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The importance of coastal sand dunes for terrestrial invertebrates in Wales and the UK, with particular reference to aculeate Hymenoptera (bees, wasps & ants)

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Abstract Although most UK sand dune systems are now fossilized, with little mobility and reducing amounts of bare sand, they support important populations and assemblages of terrestrial invertebrates. Offering open conditions, warm substrates and a range of habitats and habitat structures, they have become increasingly significant as other coastal habitats have been lost. In Wales, 680 Red Data Book and Nationally Scarce species have been recorded from dunes. 109 species in the UK are restricted to dunes, and in Wales there are an additional 145 species confined to dunes and 208 species strongly associated with dunes. Of these, 172 species are dependent upon bare and sparsely-vegetated sand, in grey dunes and early-successional dune grassland, at some stage of their life cycle, rising to 292 species if those associated with the strandline, foredunes, yellow dunes and pioneer dune slacks are included, equating to 63% of the 462 dune species. Bees and wasps are particularly well represented, with 278 species (68% of the Welsh fauna) recorded on Welsh dunes, including 17 obligates and 44 species with a strong dependence, 52 of which are associated with bare and sparsely-vegetated sand. Key to maintaining invertebrate populations on UK dunes is the provision of bare sand but in Wales, bare sand accounts for only 1.7% of the total sand dune resource. As a more appropriate bare sand threshold is likely to range between 10 and 30%, radical action is required to re-mobilize at least the key sand dune systems.

Keywords Coastal sand dunes · Bare sand · Terrestrial invertebrates · Aculeate bees, wasps & ants

Abbreviations

NNR	National Nature Reserve
RDB	Red Data Book
NS	Nationally Scarce
SSSI	Site of Special Scientific Interest

Introduction

Recent studies on the terrestrial invertebrate faunas of coastal sand dunes have focussed on the response of species or suites of species to habitat management and habitat creation (Bonte 2005; Bonte and Maelfait 2001; Bonte et al. 2000, 2003, 2004a, b; Desender et al. 1991, 2007; Maelfait et al. 2007; Maes et al. 2006; WallisDeVries and Ramaekers 2001). A recent survey of Welsh dunes by the World Museum Liverpool and the Countryside Council for Wales focussed on their importance for bee and wasp faunas (Knight et al. 2009). Other than a Buglife report which looked at the management of coastal sand dunes for invertebrates (Colenutt et al. 2003), there has been no published attempt to identify all the invertebrate species that are dependent upon or strongly associated with coastal dunes, either in Europe or within the UK. This is surprising given that dunes are known to support the richest thermophilic invertebrate faunas in Britain (Kirby 1992), which includes many of our rarer species of bees and wasps.

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Open conditions and warm substrates are key to the importance of dune systems for invertebrates, as well as the juxtaposition of a wide range of habitats, including strandline debris, bare sand, marram grassland, dune slacks and pools, sparsely-vegetated open grassland, ranker grassland, scrub and woodland. Dunes have become increasingly important refuges for invertebrates as flower-rich grasslands and heathlands have been lost or fragmented, and they often represent the last remaining areas of extensive semi-natural habitats on the coast. The reliance of terrestrial invertebrates upon coastal sand dunes is not a constant throughout Europe or, indeed, the UK where species can be much more eurytopic. In southern Europe particularly, warm, open and varied conditions are found on a wide range of habitats including heaths, grasslands and farmlands, and are not restricted to the coast but can be encountered at much higher altitudes. The sandy heaths of Dorset, Hampshire and Surrey and the Breckland of East Anglia support thermophilic and psammophilic species confined to coastal dunes elsewhere in the UK. The importance of sand dunes is perhaps most evident in western and northern European localities where there are few or no alternative habitats available for this suite of species.

Bare ground is a vital component of habitats such as coastal dunes, dry heaths, sandy and calcareous grassland and coastal soft cliffs for many invertebrates (Howe 2003; Key 2000; Kirby 1992). Bare substrates offer significantly warmer and drier conditions than surrounding areas of vegetation and are exploited by thermophilic species. Some invertebrates prefer to lay their eggs on bare soils at the edge of vegetation to promote more rapid development, whilst a suite of species, typified by solitary bees and wasps, utilizes bare, sandy soils in which to construct underground nests. The substrate has to be friable enough to dig into but firm enough to prevent nest chambers from collapsing. Burrows are also used as nocturnal refugia or to escape from inclement weather conditions. Visual predators such as ground beetles, tiger beetles and jumping spiders actively hunt on bare ground, whilst the larvae of tiger beetles and ant-lions construct pits, in firm and loose sand respectively, to entrap prey. The predatory larvae of some stilleto flies 'swim' through loose sand to attack prey on the surface, and some scarab and darkling beetles search for plant detritus at or just below the surface of bare, loose sand. Bare ground provides germination sites for ruderal and pioneer plants, many of which are important to phytophagous and flower-visiting invertebrates. Heat- and drought-stressed plants are often more floriferous, making them more attractive to invertebrates, and a number of seed-feeding bugs and beetles are found only amongst ruderal plants growing in very hot areas of bare soil.

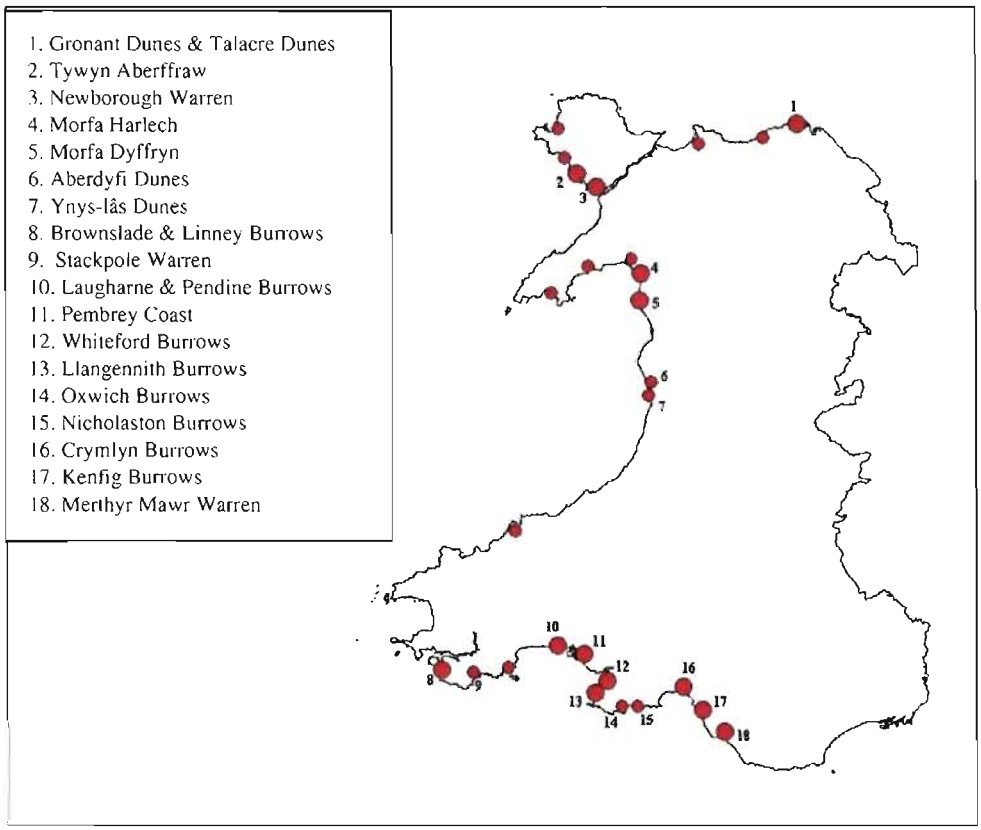

Fig. 1 The distribution of key coastal sand dune systems in Wales

Table 1 Key Welsh sand dunes for terrestrial invertebrates. RDB=Red Data Book. The totals given in the final row are for all Welsh dunes and not just those sites listed

Site	RDB Species	Nationally Scarce species	Total
OXWICH & NICHOLASTON BURROWS	43	169	212
NEWBOROUGH WARREN	20	162	182
WHITEFORD BURROWS	22	130	152
KENFIG BURROWS	30	107	137
MERTHYR MAWR WARREN	24	96	120
PEMBREY COAST	24	96	120
MORFA HARLECH	12	76	88
YNYS-LAS DUNES	8	63	71
LLANGENNITH BURROWS	17	48	65
GRONANT DUNES & TALACRE WARREN	7	55	62
TYWYN ABERFFRAW	10	51	61
TOTAL FOR ALL WELSH DUNES	130	550	680

This paper provides an assessment of the importance of coastal sand dunes in Wales and the UK for terrestrial invertebrates, with a particular focus on bees, wasps and ants.

Welsh sand dunes and their invertebrate faunas

The 8,000 hectares of coastal sand dunes in Wales (see Fig. 1) support 680 species of Red Data Book (RDB) and Nationally Scarce terrestrial invertebrates — species of high conservation interest. Key sites include Oxwich & Nicholaston Burrows with 212 species, Newborough Warren (182 species) and Whiteford Burrows (152 species) (Table 1). Their importance for invertebrate conservation is recognised by the presence of 52 invertebrate 'features' on Welsh sand dune Sites of Special Scientific Interest (SSSI). A 'feature' is the key conservation interest on a SSSI and should both be maintained and drive management on the site. Invertebrate features are either single species, such as the vernal bee *Colletes cunicularius*, the strandline beetle *Nebria complanata* and the shieldbug *Odontoscelis fuliginosa*, or groups of species (assemblages) comprising variable numbers of RDB, Nationally Scarce and local species (Table 2). Most of the large sand-dune SSSI in Wales support an assemblage 'feature' and at least one species 'feature'.

Sand-dune invertebrates

A variety of published and unpublished sources on the distribution and conservation statuses of invertebrates has been used to identify species restricted to sand dunes in Wales and the UK, and species with a high fidelity to Welsh dunes. Many taxonomic groups, such as the parasitic Hymenoptera, are poorly known and have had to be omitted from these analyses and figures presented here will underestimate the numbers dependent upon dunes. Even within groups with better ecological and distributional information, information is rarely comprehensive and a species which currently appears to be confined to coastal sand dunes may subsequently be found elsewhere, thus removing its obligate status. With these caveats, obligate and high fidelity species have been assigned to one of the three following categories:

Table 2 Invertebrate features on Welsh sand dune Sites of Special Scientific Interest (SSSI). A feature represents the key conservation interest on a SSSI and should be maintained in perpetuity and be a driver of site management. Invertebrate features can be either a single species or a suite of species (assemblage) characteristic of the habitat

	Species/Assemblage	No. features
ACULEATE HYMENOPTERA (bees, wasps & ants)	4	13
COLEOPTERA (beetles)	5	8
HEMIPTERA (true bugs)	1	1
LEPIDOPTERA (butterflies & moths)	5	8
ANNELIDA (leeches)	1	2
MOLLUSCA (snails)	1	3
ARANEAE (spiders)	1	1
DUNE ASSEMBLAGE	1	15
COASTAL ASSEMBLAGE	1	1
TOTAL	20	52

Table 3 Invertebrate species restricted to UK dunes or strongly associated with Welsh dunes. For the better represented orders of invertebrates on coastal sand dunes, the number of Welsh Grade 1 to 3 species is given in relation to the total Welsh fauna. Note that these figures will change as a better understanding of ecology and distribution of species is gained

	UK Grade 1 species	Grade 1 species in Wales	Grade 2 species	Grade 3 species	Total in Wales	Total Welsh species	% Total Welsh fauna
MOLLUSCA (snails)	0	0	1	1	2		
ORTHOPTERA (grasshoppers)	0	0	0	1	1		
DICTYOPTERA (cockroaches)	0	0	0	1	1		
HEMIPTERA (true bugs)	14	8	13	25	46	708	6.5
NEUROPTERA (lacewings)	2	2	0	0	2		
COLEOPTERA (beetles)	27	18	65	70	153	2845	5.4
LEPIDOPTERA (butterflies & moths)	17	6	10	14	30	1756	1.7
DIPTERA (true flies)	30	17	34	35	86	3330	2.6
All HYMENOPTERA (sawflies, parasitic wasps, gall wasps, bees, wasps etc)	11	4	15	45	64		
ACULEATE HYMENOPTERA (bees, wasps & ants)	9	2	15	44	61	409	14.9
ISOPODA (woodlice)	0	0	1	0	1		
PSEUDOSCORPIONES (pseudoscorpions)	1	1	0	0	1		
ARANEAE (spiders)	7	2	6	16	24	482	5.0
TOTAL	109	58	145	208	411		

Grade 1 Species (UK OBLIGATES) are restricted to coastal sand dunes in the UK.

Grade 2 Species (WELSH OBLIGATES) are restricted to coastal sand dunes in Wales, additional to UK obligates found in Wales.

Grade 3 Species (HIGH FIDELITY WELSH SPECIES) are most frequently found in Wales on coastal sand dunes.

This has identified 109 species considered to be restricted to coastal sand dunes in the UK (Table 3), with beetles, flies, moths and bugs being the best represented groups. Of these, 58 occur or have occurred in Wales which, when combined with the 145 Grade 2 species, gives an overall figure of 203 species restricted in Wales to coastal sand dunes. With a further 208 Grade 3 species, a total of 411 species that are confined or strongly associated with coastal dunes in Wales is realised. Whilst the majority of species are beetles and flies (Fig. 2), the importance of coastal sand dunes for bees, wasps and ants is highlighted when numbers are considered in the context of the total Welsh fauna, with 15% of the aculeate fauna being restricted to or strongly dependent upon the habitat (Table 3).

Assigning the 462 Grade 1–3 species to a dune habitat type, a strong association with bare and sparsely-vegetated sand is apparent (Table 4). The requirements of many of these species will be complex, with different habitats for nesting, foraging and other activities, but for the purposes of this analysis, species have been attributed to a single habitat which can range from rather broad categories such as dune grassland to the more specialised niches of a dependence upon fungal fruiting bodies growing on dunes. A total of 172 species, 37% of all species, show a high dependence upon bare and sparsely-vegetated sand. Combining all habitats with a large element of bare sand (strandline, marram zone, bare & sparsely-vegetated sand, pioneer dune slacks and a reliance on bee and wasp nests in sand) demonstrates an even more pronounced dependence, with 292 species (63% of the total) being associated with

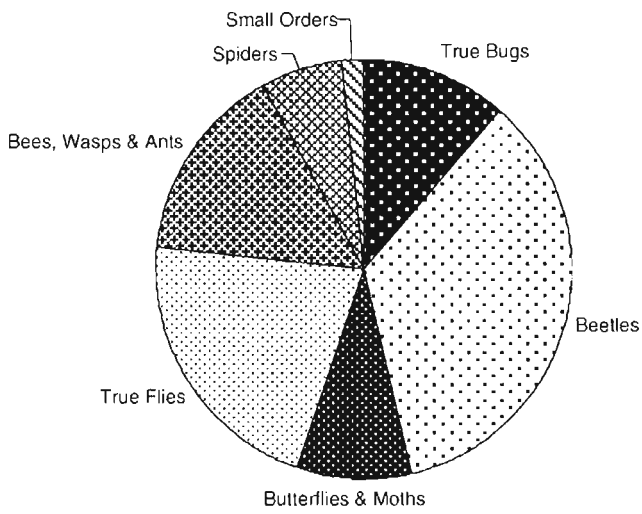

Fig. 2 Pie-chart of the 462 Grade 1 to 3 species by the relevant invertebrate order. Small Orders comprises snails, grasshoppers, cockroaches, lacewings, woodlice and pseudoscorpions

Table 4 The dune habitats used by Grade 1 to 3 species. Each species has been assigned to a single category even where there is a known dependence on more than one habitat

Habitat	Grade 1 spp	Grade 2 spp	Grade 3 spp	Total
STRANDLINE & BEACH FLORA	7	11	15	33
MARRAM ZONE	20	8	8	36
BARE & SPARSELY-VEGETATED SAND	42	48	82	172
DUNE SLACKS	7	20	23	50
DUNE GRASSLAND	10	18	33	61
DUNE HEATH	1	0	0	1
DUNE SCRUB	3	8	13	24
BEE & WASP NESTS IN SAND	2	5	13	20
DUNE FUNGI	1	2	1	4
DUNG & CARRION	6	11	6	23
Unknown Habitat Association	10	14	14	38
TOTAL	109	145	208	462

these habitats (Fig. 3). Not all species groups are equally dependent upon bare and sparsely-vegetated sand, which supports a preponderance of beetles, bugs, bees and wasps (Table 5). Many of the beetles and bugs feed on low-growing plants such as stork's-bill *Erodium*, common restharrow *Ononis repens* and kidney vetch *Anthyllis vulneraria*, plants which require open, sandy conditions, and the bees and wasps build their nests in loose or firm bare sand.

Thirty-three species are associated with strandline debris and plants such as sea rocket *Cakile maritima*, sea beet *Beta vulgaris maritima* and sand couch *Elytrigia juncea*, and 36 species are dependent upon open stands of marram grass growing on yellow dunes. Sixty-one species are affiliated to dune grassland, the majority of which are associated with short, flower-rich swards supporting such plants as common bird's-foot-trefoil *Lotus corniculatus*, stonecrops *Sedum*, thyme *Thymus*, lady's bedstraw *Galium verum* and low-growing hawkweeds *Hieracium*. Pioneer dune slacks are critical to 31 species requiring wet sand and mud whilst more mature slacks support 19 species, including several phytophagous invertebrates which are dependent upon creeping willow *Salix repens*.

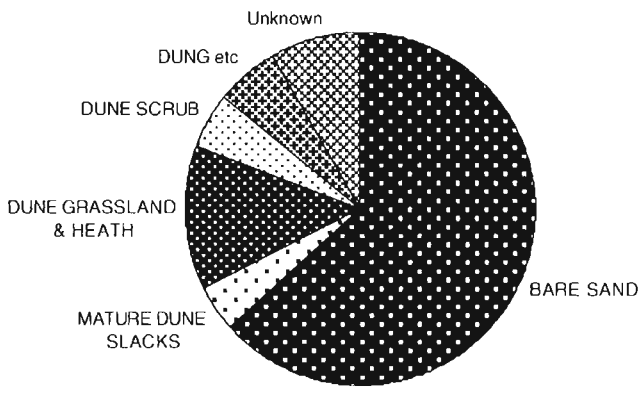

Fig. 3 Pie-chart of the 462 Grade 1 to 3 species by dune habitats. Bare sand comprises strandline, marram, bare and sparsely-vegetated sand, pioneer dune slacks and bee & wasp nests in sand. Dung etc. includes dung, carrion and dune fungi

The importance of sand dunes for bees, wasps and ants

With a few notable exceptions, bees, wasps and ants are warmth-loving species and coastal sand dunes therefore can offer ideal conditions. Some species have long flight periods and others are bivoltine, and those dependent upon pollen and nectar require similarly long flowering periods for key plants such as *Anthyllis vulneraria*, *Lotus corniculatus* and red clover *Trifolium pratense* or a variety of plants available at different times — viper's bugloss *Echium vulgare* and sea holly *Eryngium maritimum* are important late-flowering species. Other than dunes, few habitats offer such extended flowering periods or such variety.

In Wales, 278 species (68% of the total Welsh fauna) have been recorded from sand dunes including 17 dune obligates, 44 species with a strong association with dunes and 52 species of high conservation concern (Table 6; Table 11). 37 of the 61 Grade 1 to 3 species are dependent upon bare or sparsely-vegetated sand, including the marram zone, either for nesting or for foraging on low growing plants that are associated with bare ground, and a further 15 species are cleptoparasitic in the nests of bees and wasps nesting in bare sand, such that 85% are dependent upon bare sand. For the 68 UK species, the equivalent figures are 41 bare sand species and 16 cleptoparasites, equating to 84% of species (Table 7). Key Welsh species include *Colletes cunicularius* and *Oxybelus argentatus*, for which Welsh populations are significant in a UK context, *Arachnospila consobrina*, *Megachile dorsalis*, *Oxybelus mandibularis* and *Coelioxys mandibularis*, which is a cleptoparasite of *Megachile dorsalis*. Whilst *Colletes*

Table 5 Grade 1 to 3 species associated with bare sand. Bare sand comprises the following habitats: strandline & beach flora, marram zone, bare & sparsely-vegetated sand, bee & wasp nests in sand and pioneer dune slacks

	All bare sand habitats
HEMIPTERA (true bugs)	38
COLEOPTERA (beetles)	105
LEPIDOPTERA (butterflies & moths)	22
DIPTERA (true flies)	42
All HYMENOPTERA (sawflies, parasitic wasps, gall wasps, bees, wasps, etc.)	58
ACULEATE HYMENOPTERA (bees, wasps & ants)	57
ARANEAE (spiders)	21
Small Orders	6
TOTAL	292

cunicularius has been assigned to the bare sand category as it nests colonially in areas of fixed, bare or sparsely-vegetated sand, females forage mostly on *Salix repens* growing in mature slacks and it could have been considered a dune-slack species. *Mimumesa littoralis* is confined to marram grass growing in yellow dunes.

Important aculeate assemblages are found at ten dune systems in south Wales, the dunes on the Castlemartin peninsula in Pembrokeshire and on six systems in north Wales, and more than 100 species have been recorded from seven sites (Table 8). Four species, *Bombus sylvarum*, *Chrysis fulgida*, *Colletes cunicularius* and *Podalonia affinis*, are 'features' on Welsh SSSI, with *Colletes cunicularius* being a 'feature' on eight sites, and bees, wasps and ants are key components of 16 assemblage 'features' (Table 9).

Discussion and implications for conservation

Despite the fact that sand dunes are relatively rare, fragmented and localised in Wales and the UK, they support significant numbers of terrestrial invertebrate species which are either restricted to or strongly associated with this habitat. The only comparable published review (Colenutt et al. 2003) recognised 209 invertebrate species associated with dunes of which 30 appear to be restricted to dunes, although it is difficult to tease out these statistics.

Table 6 The importance of Welsh sand dunes for bees, wasps & ants. RDB and Nationally Scarce species are regarded as being of high conservation value

Total No. Welsh Species	409
Total No. Recorded on Welsh Dunes	278
RDB Species	14
Nationally Scarce Species	38
Dune Obligates (Welsh Grade 1+2)	17
High Fidelity Species (Grade 3)	44
All Bare Sand Habitats	52

Significantly, that review did not include bees, wasps and ants. The total of 411 Grade 1 to 3 species on Welsh sand dunes presented here is striking when compared to floristic equivalents. Rhind and Jones (1999) calculated that 32 species of vascular plants, 22 species of bryophytes and 10 species of fungi were wholly dependent or strongly associated with Welsh dunes. As a general rule, and as highlighted by Doody (1989), the most specialized dune invertebrates tend to occur in the earlier stages of dune succession such as the strandline, marram in yellow dunes, bare and sparsely-vegetated sand in the grey dunes and blow-outs further inland, early-successional dune grassland and pioneer dune slacks. As the proportion of bare sand declines and plant cover and humic content increase, the number of specialists also declines. This mirrors the situation with some plant groups. Vascular plant dune specialists favour mobile and semi-fixed dunes, the richest dune mycofloras are associated with semi-fixed dunes and young dune slacks, as well as more mature slacks, and most of the obligate dune bryophytes are confined to early successional stages of dune slack development (Rhind and Jones 1999; Wrench 2001).

The aim of conservation management should be to promote dynamic dune systems and natural sand movements (Houston 1997; Richie 2001), which would be highly beneficial to invertebrates as it would provide early successional habitats and inland blow-outs, maintain habitat connectivity and improve habitat patch quality (Maes et al. 2006; Provoost and Bonte 2004). However, wider public interests often inhibit such an approach and, in such cases, management is often driven by 'charismatic' species such as sand lizard, natterjack toad, some vascular plants (Houston 1997) and birds. Davies (2001) found that where Welsh dunes were managed at least in part for species, birds were the most popular focus. In Wales, major efforts have been made over the last 15–20 years to maintain populations of the fen orchid *Liparis loeselii* at Kenfig Burrows by bulldozing and mowing over-mature slacks (Jones 1998; Jones and Etherington 1992). Although Wrench (2001) notes that dune slack management on the Sefton Coast in

Table 7 The dune habitats used by the Grade 1 to 3 bees, wasps & ants. Each species has been assigned to a single category even where there is a known dependence on more than one habitat. Note that these figures will change as a better understanding of ecology and distribution of species is gained

Habitat	Grade 1 spp	Grade 2 spp	Grade 3 spp	Total
MARRAM ZONE	0	1	0	1
BARE & SPARSELY-VEGETATED SAND	5	11	24	40
DUNE GRASSLAND	1	0	3	4
DUNE SCRUB	0	2	4	6
BEE & WASP NESTS IN SAND	2	1	13	16
Unknown Habitat Association	1	0	0	1
TOTAL	9	15	44	68

Lancashire rarely considers the conservation of bryophytes despite their being particularly well adapted to dynamic processes, the inclusion of petalwort *Petalophyllum ralfsii* in the EU Habitats Directive has raised the profile of this species at least. It is a rare event for dunes in the UK to be managed specifically for invertebrates, despite their significance and their unique vulnerability to unsympathetic management.

A range of factors makes many invertebrates susceptible to even small-scale changes in land management. Many species have an annual life cycle and, as such, they require a high level of habitat continuity. They often occupy small patches of habitat which can be damaged or destroyed unwittingly, and are sensitive to changes in microclimate and vegetation structure. Many have poor dispersal abilities, at least at some stage in their life cycle, and the various stages (egg, larva, pupa and imago) can have very different requirements, often within close proximity, resulting in a need for habitat heterogeneity. As already highlighted, many species occupy pioneer habitats which are, by their nature, transient and, at least on sand dunes, either require active processes to maintain them or frequent management intervention.

Coastal sand dunes support rich invertebrate faunas despite the fact that the majority of our systems have become fossilized, with little mobility, much reduced amounts of bare sand and the loss of early-successional habitats. Much of the 1260 ha of dunes at Newborough Warren was dominated by bare sand in the 1950s and as little as 7 ha now remains (Rhind et al. 2001; Saye 2003). This process of extreme stabilisation is mirrored on other Welsh dunes and bare sand now accounts for only 1.7% of the total sand dune resource (Saye 2003; see Table 10). One quarter of the Welsh bare sand resource is found on Morfa Dyffryn, and half of the resource is found on just three sites — Morfa Dyffryn, Brownslade & Linney Burrows and Merthyr Mawr Warren. Those species dependent upon open conditions will be at risk of extinction on sites where bare sand is at a premium. Key (2000) suggests that 2–5% bare

Table 8 Key Welsh sand dunes for bees, wasps & ants

Site	Grade 1–2 species	Grade 3 species	RDB & Nationally Scarce species	All species
MERTHYR MAWR WARREN	14	34	21	133
PEMBREY COAST	13	32	16	132
OXWICH BURROWS	12	31	18	123
WHITEFORD BURROWS	12	31	13	107
YNYS-LAS DUNES	11	26	14	99
NICHOLASTON BURROWS	11	26	12	68
LLANGENNITH BURROWS	10	31	15	109
NEWBOROUGH WARREN	10	28	13	86
KENFIG BURROWS	9	30	15	96
TYWYN ABERFFRAW	9	25	9	59
MORFA HARLECH	9	18	8	52
MORFA DYFFRYN	8	26	8	78
CRYMLYN BURROWS	7	24	9	80
ABERDYFI DUNES	6	16	5	51
STACKPOLE WARREN	5	29	5	59
LAUGHARNE & PENDINE BURROWS	5	28	6	75
BROWNSLADE & LINNEY BURROWS	5	27	11	102
GRONANT DUNES & TALACRE WARREN	4	20	9	111

Table 9 Welsh SSSI 'features' involving bees, wasps and ants. There are 4 single species 'features' and 2 assemblage 'features'

Bombus sylvarum	Castlemartin Cliffs & Dunes SSSI (Brownslade & Linney Burrows)
	Cynffig SSSI (Kenfig Burrows)
Colletes cunicularius	Cynffig SSSI (Kenfig Burrows)
	Dyfi SSSI (Ynys-lâs)
	Gronant Dunes & Talacre Warren SSSI
	Morfa Dyffryn SSSI
	Morfa Harlech SSSI
	Newborough Warren-Ynys Llanddwyn SSSI
	Tywyn Aberffraw SSSI
	Twyni Chwitffordd SSSI (Whiteford Burrows)
Chrysis fulgida	Arfordir Pen-bre SSSI (Pembrey Coast)
	Twyni Chwitffordd SSSI (Whiteford Burrows)
Podalonia affinis	Gronant Dunes & Talacre Warren SSSI
Sand Dune Invertebrate Assemblage	Arfordir Pen-bre SSSI (Pembrey Coast)
	Broomhill Burrows SSSI
	Cynffig SSSI (Kenfig Burrows)
	Crymlyn Burrows SSSI
	Dyfi SSSI (Ynys-lâs)
	Gronant Dunes & Talacre Warren SSSI
	Twyni Lacharn-Pentywyn SSSI
	Merthyr Mawr SSSI
	Morfa Dyffryn SSSI
	Morfa Harlech SSSI
	Newborough Warren-Ynys Llanddwyn SSSI
	Oxwich Bay SSSI (Oxwich & Nicholaston Burrows)
	Stackpole SSSI
	Twyni Chwitffordd SSSI (Whiteford Burrows)
	Tywyn Aberffraw SSSI
Coastal Invertebrate Assemblage	Castlemartin Cliffs & Dunes SSSI (Brownslade & Linney Burrows)

ground ought to be acceptable in any habitat, with up to 10–15% desirable in some, and Richie (2001) states that values of 2.5–5% bare sand should be considered the norm for mature dune systems in temperate latitudes. However, a more appropriate threshold on sand dunes for invertebrates is likely to range somewhere between 10 and 30% bare sand — the most mobile system in Wales, Morfa Dyffryn, comprises 12% bare sand — and to reach such levels, radical action is required to re-mobilize at least the key sand dune systems.

Table 10 Measures of bare sand found on Welsh sand dunes. Only those sites with more than 5 ha of bare sand are included. Bare sand figures are taken from Saye (2003)

Site	Total area ha	Bare sand area ha	Bare sand as % of total area
MORFA DYFFRYN	313	35.91	11.5
BROWNSLADE & LINNEY BURROWS	252	18.51	7.3
MERTHYR MAWR WARREN	342	13.76	4.0
NEWBOROUGH WARREN	1257	6.96	0.6
GRONANT DUNES & TALACRE WARREN	190	6.6	3.5
LLANGENNITH BURROWS	224	5.96	2.7
TYWYN ABERFFRAW	248	5.85	2.4
MORFA HARLECH	341	5.85	1.7
TOTAL WELSH DUNE HABITAT	8051	134.86	1.7

The management strategies in Wales adopted to-date have been ineffective at producing bare and open habitats, and techniques such as extensive grazing, if heavy and prolonged, may be detrimental if there is a significant reduction in the inflorescences of flowering plants. At Ainsdale NNR, the dunes are winter-grazed by Herdwick sheep (Houston 1997) which avoids such impacts. On Belgian coastal dune reserves, grazing is used to introduce secondary dynamics and has been shown to be beneficial for butterflies (WallisDeVries and Ramaekers 2001), grasshoppers (van Wingerden et al. 1991) and spiders (Bonte et al. 2002), although it may be detrimental to burrowing species such as the tiger beetle *Cicindela maritima* and the solitary wasp *Bembix rostrata*, especially where trampling pressures are high (Bonte 2005). Grazing does promote an associated dung fauna, and the current review recognises 23 species which are restricted to (17) or strongly associated with (6) dung on sand, including 19 Welsh species. Bonte et al. (2000) found that spider diversity was highest in the transition zone between cattle-grazed and ungrazed areas, with common species occurring in tall grass and very short swards supporting common aeronauts and dune rarities. In Wales and the UK, most spider dune specialists are associated with marram grass in yellow dunes (this review; Colenutt et al. 2003), an area not traditionally subject to livestock grazing. The results for invertebrate colonisation of newly-created sand dunes are relatively encouraging. Desender et al. (2007) found an increase in both the number of species of ground beetles and the population size of rare species in restored dune slacks at a site in Belgium, although many failed to establish viable populations. They emphasise that dynamic processes have to be ongoing if species are not to be rapidly lost. On the same dune sytem, Maelfait et al. (2007) reported a rapid colonisation of new sandhills by good-dispersing species of ground beetles and spiders although, on a cautionary note, they found that many of the more specialised dune species failed to establish over the course of the four-year study period.

As early as 1973, Hammond (1974) was highlighting the plight of psammophilic ground beetles in the UK, although sharp declines at that time were the result of habitat destruction rather than the loss of early-successional habitats. Haeseler (1989) reported on the population losses and extinctions of aculeate Hymenoptera and beetles associated with coastal sand dunes in the western Mediterranean as a result of habitat loss from industrial-scale sand extraction and subsequent habitat fragmentation. Whilst species extinctions on Welsh and UK dunes will be more insidious, as the bare sand resource on our systems continues to decline, they will be no less final.

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Appendix

Table 11 A list of the 68 Grade 1 to 3 bees, wasps and ants of Welsh and UK coastal dune systems. For each species, its preferred single habitat is provided. Species in emboldened text have been recorded in Wales. RDB=Red Data Book, NS=Nationally Scarce

Grade	Species	Family	UK Status	Preferred habitat
1	*Myrmica specioides*	Formicidae	RDB3	dry bare/sparsely vegetated sand
1	*Evagetes pectinipes*	Pompilidae	RDB1	nests of spider-hunting wasps in dry bare or sparsely vegetated loose sand
1	*Tachysphex obscuripennis*	Crabronidae	Extinct	dry bare or sparsely vegetated firm sand
1	*Miscophus ater*	Crabronidae	RDB2	dry bare or sparsely vegetated loose sand
1	*Gorytes punctatus*	Crabronidae		habitat unknown
1	*Colletes floralis*	Apidae	RDB3	dry bare or sparsely vegetated firm sand
1	*Colletes cunicularius*	Apidae	RDB3	dry bare or sparsely vegetated firm sand
1	*Coelioxys mandibularis*	Apidae	RDB3	nests of solitary bees in sand
1	*Bombus pomorum*	Apidae	Extinct	dry herb-rich grassland (fixed dune)
2	*Hedychridium cupreum*	Chrysididae	NS	nests of digger wasps in sand
2	*Chrysis fulgida*	Chrysididae	RDB1	nests of potter wasps in scrub
2	*Anoplius viaticus*	Pompilidae		dry bare/sparsely vegetated sand
2	*Podalonia affinis*	Sphecidae	RDB3	dry bare/sparsely vegetated sand
2	*Dryudella pinguis*	Crabronidae		dry bare/sparsely vegetated sand

Table 11 (continued)

Grade	Species	Family	UK Status	Preferred habitat
2	*Tachysphex nitidus*	Crabronidae		dry bare or sparsely vegetated firm sand
2	*Oxybelus argentatus*	Crabronidae	NS	dry bare/sparsely vegetated sand
2	*Oxybelus mandibularis*	Crabronidae	NS	dry bare/sparsely vegetated sand
2	*Mimumesa littoralis*	Crabronidae	RDB3	tussocks/litter in yellow dunes (marram and lyme grass)
2	*Mimesa bicolor*	Crabronidae	RDB2	dry bare or sparsely vegetated firm sand
2	*Mimesa bruxellensis*	Crabronidae	NS	dry bare/sparsely vegetated sand
2	*Colletes marginatus*	Apidae	NS	dry bare/sparsely vegetated sand
2	*Dasypoda hirtipes*	Apidae	NS	dry bare/sparsely vegetated sand
2	*Stelis ornatula*	Apidae	RDB3	nests of solitary bees in hollow plant stems
2	*Megachile dorsalis*	Apidae	NS	dry bare or sparsely vegetated firm sand
3	*Hedychridium ardens*	Chrysididae		nests of digger wasps in sand
3	*Cleptes semiauratus*	Chrysididae	NS	parasitoid of sawflies associated with scrub
3	*Tiphia femorata*	Tiphiidae		parasitoid of scarab beetle larvae in dry herb-rich grassland (fixed dune)
3	*Myrmosa atra*	Mutillidae		nests of digger wasps in sand
3	*Sapyga quinquepunctata*	Sapygidae		nests of solitary bees in sand
3	*Cryptocheilus notatus*	Pompilidae	RDB2	dry bare or sparsely vegetated loose sand
3	*Pompilus cinereus*	Pompilidae		dry bare or sparsely vegetated loose sand
3	*Arachnospila consobrina*	Pompilidae	RDB3	dry bare or sparsely vegetated loose sand
3	*Arachnospila trivialis*	Pompilidae		dry bare or sparsely vegetated loose sand
3	*Arachnospila wesmaeli*	Pompilidae	NS	dry bare or sparsely vegetated loose sand
3	*Evagetes crassicornis*	Pompilidae		nests of spider-hunting wasps in dry bare or sparsely vegetated loose sand
3	*Anoplius infuscatus*	Pompilidae		dry bare or sparsely vegetated loose sand
3	*Episyron rufipes*	Pompilidae		dry bare or sparsely vegetated loose sand
3	*Ceropales maculata*	Pompilidae		nests of spider-hunting wasps in sand
3	*Symmorphus crassicornis*	Vespidae	RDB3	dune scrub (aspen, hawthorn, burnet rose)
3	*Ammophila sabulosa*	Sphecidae		dry bare or sparsely vegetated loose sand
3	*Podalonia hirsuta*	Sphecidae	NS	dry bare or sparsely vegetated loose sand
3	*Tachysphex pompiliformis*	Crabronidae		dry bare or sparsely vegetated firm sand
3	*Crabro cribrarius*	Crabronidae		dry bare or sparsely vegetated firm sand
3	*Crabro peltarius*	Crabronidae		dry bare or sparsely vegetated firm sand
3	*Crossocerus wesmaeli*	Crabronidae		dry bare or sparsely vegetated firm sand
3	*Oxybelus uniglumis*	Crabronidae		dry bare or sparsely vegetated loose sand
3	*Nysson dimidiatus*	Crabronidae	NS	nests of digger wasps in sand
3	*Harpactus tunidus*	Crabronidae		dry bare or sparsely vegetated firm sand
3	*Cerceris arenaria*	Crabronidae		dry bare or sparsely vegetated firm sand
3	*Colletes fodiens*	Apidae		dry bare or sparsely vegetated firm sand
3	*Colletes similis*	Apidae		dry bare or sparsely vegetated firm sand
3	*Andrena barbilabris*	Apidae		dry bare or sparsely vegetated loose sand
3	*Lasioglossum prasinum*	Apidae		dry bare or sparsely vegetated firm sand
3	*Melitta leporina*	Apidae		dry bare or sparsely vegetated firm sand
3	*Osmia xanthomelana*	Apidae	RDB1	dry bare or sparsely vegetated firm sand
3	*Osmia aurulenta*	Apidae		dry herb-rich grassland (fixed dune)
3	*Osmia bicolor*	Apidae	NS	dry herb-rich grassland (fixed dune)
3	*Hoplitis claviventris*	Apidae		hollow plant stems (bramble etc.)
3	*Hoplitis spinulosa*	Apidae		hollow plant stems (bramble etc.)
3	*Megachile circumcincta*	Apidae		dry, bare or sparsely vegetated sand
3	*Megachile maritima*	Apidae		dry bare or sparsely vegetated loose sand
3	*Coelioxys quadridentata*	Apidae	RDB3	nests of solitary bees in sand
3	*Coelioxys elongata*	Apidae		nests of solitary bees in sand

Table 11 (continued)

Grade	Species	Family	UK Status	Preferred habitat
3	*Coelioxys inermis*	Apidae		nests of solitary bees in sand
3	*Coelioxys conoidea*	Apidae		nests of solitary bees in sand
3	*Coelioxys rufescens*	Apidae		nests of solitary bees in sand
3	*Epeolus cruciger*	Apidae		nests of solitary bees in sand
3	*Epeolus variegatus*	Apidae		nests of solitary bees in sand

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