Machair invertebrates: the importance of ‘mosaiciness’

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ABSTRACT
Machair systems are not particularly rich in invertebrate species but do contain a much more diverse range of invertebrates than would normally be expected from what is generally thought of as a dry grassland habitat. This invertebrate diversity is driven by the fine-scale, field-scale and landscape-scale mosaic-iness produced by variations in underlying soil conditions, the impact of wind and sea-spray on the soil, the range of markedly different habitat types occurring in close proximity to each other and the strong over-arching influence that cropping and grazing management has on those habitats. The occurrence of these varied invertebrate assemblages is one of the more important reasons why the machair system holds such large and important populations of breeding birds such as dunlin, Calidris alpina, lapwing, Vanellus vanellus, oystercatcher, Haematopus ostralegus, redshank, Tringa tetanus, and snipe, Gallinago gallinago. Without the invertebrates the birds would not be there in such high numbers and without the continued combination of environmental and management factors, the diversity of invertebrates occurring on the machair would be much less.

MACHAIR INVERTEBRATES: WHAT’S KNOWN ABOUT THEM?
The machair grassland systems of the west of Scotland are well known for their botanical and ornithological richness but very little is actually known about their associated invertebrate assemblages. Other than the work on great yellow bumblebee, Bombus distinguendus, and northern collettes, Colletes floralis, reported elsewhere in this issue (this version), most of what is known about machair invertebrates is based on a single survey (using ultraviolet light traps for Lepidoptera and pitfall trapping of surface-active invertebrates) conducted by the Institute of Terrestrial Ecology (ITE) at 24 sand grassland locations in the Outer Hebrides during June and July 1976 (Welch, 1979, 1989).

The pitfall trapping indicated that although the invertebrate assemblages that can be surveyed by this method (such as beetles, centipedes, millipedes, slugs and snails and spiders) were not particularly rich in species, the assemblages themselves did contain a much more diverse range of invertebrates (with differing ecological requirements) than would normally be expected from such dry grassland habitats. However, the ITE survey was relatively limited in terms of the focus on only one element (the sand grassland component) of the wider machair system, the small number of those sites sampled, the duration of the trapping period and the relatively small range of invertebrates that can be surveyed accurately by these trapping methods. As a result, this article will not attempt to describe the invertebrate assemblages occurring on machair in any great detail but rather will try to highlight the underlying environmental and management factors influencing machair invertebrate assemblages in general.

PATCH MOSAICINESS: THE INFLUENCE OF THE ENVIRONMENT
Many terrestrial invertebrates spend all or some part of their life-cycle either on or under the ground, and so soil type and condition is a good place to start. Calcareous sand underlies many of the elements of the machair system and this can influence invertebrates in a variety of ways:

• Despite relatively high rainfall levels, the sand allows large areas of the machair to be reasonably free-draining for a large part of the year. These relatively dry soil conditions not only provide a good medium through which the predatory larvae of ground beetles (Carabidae) and rove beetles (Staphylinidae) can move but also serve to enhance the survival of the larval and pupal stages of other beetles which live underground. For example, the brown chafer, Serica brunnea, is one of the most characteristic beetle species of sand grassland systems and its larvae can spend many months in the soil feeding on the roots of grasses and other plants.

• The calcareous nature of the sand also means that snails can obtain the basic building blocks for their shells. The presence of the snails also provide a greater range of potential prey for predatory beetles, such as the ground beetles and rove beetles already mentioned and also for snail-feeding specialists such as Silpha species of carrion beetles.

• The relatively dry and calcareous nature of the soil also helps drive the botanical richness of the machair, with the nutrient poor conditions allowing a wider range of broad-leaved plants to compete effectively with the grasses. The occurrence of such a wide range of broad-leaved plants provides ideal conditions for a wider range of invertebrates, not only those, such as bees, attracted to the flowers of these plants but also just as importantly others, such as
weevils (Curculionidae), which feed on the roots, stems and leaves of these plants. The sand or marram weevil, *Philopedon plagiatus*, is another characteristic species of herb-rich machair systems.

- The inherently fragile nature of the soil combined with exposure to wind and sea-spray creates a range of sizes of open, sandy patches which not only warm up quickly in the spring and summer (and hence provide good basking opportunities for invertebrates) but also provide good hunting areas for ground beetle species such as *Notiophilus aquaticus* which need open, unobstructed areas in which to spot (using their very large eyes) and then run down their prey.

**FIELD MOSAICINESS: THE INFLUENCE OF CROPPING AND GRAZING**

The management superimposed on the machair system by crofters also adds to the variety of conditions available for invertebrates to exploit:

- The planting of small patches of crops within the machair also serves to help create open, sandy areas with their associated fauna (as described above). In addition, the use of seaweed or livestock dung to fertilise these patches of crops helps increase the organic matter and moisture content of the soil. These patches of moister, more nutrient-rich soil provide suitable conditions for the development of more moisture-loving invertebrates such as the larvae of root-feeding Bibionidae flies and the predatory larvae of soldier flies (Stratiomyidae) which also prefer higher organic matter soils.

- Grazing and trampling by sheep, and especially cattle, also helps to open up the swards at ground level, providing a greater range of microclimates for a wider range of invertebrates to make use of. Providing the grazing is not too intense, this also creates a wide variety of vegetation heights and structures. These tall and short patches of vegetation can support a greater range of different assemblages of invertebrates than would be possible if the vegetation was all of a similar height and structure. Livestock dung is also an important component of the machair system in its own right and contains its own characteristic fauna of dung beetles (such as the wide variety of *Aphodius* spp.) and dung flies (such as *Scatophaga stercoraria*).

**THE IMPORTANCE OF LANDSCAPE MOSAICINESS** All of the above factors are important in their own right in driving the fine and field-scale invertebrate assemblage structures seen on the machair system. The additional important feature of the machair is that by its very nature its differing soil conditions mean that a wide range of different habitats occur in close proximity to each other. So for example, within a 200 m radius of any one point there is likely to occur a close-knit combination of blown sand, patches of crops, grassland with varying heights and structures and lower-lying areas of wetter vegetation. This additional mosaiciness at the landscape scale helps to ensure that the conditions needed to sustain the different invertebrate assemblages occurring on the machair may change locations but nevertheless are still likely to occur somewhere close by throughout the year.

**THE WIDER IMPORTANCE OF MACHAIR INVERTEBRATES**

Finally, since many of these component parts of the machair system are managed at low intensity, they are, from an invertebrate point of view, relatively undisturbed. Consequently, many of the characteristic machair species of invertebrates take a relatively long time to complete their life-cycles and grow to a relatively large size (e.g. the brown chafer, ground beetles such as *Calathus fuscipes*, or *Geotrupes* spp. dung beetles). Other characteristic species (such as the sand weevil or *Aphodius* spp. beetles) may not be large species but the varied conditions across the machair are such that these species can be particularly abundant. All these species are good food for insectivorous birds and the occurrence of these invertebrates on the machair is one of the more important reasons why the machair system holds such large and important populations of breeding unlin, *Calidris alpina*, lapwing, *Vanellus vanellus*, oystercatcher, *Haematopus ostralegus*, redshank, *Tringa tetanus*, and snipe, *Gallinago gallinago* (Fuller et al., 1986). Without the invertebrates the birds would not be there in such numbers and without the continued combination of environmental and management factors acting on the machair, the diversity of invertebrates occurring on the machair would be much less.

**REFERENCES**

