblers.

Heinroth had intuitively combined two ideas, as is now common practice in ecomorphology. First, that the demands of a habitat are reflected in the body structure of a bird and, secondly, that this interrelationship manifests itself by some linking behaviour, in this case the specialized climbing method. In ecomorphological studies, data gained from observations in the field or aviary are integrated with morphological parameters – usually a series of measurements from museum skins or skeletons – using complex statistical procedures such as principal component analysis (PCA) or multiple regression. In this way, relationships can be identified, that would otherwise remain hidden, between ecology and both body structure and behaviour (which develop in tandem in the course of their evolution). In studies involving several species the additional question arises as to which traits can be explained by adaptations to environmental demands and which have their origins in a phylogenetic relationship.

Even the apparently uniform acrocephalids, whose members appear to lack any species-specific characteristics, can be separated from each other in their ecological and phylogenetic aspects by employing ecomorphological methods (section 2.1). Not only do they show very little variation in basic shape (see below) and colouration, but with a weight of 8-20 g they mainly belong to the small to medium-sized warblers, with Blunt-winged and Booted Warblers being the smallest. Only a quarter of the species are larger at 25-35 g (the large reed warblers), and just a few island species are larger still, such as Tahiti Warblers, which weigh in at more than 40 g (chapter 1). Several factors can shape the size or body mass of a species; interspecific size differences are determined by, for example, phylogeny, physiology, habitat productivity and structural complexity, habitat use, and competition (e.g. Polo & Carrascal 1999). Despite the special effect of phylogeny on body size, which varies only slightly between closely related taxa (section 5.4), there are exceptions where sister species actually do differ considerably in body size. We are thinking here of the species pairs Upcher’s and Olive-tree Warblers or Cape Verde and Greater Swamp Warblers. The insular forms also display a certain plasticity within the group for either decreasing or increasing body size, depending on ecological conditions (chapter 12). On the other hand, size difference between the sexes remains slight.

Using the results of ecomorphological studies, this chapter will illustrate how a range of ecological challenges, such as climbing on vertical stems or long-distance migration, were solved, and which structural characters were required. These examples are good illustrations of both the working methods of integrated ecomorphology and the fact that birds in the wild and in laboratory conditions behave and act precisely according to their morphologically defined capacities. A further issue with far-reaching implications is how young birds explore their own species-specific and individual abilities. Finally, by analysing the morphology of the different species and clades in the light of their phylogeny, conclusions can be drawn regarding a possible diversification in this superficially homogeneous family.