An annotated list of wetland ground beetles (Carabidae) and rove beetles (Staphylinidae) found in the British Isles including a literature review of their ecology

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An annotated List of Wetland Ground Beetles (Carabidae) and Rove Beetles (Staphylinidae) found in the British Isles including a literature review of their ecology

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Summary

1. Non-aquatic groups are a largely overlooked species-rich component of the wetland invertebrate fauna. Faunal studies have shown that the ground-living non-aquatic fauna is dominated by rove beetles (Staphylinidae) and ground beetles (Carabidae).

2. A definition of wetlands is given which encompasses riverbanks, because of the high degree of overlap of their beetle fauna with other wetland types.

3. A review is given of the ecological literature on wetland and riparian species, encompassing morphological, behavioural and life history adaptations, habitats, studies on species assemblages and use in conservation assessment. Many species have habitats which do not fit standard habitat classifications, but certain habitat structures, such as exposed riverine sediments, seepages, floodplain wetlands and certain coastal features have been identified as being rich in characteristic species of ground beetles and rove beetles.

4. Because of their habitat specificity and sensitivity to different disturbance and hydrological regimes, it is concluded that rove beetles and ground beetle assemblages together have the capacity to be useful biotic indicators of environmental change. Identification of important disturbance and hydrological gradients, which can be related to fluvial and coastal processes, will have value for informing wetland management protocols at a number of different spatial scales.

5. More comprehensive base-line data is needed to develop authoritative rarity and fidelity scores for use in site quality evaluation, but the need for complex ranking systems is questioned. Site quality evaluations are best used as part of a strategic approach that takes account of fluvial and coastal processes operating at the landscape or catchment scale.

6. A guide to sampling methods and sources of information on species identification, distribution and ecology is given. Attention is drawn to the need for an improved regional network of museum reference collections.

7. 422 rove beetles and 175 ground beetles are listed as wetland species in the British Isles with varying degrees of affinity for wetland habitats. Selection of species was based on the literature and a database of 870 samples. Each species is annotated with summary details of conservation status, main habitat and microhabitat and also an estimate of fidelity status. The list is intended to be inclusive rather than exclusive, but the fidelity status can be used to filter out the less specialist species if so desired. Changes in conservation status are recommended for a limited number of species.

8. The number of ground beetle and rove beetle species listed far exceeds the number of aquatic beetles recorded from Britain and lends credence to the claim that non-aquatic invertebrates have a higher species diversity in wetlands than aquatic invertebrates, at least in freshwater systems.

Contents

1. Introduction

Until recently, conservationists have generally regarded wetland invertebrate biodiversity as being concentrated in aquatic organisms. However, wetland specialist species can also be found among several families of terrestrial insects that complete their whole life cycle around the edge of the water or on emergent vegetation (Williams & Feltmate 1992). 2,773 species of freshwater aquatic macroinvertebrates are believed to occur in Britain (RSPB, NRA & RSNC 1994). It has been estimated that the species richness of non-aquatic species found in freshwater wetlands is approximately twice that of aquatic species (Hammond 1998). Table 1 shows the numbers of species in non-aquatic invertebrate groups found in faunal surveys conducted in various temperate wetlands and river systems. These studies reveal an important, but often overlooked component of wetland biodiversity whose conservation is only now starting to be addressed in certain well-defined areas.

Eyre & Lott (1997) reviewed issues relating to the conservation of invertebrates on exposed riverine sediments and made recommendations for further work, which has followed in England and Wales (Sadler & Petts 2000) and Scotland and northern England (Eyre 1998, Eyre, Luff & Phillips 2001, Eyre, Lott & Luff 2001, Eyre & Luff 2002). Lott, Proctor & Foster (2002) reviewed the effects of site management on non-aquatic invertebrates in East Anglian fens and identified priorities for future research, following similar work on Welsh peatlands (Holmes, Boyce & Reed 1993, Holmes *et al.* 1993). Boyce (2002) reviewed the conservation value of seepages for invertebrates and recommended several priority areas for research. Other important areas of interest in the UK that have been identified include floodplains (Hammond 1998) and coastal habitats (Sherwood, Gardner & Harris 2000), but as yet they lack a coherent conservation strategy at the national scale. What is also lacking is an overview of non-aquatic invertebrates in wetlands. This would be useful not only to identify further priorities for action, but also to inform discussions on habitat fidelity and what constitutes a specialist species.

The predominant non-aquatic groups appearing in samples of the wetland ground fauna are two families of mostly predatory beetles. The rove beetles (Staphylinidae) are often the most speciose group followed by the ground beetles (Carabidae). The prevalence of these two families in beetle assemblages is repeated in a wide range of temperate wetland types (see table 1, also Köhler 1996, Hammond 1998, 2000, Lott 2001). This report is the first stage of an overview of the wetland species in these families. It reviews the current literature on their ecology and conservation and includes an annotated list of species occurring in the British Isles. It is primarily intended to be an information tool, but it also identifies some strategic conservation issues, particularly in the area of habitat characterisation. It also provides a broader ecological context to work currently in progress in more specific habitats such as fen, seepages and exposed riverine sediments.

Further non-aquatic wetland specialists in the British Isles are found in other beetle families, but the numbers of species are much lower. In addition, all aquatic species pass through at least one non-aquatic stage in their life cycle.These families are listed in table 2.

Wetland has been defined as *an area of low-lying land, submerged or inundated periodically by fresh or saline water* (Lincoln & Boxshall 1987). This definition applies to low-lying sediments by rivers and there is a high degree of overlap between beetle assemblages on riverbanks and assemblages in other types of wetland. Consequently, riparian species are included in both the literature review and the species list.

Table 1. Number of non-aquatic invertebrate species recorded in some faunal studies of temperate wetlands

Location	Major groups recorded together with no. of species	Source
7 rivers in southern Karelia	Coleoptera (295)	Palmén & Platanoff (1943)
lake margin in SW Finland	Orthoptera (2), Lepidoptera (27), Diptera (322), Coleoptera (323), Hymenoptera (89), Heteroptera (37), Auchenorrhyncha (42)	Krogerus (1948)
2 rivers in Tuscany	Coleoptera – Carabidae & Staphylinidae (88)	Bordoni (1967, 1969)
reedbed in Czech Republic	Coleoptera (95)	Obrtel (1972)
10 gravel pits in the Rhein valley, Germany	Coleoptera (78)	Koch (1977)
9 streams in Ohio (USA)	Coleoptera – Carabidae, Staphylinidae & Heteroceridae (90)	Holeski & Graves (1978)
R. Ourthe, Belgium	Diptera – Dolichopodidae (26)	Pollet, Mercken & Desender (1988)
shingle banks on 2 rivers in Wales	Orthoptera (2), Heteroptera (1), Diptera – Empidoidea (6), Hymenoptera – Formicidae (3), Coleoptera (70), Araneae (44)	Fowles (1988)
8 streams in Hesse (Germany)	Araneae (77), Coleoptera (55)	Smit *et al.* (1996)
R. Soar floodplain in Leicestershire	Coleoptera – Carabidae (86), Staphylinidae (187), Heteroceridae (2) & Elateridae (6)	Lott (1998b)
19 saline lagoons in SW Ireland	Coleoptera – Carabidae (64) & Staphylinidae (145)	Good & Butler (1998)
4 turloughs in W Ireland	Coleoptera - Carabidae (37) & Staphylinidae (78)	Good & Butler (2001)
East Anglian fenland	Mollusca (37), Araneae (182), Auchenorrhyncha (117), Diptera (543+), Coleoptera – Carabidae (55), Staphylinidae (133+), phytophagous spp. (78)	Lott, Proctor & Foster (2002)

Table 2. British beetle families containing wetland species.

Family	aquatic	non-aquatic
Carabidae		x
Haliplidae	x	x (pupae)
Hygrobiidae	x	x (pupae)
Noteridae	x	x (pupae)
Dytiscidae	x	x (pupae)
Gyrinidae	x	x (pupae)
Microsporidae		x
Spercheidae	x	x (pupae)
Georissidae		x
Hydrochidae	x	x (pupae)
Hydrophilidae	x	x
Hydraenidae	x	x (pupae)
Ptiliidae		x
Scydmaenidae		x
Staphylinidae		x
Scarabaeidae		x
Clambidae		x
Scirtidae	x (larvae)	x (adults)
Byrrhidae		x
Psephenidae	x (larvae)	
Heteroceridae		x
Limnichidae		x
Dryopidae	x	x
Elmidae	x	x (pupae)
Elateridae		x
Cantharidae		x
Melyridae		x
Rhizophagidae		x
Silvanidae		x
Cryptophagidae		x
Phalacridae		x
Coccinellidae		x
Anthicidae		x
Cerambycidae		x
Chrysomelidae	x	x
Apionidae		x
Curculionidae	x	x

2. Literature review

2.1 Morphological and behavioural adaptations

2.1.1 Survival in floods

An ability to survive or react to permanent or intermittent inundation is probably the major adaptive factor that defines a wetland species. Many non-aquatic species with wetland habitats are not incapacitated by the presence of standing water. Ahrens and Bauer (1987) reported that *Blethisa multipunctata* is quite active when it enters the water and suggested that it habitually enters water in order to escape predation and to hunt. *Carabus clathratus* can search for prey under water for over 15 minutes by storing air under its elytra like Dytiscidae, and larvae of the non-British *Carabus variolosus* can reach down underwater to take aquatic prey while swimming on the surface (Sturani 1962). *Agonum thoreyi, Oodes helopioides* and the non-British rove beetle, *Acylophorus wagenschieberi,* have been observed by the author purposefully entering water when their environment was disturbed by trampling during sampling, while *Stenus* species walk on the water surface in order to traverse small areas of open water (Betz 1999).

More or less permanently waterlogged environments can be found in fens, bogs and lake margins with emergent vegetation. These biotopes support several species of ground beetles and rove beetles capable of climbing plants. *Demetrias* species have enlarged bilobed tarsal segments similar to Chrysomelidae and Coccinellidae that habitually climb plants. Within the large rove beetle genus, *Stenus,* widened tarsal segments and associated adhesive setae are used to grip smooth plant surfaces (Betz 2002). *Quedius maurorufus* and *Hygronoma dimidiata* are adept at climbing the vertical walls of glass tubes (personal observation), an ability linked to the need to climb smooth, vertical plant stems in their fenland and marshland habitats. Landry (1994) found that, out of four species of *Agonum* in a Canadian lakeside fen, *A. nigriceps* had the most proficient climbing ability and also the longest tarsi. He associated this climbing ability to a preference on the part of *A. nigriceps* for flooded areas with tall emergent vegetation.

Intermittent flooding can be regarded as a type of disturbance. Sousa (1984) described five attributes of disturbance regimes that could be selective on adaptations in species affected by the disturbance. These can be adapted to flooding regimes as follows:

1. spatial scale (size of area subject to floods),
2. magnitude (expressed either as intensity measured as the strength of the disturbing force, eg current power, or as severity measured as the damage caused by the disturbance, eg habitat change),
3. frequency (number of floods per unit time),
4. predictability (variance in mean time between floods),
5. turnover rate (mean time required to disturb entire area, or proportion of area affected by average flood event).

Flooding regimes with high predictability fall into two discrete classes that can be separated by frequency. River floodplains are subject to annual flood pulses following winter rain or spring snow melts, while sea shores and estuaries are subject to a tidal regime which has a monthly period superimposed onto an almost twice daily pulse. A variety of different behavioural and life history adaptations have been acquired to deal with 1) annual flooding, 2) tidal flooding and 3) unpredictable flooding.

Wetland species in habitats affected by annual flooding can adapt their life cycle by developing hibernation strategies for surviving winter floods and these are considered in the section on life histories. Many intertidal beetles occupy burrows or rock crevices where they can remain in an air pocket during submersion by the tide (Bro Larsen 1936, Elliott, King & Fordy 1983a, Wyatt 1986). Littoral *Bledius* burrows are bottle-shaped to prevent ingress of water during tidal inundations (Wyatt 1986). The parental care of eggs and larvae exhibited by *Bembidion pallidipenne* and four species of saltmarsh *Bledius,* includes ventilation of larval chambers between tides and confers protection against flooding of burrows as well as protection against attack by fungi, parasitoids and predators (Bro Larsen 1952, Foster 2000). Foster (2000) described strategies used by surface-active arthropods to prevent their activity patterns co-inciding with high tides. The nocturnal ground beetle, *Dicheirotrichus gustavi*, is able to suppress its normal circadian rhythm in response to tidal inundation of its feeding grounds (Foster 1983), but the intertidal ground beetle, *Cillenus lateralis* (formerly in *Bembidion*), has an endogenous tidal activity rhythm (Elliott, King & Fordy 1983).

A range of behavioural and physiological strategies have been developed to survive unpredictable flooding caused by spates and storm surges. Firstly, preventative action can be taken to avoid contact with water. Just as intertidal beetles can survive tidal submersion in burrows, so riverbank species are well placed to sit out unexpected floods, if through cryptic behaviour during periods of inactivity, they are occupying burrows, grass tussocks and rotten wood in tree stumps, where air pockets can persist during inundation (Hammond 1998). Andersen (1968) studied the response of riverbank beetles to rising floodwater and suggested that burrowing adults and larvae tend to remain in the substrate, however some adults are forced out of coarser substrates, where the current tends to be stronger. Cursorial species retreat up the bank as the flood advances.

There are two main strategies for dealing with contact with water: escape or survival of submersion. Joy (1910) studied the behaviour of beetles during flooding of main river channels and identified four types of active locomotion over the water surface to escape from submersion. Firstly, several species of rove beetles in the subfamily Steninae together with the ground beetle, *Paranchus albipes* (formerly in *Agonum*), can skim over the water surface. In order to do this they secrete a substance which lowers the surface tension behind them and propels them forward. Some species of *Stenus* together with several species of *Bembidion* swim with their legs, whereas other species of *Stenus* raise themselves above the water surface and walk. Joy also observed the rove beetle, *Gnypeta carbonaria,* raising itself above the surface with its abdomen held aloft like a sail to be propelled by the wind. This behaviour has also been observed in a species of *Myllaena* in Spain (G.N. Foster, pers. comm.). Andersen (1968) recorded two species of *Bembidion* flying from the water surface at temperatures above 25^{o} C and suggested that species of *Bledius* and *Gnypeta* can fly from the water at lower temperatures. Other rove beetle genera that can fly directly from the water surface include *Carpelimus, Thinobius* and *Ischnopoda* (Hammond 1998). When on the water surface, many beetles orientate themselves toward the largest dark object on the horizon which is usually the bank (Jenkins 1959, Andersen 1968). Zulka (1994) reported that some ground beetles associated with floodplains were relatively fast at reaching the bank when stranded on water.

Joy (1910) noted that several species of *Quedius* and many smaller rove beetles are very poor at moving in the water. Adults of these species and fenland beetles such as *A. thoreyi* and *Paederus riparius* can survive flooding by clinging to submersed vegetation and becoming torpid (Palmén 1945). In this state, they require less oxygen and can wait until the waters recede or they are passively deposited on a river bank. Palmén (1945, 1949) showed that many species can survive submersion in this way at least in cold water for long periods of time and similar results have been obtained for littoral species immersed in sea water (Elliott, King & Fordy 1983b). Escape from inundation as a strategic option is not available to eggs and pupae because of their immobility. Many insect eggs, even those of terrestrial species, use plastron respiration to extract oxygen from water during periods of submersion (Hinton 1961, Hammond 1998).

2.1.2 Body form related to locomotion and cryptic behaviour

Adult ground beetles show a variety of morphological adaptations to different lifestyles (Forsythe 1987). Evans (1990) classified ground beetles into three groups according to the anatomy of their legs, which suited them to different locomotor lifestyles. *Rapid runners* have long thin legs and are able to sprint over the surface, but they are weak at pushing against a force. *Strong wedge-pushers* have thicker legs and are slower runners, but their large hind trochanters enable them to push horizontally into crevices. *Powerful burrowers* have shorter legs still and so are much less mobile above ground. However, their powerful leg muscles enable them to burrow into the ground. Often the front tibia are flattened and equipped with teeth to facilitate digging and their bodies are elongate and pedunculate. Evans (*op. cit.*) found that most ground beetles were *strong wedge-pushers,* but noted the high numbers of *rapid runners* and *powerful burrowers* in riparian habitats where their adaptations are suited either to a cursorial or fossorial lifestyle in areas of bare sand. *Strong wedge-pushers* are suited to a compromise lifestyle and are equipped both for activity on the surface and also for pushing into hiding places at the end of activity periods. They are also well equipped for activity in deciduous litter which requires pushing against vegetative obstacles (Evans & Forsythe 1984). A remarkable morphological adaptation is exhibited by species of *Omophron* which have a leg structure similar to *rapid runners*, but the body shape of a dytiscid water beetle and this enables them to move through loose sand (Forsythe 1991). Andersen (1978) found that species of *Cicindela, Omophron* and *Bracteon,* which have long legs for running as well as the ability to burrow into sand, have similar modifications to the front tibiae.

A similar gradient in leg morphology can be seen in the rove beetles. Within the genus *Stenus*, agile species that run over the surface on bare substrates have longer legs and slenderer tarsi than species that climb plants or live in moist humus and plant debris (Betz 1998). In other genera, species of *Paederidus* and *Ischnopoda* have long thin legs and are often encountered running over bare sediments in riparian habitats. Coiffait (1972) referred to modifications of the front tibiae in fossorial *Bledius* and the non-British Osoriinae, which are short, broad and toothed. However, Herman (1986) observed that several species of *Bledius* excavate burrows with their mandibles rather than their legs, so these modifications may be an adaptation for moving through burrows rather than digging. Remarkably few, if any, authors mention the long thin body shape of rove beetles which would appear to be an adaptation for moving through fissures in the ground and tangled vegetation in litter and tussocks. It is also useful for sheltering in hollow plant stems during hibernation (Palmén 1949).

Andersen (1985a) divided Norwegian species of *Bembidion* into three groups according to their hind body shape. He found that flat parallel-sided species are confined to gravel or stone shores and banks, whereas more convex species, which tend to have more rounded elytra, live in more or less vegetated sites on fine sand, silt or clay. Species of intermediate morphology tended to occur on a wider range of substrate types. These results were supported by Desender (1989) in a study of seven Belgian species of riverbank *Bembidion*, who found a similar relationship between the convexity of body type and particle size of the preferred substrate type. Andersen (1985a) proposed that a flattened body-form in *Bembidion* is an adaptation for moving in a restricted environment under stones to find food and breeding partners. He lists several further beetles which are confined to coarse substrates and which have flattened bodies. These include ground beetles in the genera *Perileptus* and *Nebria,* and rove beetles in the genera *Thinobius, Hydrosmecta* and *Aloconota.* However this group exhibit a wide range of leg morphology and fall into several groups as classified by Evans (1990). Beetles such as *Nebria* and *Aloconota* have long legs which are adapted to running fast over the surface and which would be disadvantageous when moving through gravel or under stones. Possibly their flattened body shape is adapted less for activity in this environmental and more for hiding during periods of inactivity. Similar flattened body forms are also found in intertidal beetles that hide in rock crevices such as *Aepus robini* (King, Al-Khalifa & Fordy 1980), *Cillenus lateralis* (Elliott, King & Fordy 1983a) and *Micralymma marina* (Elliott, King & Fordy 1983b), while the elongated flattened body shape of some marshland beetles, such as *Dromius longiceps, Hygronoma dimidiata* and *Alianta incana* facilitates sheltering in the leaf sheaths of tall monocots.

2.1.3 Feeding

Species of ground beetles and rove beetles are traditionally regarded as predominantly predatory, although it is now recognised that many species are omnivorous (Lindroth 1949) and that some ground beetles predominantly feed on seeds, while some rove beetles feed on algae, fungal mycelia and other plant material (Good & Giller 1991). Good & Giller (1991) considered it likely that the extent of scavenging by rove beetles as opposed to predation had been underestimated in previous work. The same could be true for ground beetles. For example, the non-British ground beetle, *Oodes gracilis,* has been observed to attack only those insects that were severely injured (Lindroth 1942).

Hering & Plachter (1997) reported that scavenging the exuviae of aquatic insects, as well as preying on pre-emergent aquatic nymphs, was the prevailing food-gathering activity practised by riparian species of *Nebria* and *Bembidion* on exposed sediment by an alpine river. On streams in the same catchment, where this source of food was less abundant, terrestrial insects formed a larger proportion of the diet of *Bembidion* species, but it is not known whether these were obtained by predation or by scavenging surface drift. Aquatic Diptera and caddisfly larvae were also found to be an important dietary component for riverbank ground beetles in an American study (Hering 1998).

True predatory behaviour has been reported in several wetland species. Hunting springtails by sight during the day has been recorded in both ground beetles and rove beetles in the genera *Asaphidion* (Bauer 1985), *Elaphrus* (Bauer 1974) and *Stenus* (Betz 1999), whose species all possess large eyes. Wetland species of the rove beetle genus, *Quedius* also have large eyes and probably also hunt by sight. Several *Quedius* species have been observed by the author consuming smaller rove beetles in the collecting tube during sampling. *Asaphidion* and *Stenus* species stalk their prey with short punctuated walks or runs until they get within striking distance (Bauer 1985, Betz 1999). As well as using visual stimuli, *Stenus* species may use their antennae to identify prey items when within striking distance (Betz 1999). They sometimes make mistakes and strike at soil particles and other non-prey items which contrast against their background. *Stenus* species can secure their prey either by picking them up with their mandibles or by harpooning them with a sticky protrusible labium (Bauer 1991, Betz 1999), while *Loricera pilicornis* uses a setal trap on its antennae to capture springtails (Hintzpeter & Bauer 1986) and larvae of *Pselaphus heisei* and several other pselaphine species have a structure on the head which assists in capture of prey (De Marzo 1988). *Elaphrus* larvae hunt on the surface at night, but hide under the surface by day, thereby avoiding predation by conspecific adults (Bauer 1974).

Springtails probably provide an important source of food in a variety of wetland environments. They are reported as being taken by the fenland ground beetle species, *Demetrias imperialis* and *Odacantha melanura* (Lindroth 1949) and the intertidal beetles, *Aepus robini* and *Micralymma marina,* which feed predominantly on springtails in rock crevices (Doyen 1976, Glynne-Williams & Hobart 1952). They also constituted an important dietary component for *Agonum, Oxypselaphus* and *Pterostichus* species in a study of marshland ground beetles in Oxfordshire (Dawson 1965). Other important food items in that study included mites, Diptera and spiders and it is probably the case that most predatory wetland ground beetles and rove beetles are fairly catholic in their choice of food. Traditionally, rove beetles in the subfamily Pselaphinae have been regarded as specialist predators on mites (eg Koch 1990), but, in fact, many free-living species take a variety of prey (Chandler 1997). The large sea shore species, *Nebria complanata,* has been recorded feeding almost exclusively on amphipods, but in the laboratory it takes a variety of food and its dependence on amphipods is probably related to their abundance in its favoured habitat (Thiele 1977). Similarly, *Cafius xantholoma* preys largely on Diptera larvae and adults in wrack beds (Egglishaw 1965), but in the laboratory will also take beetle larvae and dead amphipods (Backlund (1945). The supposed specialist predation of *Dyschirius* species (Carabidae) on *Bledius* species (Staphylinidae) is probably also a result of sharing the same habitat (Herman 1986). Lindroth (1949) found no evidence of any enhanced ability to locate and prey on *Bledius* by *Dyschirius* species. In fact they are opportunistic feeders and various species have been recorded feeding on nematodes and beetles in the genera, *Carpelimus* and *Heterocerus*.

Specialised predation, therefore, appears to be rare among British wetland beetles in comparison with terrestrial species. The aleocharine tribe Lomechusiini contains 13 species of specialist ant predators in the British Isles, but apart from *Drusilla canaliculata,* a normally terrestrial species which is occasionally found in bogs, only one species, *Zyras collaris,* has a specifically wetland habitat. *Z. collaris* adults and larvae have been found in a nest of the ant, *Myrmica rubra,* in cut sedge litter (Donisthorpe 1927). The genus *Aleochara* contains 30 British species, whose larvae develop as parasitoids of various species of Diptera (Peschke & Fuldner 1977). Of these, four species attack flies in tidal wracks of seaweed (Scott 1916, Peschke & Fuldner 1977), while a fifth, *A. brevipennis,* is hygrophilous and partly associated with wetland habitats (Welch 1997). None of the beetle species that specialise in feeding on snails are particularly associated with wetlands. By contrast, wetland species constitute a large proportion of the British Sciomyzidae, a Dipteran family that are specialist predators and parasitoids of molluscs (Berg & Knutson 1978).

Several fossorial rove beetles living in sparsely vegetated damp sediments subsist predominantly on algae. Algae form most if not all of the diet of *Bledius* and three coastal

Carpelimus species (Bro Larsen 1936, Herman 1986), and it has been suggested that the same is probably true for *Thinobius* species as well (Hammond 1998). There are conflicting reports on whether *Diglotta* species are predatory or algal grazers (Good 1998). The littoral species, *Bledius furcatus* and *B. diota* collect and store algae after rain when the salt content is lower in order to reduce problems associated with osmoregulation (Bro Larsen 1952). Rove beetles in other wetland habitats can also be vegetarian. *Eusphalerum* species feed on pollen as adults (Klinger 1983) while *Anotylus* species appear to be saprophagous (Hammond 1976, 2000). Fungus-feeders are not well represented in wetlands. Only two of the 20 British species in the fungus-feeding subtribe Gyrophaenina and single species of *Micropeplus* and *Sepedophilus*, can be regarded as wetland species. However, it seems likely that omnivorous species in the subfamilies, Proteininae, Omaliinae and Aleocharinae include fungal mycelia in their diet.

2.2 Life histories

2.2.1 Breeding season

In temperate regions, ground beetles undergo one generation per year, and generally either breed in the spring and overwinter as adults, or breed in the autumn and overwinter as larvae (Larsson 1939, Thiele 1977, den Boer & den Boer-Daanje 1990). In wetlands, many individuals die after breeding (Krogerus 1948), but some *Agonum* species can survive for longer than one year and breed for a second time (Wasner 1979).

Lehmann (1965) found that in ground beetle assemblages along the banks of the Rhine, *autumn breeders* predominated in woods and meadows above the riverbank but in areas regularly inundated by the river they were almost entirely replaced by *spring breeders*. The only *autumn breeder* present on the bank was *Amara fulva*, which was confined to the topmost zone. Lehmann reviewed faunal lists of riverbank ground beetles from Scandinavia and found that they were composed almost entirely of *spring breeders*. He attributed the scarcity of *autumn breeders* to the difficulty of their larvae in escaping the effects of high winter flows. A similar pattern is found in other types of wetlands. Murdoch (1967) studied the life histories of 21 wetland ground beetles in marshes in Britain and found that all but one are *spring breeders*. Furthermore he examined data on Scandinavian ground beetles and found that only 11 out of 124 hygrophilous species were *autumn breeders*. Like Lehmann he suggested that larvae are vulnerable to inundation during the winter, whereas adults can escape more easily into hibernation quarters. However, the proposed vulnerability of larvae to flooding does not explain the preponderance of *spring breeders* along the banks of the Rhine (Lehmann 1965) and rivers in Norway (Andersen 1969) whose seasonal high water levels occur in the spring or early summer when the larvae are present along the bank. Lehmann's suggestion that the majority of larvae along the Rhine are killed each summer and that populations are sustained by annual immigrations each spring implies that the banks of the Rhine act as a huge mortality sink for local riparian populations and seems implausible. Furthermore, Andersen (1968) reported high survival rates of eggs, larvae and pupae during submersion and even recorded a higher survival rate for larvae than adults. Adis & Junk (2002) suggested that life cycle adaptations provided useful survivorship strategies in areas such as central Amazonia, where there is a predictable monomodal flood pulse, than in central European lowland rivers where flooding is more unpredictable and survivorship strategies rely more on opportunism.

There are some wetland species which overwinter as larvae. *Nebria gyllenhali, Bembidion lunatum* and *Trechus secalis* are classified by Andersen (1969) as exclusively *larval hibernators*. In addition the reproductive cycles of wetland ground beetle species are not always constant. Meissner (1983) reported that a population of *Bembidion femoratum* by a German gravel pit was sexually active all year round and egg laying occurred over a long period from March to September. Andersen (1969) recorded teneral adults of several riparian species of *Bembidion* in early spring suggesting occasional larval or pupal overwintering. He also found that *Asaphidion pallipes* hibernates commonly as both larvae and adults. In Britain, the coastal species, *Nebria complanata*, is active throughout the summer, but further south around the Mediterranean it undergoes a summer diapause (Colombini & Chelazzi 1991).

It is not known whether the domination of *spring breeders* amongst wetland ground beetle assemblages is reflected amongst rove beetles. Methodically collected information on rove beetles is lacking, although Horion (1963, 1965, 1967) gives records of many wetland species overwintering as adults. On the other hand Steel (1970) reported that species of *Lesteva* breed in autumn and overwinter as larvae. He also found larvae of the riparian species *Geodromicus nigrita* in September and October but suspected that it hibernated in the adult stage. It has been suggested that *Micralymma marina* may overwinter as an egg (King, Fordy & Al-Khalifa 1979). It is possible that a wider range of life cycles remains to be discovered among rove beetles. Bordoni (1982) mentioned that some Oxytelinae and Aleocharinae have three generations per year. Herman (1986) quoted reports of two or more breeding periods in Danish and Japanese species of *Bledius,* but it is unclear whether this is due to more than one generation per year or a prolonged breeding season of a single generation.

Evidence of breeding in wetland environments has usually relied on examination of the female ovaries or the presence of teneral adults (eg Dawson 1965, Kurka 1975, 1976) However Krogerus (1948) included field observations of developmental stages when he studied the riparian insect fauna of a Finnish lake, whose seasonal water levels were affected by snow-melt. His study describes how the life histories of a riparian beetle assemblage are adapted to exploiting a resource provided by substrates exposed by seasonal fluctuations in water level.

The ground beetles were nearly all *spring breeders* (except *Oxypselaphus obscurus & Amara brunnea*) but did not arrive at the breeding site until late May or June. Numbers built up very quickly with strong migrations from hibernation sites on the warm days. Some species arrived one week later than others. Young larvae first appeared in June close to the water margin. As the water level dropped, the adults moved with it and most died off several weeks later. The larvae lived deep within the soil and did not move from a zone which became progressively drier and more remote from the water margin. By July remaining adults were concentrated near the water's edge, young larvae were found higher up the bank and older larvae were found higher still. Pupation took place in flat depressions on mud under a thin layer of moss. Adults emerged from their pupation site in August. Mass emergences often followed heavy rain. The teneral adults hardened up in dry areas high up on the bank and then moved down to the water margin before migrating to hibernation sites in September. No further breeding took place at this time. There were annual fluctuations in the timing of these events which were related to weather conditions.

Published observations of oviposition and pupation sites are rare. Andersen (1978) observed *Bracteon argenteolum* in the laboratory ovipositing in burrows excavated in sand whereas

Bembidion schuppelii and *B. semipunctatum* oviposited in natural crevices. Field records of wetland rove beetle larvae and pupae are very scarce. Welch (1965) reported finding two pupae of *Stenus canaliculatus* in soft rotten timber beneath the bark of a fallen willow on the muddy banks of a stream.

2.2.2 Hibernation

Interest in the hibernation sites of riparian beetles has been generated by observations of their absence from their breeding habitat during the winter. For example, Palmen & Platanoff (1943) found that the summer fauna of Karelian riverbanks disappeared in mid September and returned suddenly in mid May. In Krogerus' (1948) study of a Finnish lake shore assemblage of ground beetles and rove beetles, most species were found in large numbers above marginal areas in leaf litter in sallow scrub in the winter. Only a few species were found by the water's edge and these were often washed up into the sallow scrub by winter floods. Some species were never found in winter and must have overwintered at some distance from the lake. There were fewer species in this group but they included many of the larger species. Krogerus reported isolated instances from elsewhere in Finland of some of these species (*Blethisa multipunctata, Pterostichus minor. P. nigrita & Agonum versutum)* being found in leaf litter around 1km from the nearest wetland. In Sweden Lindroth (1942) concluded that the ground beetle, *Oodes gracilis,* flies some distance from its summer habitat in order to hibernate.

Palmen (1945) observed that some shore habitats such as extensive reedbeds growing in shallow water do not lose their summer fauna in the winter. He investigated overwintering in six beetle species which spent the summer in a reedbed growing in the shallow margins of an almost freshwater inlet of the Baltic and found that *Agonum fuliginosum* moved higher up the bank to an area dominated by sedge during the autumn. However, there was no sudden emigration as had been reported by Palmen & Platanoff (1943). There was also a partial migration of the rove beetle, *Paederus riparius,* to the sedge zone. The other species investigated together with some *Paederus riparius* stayed throughout the winter in the inundated reedbed. Several small species including many rove beetles were found sheltering in hollow reed stems in ice (Palmen 1949). Laboratory experiments suggested that the presence of litter is important in enabling many beetles to survive freezing conditions underwater (Palmen 1945, 1949). Species of marsh *Agonum* and *Pterostichus* in Oxfordshire were found hibernating in rotten logs and grass tussocks on site, although some individuals washed out by winter floods moved to grass tussocks in surrounding grassland (Murdoch 1966).

Andersen (1968) investigated hibernation sites on rivers in Norway where winter water levels are not the highest of the year. He found that many species (several species of *Bembidion* and many rove beetles including *Bledius* species) overwintered close to their breeding grounds, albeit slightly higher on the riverbank. There is evidence that some of these species may change their hibernation site in the event of flooding. He also found overwintering larvae of the ground beetles, *Nebria rufescens* and *Bembidion lunatum* on the riverbank. Andersen suggested that *Bembidion semipunctatum* and *B. quadrimaculatum* hibernate in areas adjacent to the riverbank and that other species of *Bembidion* together with many rove beetles that probably hibernate as adults (species of *Ochthephilus, Thinobius, Stenus, Ischnopoda* and *Gnypeta*) fly to hibernation sites more distant from the river.

Similar variations in hibernation strategies are reported from elsewhere. *Paranchus albipes* was found to be absent from the banks of mountain streams in Bohemia between late October and mid March (Kurka 1976), whereas *Bembidion tibiale* was present on gravel deposits all year round (Kurka 1975). Four species of *Bembidion* (*B. ascendens, B. conforme, B. andreae* and *B. tricolor*) have been captured hibernating in traps filled with coarse sediment buried at depths of up to 75 cms in gravel bars by the River Isar in Germany (Dieterich 1996). Bauer (1974) found that in Austria *Elaphrus cupreus* and *E. riparius* moved away from the water to find dry ground into which they dug several centimetres in order to pass the winter. He found no evidence of long-distance flight to hibernation sites remote from the river as suggested by Krogerus (1948). The rove beetle, *Platystethus cornutus,* has been found hibernating in large numbers in woodland leaf litter over 100 metres from the margins of a reservoir where it had presumably bred (Lott 2001). Meissner (1983) found that *Bembidion punctulatum* and, to a minor degree, *B. femoratum,* undertook seasonal migration flights over long distances between their breeding sites by a German gravel pit and their hibernation sites which were suspected to be hedges and woodland edges.

The available information on hibernation for wetland beetles including those of open shores suggests three hibernation strategies.

1) Beetles can stay at their breeding sites and cope with winter conditions.
2) Beetles can move to adjacent areas to escape winter inundations. This can be accomplished either actively or passively in flood debris (Joy 1910).
3) Beetles can migrate to hibernation sites well away from the river.

Individual populations may adopt more than one strategy (Palmen 1945).

2.2.3 Dispersal

On the basis of three decades of pitfall trapping and window trapping in the Netherlands, den Boer (1990) considered that a dispersal phase amongst ground beetles was the rule rather than the exception. He suggested that some species, especially the larger ones, disperse by walking, but that individuals from many macropterous and wing-dimorphic species disperse by flight to new breeding sites after emergence from the pupa. Lindroth (1949) reviewed flight records of Scandinavian ground beetles and found that for *spring breeders* there was a peak of activity in the spring suggesting that dispersal takes place between hibernation and breeding. Many rove beetles also disperse by flight. Bauer (1989) found a high incidence of vagrant species in an upland site in northern England and Lindroth (1949) quotes a report that rove beetles were the most abundant beetle family in high altitude aerial plankton. There are numerous records of vagrants belonging to wetland species turning up in terrestrial habitats outside their normal geographic range (see eg Allen 1972, Wright 1990, Lott & Daws 1996) and these are presumably the result of long-distance dispersal flights aided by high altitude air currents.

There has been plenty of speculation that riparian beetles need to be good dispersers in order to recolonise riverbanks after flooding (Lindroth 1949, Lehmann 1965, Holeski 1984). Rehfeldt (1984) looked at the characteristics of ground beetles in several different habitats in a river valley in Lower Saxony and found that riverbanks contained a high proportion of both diurnal species and macropterous species. He suggested that macroptery in riparian ground beetles enabled them to colonise new habitat structures created by flooding. This hypothesis is supported by a tendency in some wing-dimorphic species for macropters to predominate in frequently flooded habitats and for brachypters to predominate in more stable habitats (Adis & Junk, 2002). In fact, macroptery is prevalent in most wetland environments. Around 83% of British ground beetles that are more or less restricted to wetland habitats are constantly macropterous according to information provided by Luff (1998), while over half the remainder have wing-dimorphic populations. In comparison, only 67% of strictly non-wetland species are constantly macropterous. However, several common wetland beetles, such as *Agonum fuliginosum, Lesteva sicula* and *Stenus boops,* are represented in most field samples entirely by short-winged specimens, even though their widespread distribution in the countryside would suggest that they are efficient dispersers. Despite their scarcity in pitfall trap samples, den Boer (1977) found that full-winged specimens of *Agonum fuliginosum* turned up frequently in window traps and it is possible that flight is a dispersal mechanism used by many species, even when their populations are predominantly short-winged.

It has been suggested that flight is a risky means of dispersal for coastal insects that could get blown out to sea or inland where suitable habitat is absent (Foster 2000). Winglessness is found in a high proportion of beetles living on rocky shores including *Aepus* species (Doyen 1976) and *Micralymma marina* (King, Fordy & Al-Khalifa 1979). Three nocturnal, flightless rove beetles live on sandy beaches in southern California (Moore 1975) and European rove beetles in the fossorial genus *Diglotta,* are wing-dimorphic. Wingless populations are found on more eposed sandy shores, while winged morphs are found by more sheltered estuaries (Lohse 1985). However, many species of sandy shores, saltmarshes and wrack beds are thought to use flight for dispersal as well as to escape danger (Hammond 2000).

2.3 Habitats

2.3.1 Typology

The variations in morphology, physiology, behaviour and life history outlined above can be viewed as adaptations to specific habitats in the environment. These habitats have usually been described qualitatively in traditional terms of habitat structures and vegetation communities such as fen, riverbanks, mammal nests etc. (eg Koch 1989, 1990). Quantitative assessments of the requirements of species in terms of physical and chemical factors such as temperature, humidity, salinity, soil particle size etc. (eg Lindroth 1949) are less common. No standard habitat classification has been successfully applied to wetland beetles, although several physical and vegetational features, such as exposed riverine sediment, seepages on soft-rock cliffs, tidal wrack beds and *Sphagnum* moss, have been recognised as habitats for a good number of characteristic species.

Studies of non-aquatic beetle habitats in fen, carr and marsh are surprisingly scarce. The distribution of species of ground beetles between different vegetation communities has been studied by Dawson (1965) and Landry (1994). At a microhabitat scale Dawson (1965) found variations between species of ground beetle in their occupation of different layers in fen, ranging from the soil through litter to low vegetation. Several species were abundant in a range of small scale habitat structures, but some species of *Agonum* preferred litter piles, while some species of *Pterostichus* preferred soil. She referred to the fact that *P. strenuus* and *P. diligens* are rarely found together, because the former species favours mineral soils, while the latter favours peat. Similarly, Landry (1994) found that some species of *Agonum* in Canadian marshes occurred across a range of microhabitats, while others were strongly associated with particular microhabitat structures such as emergent tussocks and concentrations of dead vegetation. A number of fen rove beetles, such as *Gymnusa* species, are often quoted as being associated with wet *Sphagnum* moss, although they are also occasionally found in other microhabitats. Similarly, the marsh rove beetle, *Alianta incana,* is said to be associated with *Typha*, but this could reflects the domination by this plant of its favoured habitat, tall emergent vegetation on mineral soils.

Hammond (1998) included riverine fen as a habitat of floodplain arthropods in a review that drew heavily on work carried out on beetles. Exposed riverine sediments, eyots (mid-channel islands) and wooded floodplains were also described as distinctive habitats characterised by ground beetles and rove beetles.

Habitat studies on exposed riverine sediments are relatively numerous, especially for ground beetles. Many authors have stressed the importance of substrate particle size in determining the presence of particular species of ground beetles (eg Palmen & Platanoff 1943, Andersen 1969, Reid & Eyre 1985, Desender 1989, Gerken *et al.* 1991, Hammond 1998, Sadler & Petts 2000). The vast majority of work on microhabitat preferences for riparian beetles has been done on active adults, although Andersen (1969) noted that larvae of *Bembidion* species had stricter microhabitat preferences than adults. Andersen (1969, 1983) described a number of different microhabitats using a wide range of environmental factors including height on bank, substrate particle size and organic content, vegetation cover, shade and presence of litter. He found that many species of Norwegian *Bembidion* were present in high numbers at only one or a few microhabitats, although a few species seem to change their microhabitat preferences from site to site. Similarly, in a Bavarian study, a large proportion of shingle bank ground beetle species were collected mainly in one of four microhabitats classified by distance from water and vegetation cover (Plachter 1986). Along the Weser, the activity of *Bembidion decorum* and *B. punctulatum* was found to be mainly confined to sparsely vegetated, coarse substrates, whereas *Bembidion articulatum* was active over a wide range of substrate particle size and percentage vegetation cover (Gerken *et al.* 1991). Species abundances also vary between lateral zones on the banks (Lehmann 1965) and between banks of different gradients (Palmen & Platanoff 1943). Bauer (1974) regarded shade as an important factor in separating the habitats of *Elaphrus cupreus* and *E. riparius.*

In laboratory experiments Andersen (1978) and Meissner (1984) found that several species of *Bembidion* preferred substrates of a certain particle size, but that their preferences were often affected or overridden by differences in moisture. Substrate preferences can also be affected by the presence of other species (Sowig 1986). Laboratory experiments also show that temperature and humidity responses vary with time and the physiological state of the beetle (Andersen 1985b, 1986). Evans (1988) found that riparian ground beetles are attracted to volatile chemicals collected from microflora associated with their habitats in the field and suggested that they use them to locate suitable microhabitats.

Apart from exposed sediments, other habitats associated with flowing water include wet moss by fast-flowing streams and waterfalls (Hammond 1998), while *Bembidion fluviatile* is normally found on eroding banks. Many riverbank species, such as *Bembidion atrocoeruleum, Geodromicus nigrita, Dianous coerulescens* and *Aloconota currax* are found both on coarse sediments and in wet moss. Two rove beetle species, *Lesteva sicula* and *Quedius maurorufus,* are found both in wet moss by streams and in fen.

Boyce (2002) listed invertebrate species associated with seepages, defined as very small flowing waterbodies fed by springs. Five separate habitat types were recognised: slumping cliff seepages, stable cliff trickles, woodland seepages, acid-neutral flushes and calcareous flushes. Ground beetles and rove beetles form a significant proportion of the species listed with slumping and stable cliffs as habitat. Several species associated with cliff seepages, such as *Scopaeus sulcicollis* and *Chlaenius vestitus* are also found in riparian habitats by larger waterbodies, while species found in flushes are often more widely distributed in fens and marshes.

Just as in the riparian environment inland, so on seashores, individual beetle species are often specific in their choices of substrate particle size and many species are restricted either to rocky shores, sandy beaches or mud flats (Doyen 1976, Moore & Legner 1976). Many intertidal species are restricted to a specific zone between mean low water and the reach of the highest tides (Glynne-Williams & Hobart 1952). In California, Moore and Legner (1976) recognised three zones within each substrate type which were occupied by different species of rove beetles. Accumulations of seaweed and other detritus deposited on the high tide line and known as wrack beds constitute the habitat of several rove beetles as well as other arthropods (Backlund 1945, Egglishaw 1965, Hodge & Jessop 1996).

Many riparian species are attracted to artificial habitats, such as gravel pits (Koch 1977, Plachter 1986, Gerken *et al.* 1991, Hammond 1998), sludge-drying beds (Green 1983), sewers (Hammond 1998), silage silos (Anderson 1986), compost heaps and arable fields. Indeed, some species, notably *Carpelimus fuliginosus* and *Neobisnius lathrobioides*, whose natural habitat is riparian, appear to occur predominantly or even exclusively in compost heaps in Britain. However, it is likely that many species recorded from artificial habitats are still dependent on natural habitats for sustaining their populations in the longer term. Gravel pits, for example, will only provide suitable habitat for early successional species for a limited period without intensive management of the site.

2.3.2 Stenotopy and eurytopy

In a series of laboratory experiments Lindroth (1949) showed that several Fennoscandian ground beetles traditionally regarded as limestone grassland species should more accurately be described as thermophilic and xerophilic. Lindroth concluded that the decisive influences on the local distribution of ground beetles are local climatic factors and soil factors, both physical and chemical.

Lindroth's analysis has implications for the concept of a stenotopic species. For example, ground beetles characterised as riverbank species may not be obligate riverbank-dwellers. They may be species whose physical and chemical requirements are matched by the combination of local climatic and edaphic factors found in the riparian environment. This hypothesis is supported by the fact that many species characteristic of open exposed riverine sediments are also found on similar artificial structures such as gravel pit margins (see above) or on similar natural structures such as lake margins and sea shores (Andersen 1969, 1983). Superficial differences in occupied habitat structures may sometimes mask a similarity of environmental conditions. Furthermore the same environmental conditions may be provided by different habitat structures in different regions. Table 3 shows the variation in habitat structures occupied by three species of ground beetle in Britain, Holland, Scandinavia and Central Europe. Similar variations are found in the rove beetles. For example, *Scopaeus laevigatus* is characteristic of riverbanks and associated wetlands in Central Europe (Koch 1989) and Spain (Lott, personal observation) but is one of a group of such species which have only been recorded in Britain from beside trickles on collapsing sea cliffs along the south coast (Boyce 2002).

In northern Norway, Andersen (1983) found a wide variation in the degree to which species of *Bembidion* were restricted to riverbanks. Some species were mainly confined to one type of river, whereas four species occurred in a wide range of sites including those away from water. He also reported that, although *Bembidion lunatum* was confined to sites by flowing water in northern Norway, it occurred in a wider range of sites including gravel pits and roadsides in central Norway. Palmen & Platanoff (1943) characterised beetle species along riverbanks in southern Karelia according to their habitat preferences within the region. 63 species were mostly confined to riverbanks and were described as stenotopic species. Eurytopic species were defined as those found in other damp habitats such as lake margins and woodland pools. However, Lindroth (1949) found that their list of eurytopic ground beetle species contained several which are regarded as stenotopic riverbank species in Sweden and other parts of Finland and suggested that a species is often more stenotopic at the edge of its range. The same arguments can be applied to rove beetles and to other wetland types, where variations and imprecision in definitions of habitat structure, such as fen, can bring additional problems to bear. At the edge of its range in Britain, the rove beetle, *Stenus kiesenwetteri,* is restricted to *Sphagnum* moss in bogs, but elsewhere it is simply highly hygrophilous (Smetana 1995).

These arguments show that the designation of a species as stenotopic or eurytopic has only local validity because a species' occupancy of habitat structure types may vary between regions. Furthermore these terms are subjective in that they are relative to the range and classification of habitat structures selected for analysis. The categorisation of species as eurytopic is effectively based on the number of *a priori* selected habitat structures occupied by the species, but these habitat structures may be unevenly distributed along the natural environmental gradients which are important to beetles. Eurytopy in this sense is therefore not necessarily related to true ecological amplitude. However, although the characterisation of wetland species as stenotopic may lack ecological validity, it could have some use in conservation work because it reflects the way that the landscape is divided up for land management.

Table 3. Regional variations in the occupation of habitat structures by three species of ground beetles

Species	Britain	Holland (Turin *et al.* 1991)	Central Europe (Koch 1989)	Scandinavia (Lindroth 1985)
Elaphrus riparius	barren sand or clay by freshwater (Lindroth 1974)	young moist habitats in polders and other colonisation sites	sunny sand and mud banks, brickpits	banks of standing or slow-running waters in open country
Clivina collaris	sandy soils usually near rivers (Luff 1998)	open localities, predominantly riparian	open sand and gravel banks	cultivated areas with humus-rich soil
Bembidion schuppelii	on damp fine sand and silt or fine shingle with 50-100% cover of low herbage on riverbanks (Reid & Eyre 1985)		shaded muddy banks of woodland pools	on moist silty vegetated riverbanks

2.3.3 Scale

Luff (1966) defined microhabitat as *the minimum part of the ecohabitat which supplies the requirements of the species in its particular physiological state at that time.* Information on the life histories of wetland ground beetles suggests that they could potentially have five different microhabitat requirements at different life stages, namely larva, pupa, teneral adult, hibernating adult and active adult. Furthermore breeding and feeding adults restrict their activities to different times of the day (Thiele & Weber 1968) and may use different microhabitats when resting and when active. By extending Luff's definition of microhabitat we can regard the ecohabitat (usually loosely referred to as habitat) of an organism as *the sum of all the microhabitats required to complete its life cycle.* These definitions fit use of *habitat* as an autoecological term to describe the interaction of a species with its environment (Samways 1994).

The term *macrohabitat* has been applied by some authors to riverine habitats at the landscape scale (Spence 1977, Andersen 1983). A definition of a species' macrohabitat to match other definitions given above would be *a landscape that can sustain a population of the species over an extended period of time.* Implicit within this definition, is the idea that a species can migrate from habitat to habitat within its macrohabitat and found new meta-populations. There is evidence that land use changes can affect the sustainability of populations of terrestrial ground beetle species in a landscape, in which its habitats become increasingly isolated (den Boer 1990). Because of their presumed higher powers of dispersal, it might be argued that a smaller proportion of wetland beetles should be sensitive to habitat fragmentation. However, the role of large-scale fluvial and coastal processes in shaping disturbance regimes and habitat structure distribution suggests that macrohabitat may be relatively important for wetland beetles. Fowles (1989) found that some species of ground beetles had an uneven longitudinal distribution on shingle banks along the River Ystwyth in Wales. *Bembidion punctulatum* was confined to the lower mature stretches whereas *Bembidion tibiale* was mostly restricted to the higher stretches and smaller tributaries lower down. Similarly in a study of ground beetles on gravel banks along the River Isar in Bavaria Plachter (1986) found that alpine and subalpine species were concentrated in the upper stretches although they were present in smaller numbers on gravel banks as far as 110 km north of the mountains. He reported that species confined to lower levels tended to be more eurytopic. Andersen (1983) found that several species were mainly found by rivers of a certain size category.

The majority of habitat studies on wetland ground and rove beetles have been carried out on microhabitats. Moreover, these studies have been concerned more or less exclusively with active adults. Although these studies throw valuable light on the utility of various species' adaptations, it is clear that more work on habitats at a larger scale could be very productive in achieving a more balanced picture of the habitat requirements of wetland beetles.

2.3.4 Habitat templets

In recent decades much progress in ecological theory has arisen from attempts to find a predictive relationship between habitat and species traits such as life history strategies. Southwood (1977) proposed that habitat acted as a templet which selected certain species traits. Southwood (1988) attempted to unify four major theories linking habitat and species traits and identified a habitat type in which growth potential or productivity is high, disturbance is low and interactions with other organisms (eg competition) is high as a common feature to all theories. Habitats deviate from this condition along three main axes related to disturbance, adversity (sometimes interpreted as environmental stress) and degree of biotic interaction. Consequently it is predicted that highly disturbed environments will favour r-selected organisms which invest a large proportion of their resources in reproduction and dispersal, whereas stable environments favour K-selected organisms which invest a large proportion of their resources in survivorship.

Habitat templet theory should be particularly applicable to ecological studies of wetlands, where different patterns of flooding will give rise to variations in disturbance regimes. In relatively stable habitats such as fens, we might expect K-strategists to predominate, whereas r-strategists should favour highly disturbed sites. To date, the application of habitat templet theory to wetland invertebrates has concentrated on aquatic groups (eg Townsend & Hildrew 1994, Resh *et al.* 1994).

Holeski (1984) suggested that all shore beetles are r-strategists, because they are frequently required to recolonise their sites after flooding. Similarly Adis & Junk (2002) proposed that r-strategists were well placed to exploit habitats provided by unpredictable flooding in large, lowland floodplains. Southwood (1977) stressed the importance of comparing intervals between disturbances with organisms' generation times. Consequently, Lott (1999b) concluded that very few species of ground beetles and rove beetles subject to natural flooding disturbance by the River Soar in Leicestershire were likely to be r-strategists, because flooding is too frequent in comparison with their annual life cycles. He suggested that in order to survive flooding, these species probably rely more on morphological and behavioural traits such as the ability to burrow or shelter in tussocks, rather than life history traits such as dispersal by flight to new areas. They are therefore better regarded as A-strategists (Greenslade 1983) that commit themselves to a survivorship strategy appropriate for dealing with environmental stress or adversity. However, recently reprofiled riverbanks along certain stretches of the Soar as part of flood alleviation works did attract several species absent or rare on naturally disturbed sites and it was suggested that these could be r-strategists acting as pioneer species dispersing to new sites. Some of these r-strategists, such as *Bembidion articulatum* and *B. genei,* are characteristic of other artificially disturbed sites such as gravel pits in Leicestershire, while others such as *Bledius pallipes* are much more widespread on the banks of the River Trent, a larger river 10 to 20 kilometers away. True r-strategists may be more successful along large rivers such as the Trent, and coastal sites, where large scale, severe flooding disturbances with periods greater than a year take place. In this context, it is interesting to note the results of Koch's (1977) study of gravel pits in the Rhine valley. Some species were capable of colonising pits up to 10km from their natural habitat, but others were restricted to pits closer to the main channel. This gradient in dispersal ability could be interpreted as variations in commitment to a r-strategy.

2.4 Species assemblages

2.4.1 Species composition

Multivariate analysis has been used widely to explore the relationship between environmental variables and the species composition of ground beetle assemblages. The most important axis of variation identified through ordination is invariably linked to a moisture gradient that separates dry habitats from wet habitats in both general studies covering all habitats (Day 1987, Luff, Eyre & Rushton 1989, Turin *et al.* 1991) and in studies specific to grassland (Eyre & Luff 1990, Eyre, Luff & Rushton 1990) and floodplains (Šustek 1994).

Consequently, we can conclude that wetland ground beetle communities are substantially different in their species composition from communities in dry biotopes. There is, of course, no clear separation between these communities and intermediate assemblages can be found for example in damp grassland. Equivalent studies are largely lacking for rove beetles, although an ordination of rove beetle assemblages in conifer plantations in Northumberland identified soil moisture as the second most important environmental gradient after altitude (Buse & Good 1993).

Similar studies that are more specific to wetlands are listed in table 4. Flooding is invariably identified as an important environmental gradient in river floodplain studies, but the complexities of flooding regimes has resulted in different interpretations of the important hydrological factors affecting species composition. Flooding was found to be the major factor determining ground beetle species assemblages at five sites in the floodplain of the Morava River in Austria (Zulka 1994). Similarly, Šustek (1994) separated flooded sites from non-flooded sites in a study of 26 sites in Slovakian floodplains, but also identified important variations in species composition between assemblages from oligotrophic sites flooded by fast-flowing water and eutrophic sites flooded by stagnant water. In addition, significant differences were found between assemblages in sites flooded only in early spring and those in sites flooded more frequently. In Leicestershire, Lott (1999b) identified severity of disturbance by flooding as the most important environmental gradient influencing mixed assemblages of ground beetles and rove beetles. On the most important axis of variation, unvegetated main channel sites on coarse substrates were separated from floodplain wetland sites with coarse organic matter incorporated into the substrate. It was found that grazing by cattle affected species composition in the same way as flooding and represented a similar short period disturbance that removed vegetation and litter and perturbed the substrate through trampling. The second most important gradient was related to seasonal fluctuations in water levels in floodplain sites. On axis 2, a small number of permanently wet fen and flushes were separated from seasonal pools in abandoned channels. These gradients were fitted to a successional model for floodplain wetlands, with axis 1 representing a transition from an early successional stage to fen, while axis 2 represented a transition to a carr-like stage in the process of terrestrialisation. Fluctuations in water level were also associated with the second most important axis of variation in an analysis of beetles sampled from over 100 ponds across lowland England (Lott 2001). It was concluded that the fauna of temporary ponds was not a specialist fauna, but one associated with sediment exposed by fluctuating water levels. Broader hydrological factors have also been identified as important environmental variables in studies on Welsh peatlands (Holmes, Boyce & Reed 1993) and East Anglian fens (Lott, Proctor & Foster 2002). The investigation of the significance of more precise hydrological factors should prove to be a fertile area for further research.

The importance of sediment particle size in exposed riverine sediments, previously identified by habitat studies on individual species, has been confirmed by a number of multivariate analyses of both ground beetle assemblages (Desender *et al.* 1994, Eyre, Luff & Phillips 2001) and assemblages of ground beetles plus other beetle families (Lott 1999b, Sadler & Petts 2000). Vegetation cover, which is often correlated with sediment particle size, has also been identified as important in several studies (Desender *et al.* 1994, Lott 1999b, Eyre, Luff & Phillips 2001). It is interesting that preliminary work on rove beetle assemblages points to larger scale factors such as catchment elevation and position within the catchment being more important than microhabitat features (Eyre, Lott & Luff 2001). Work at larger scales would appear to be a fruitful area of study for both ground beetles and rove beetles.

Multivariate techniques have also been applied to the effects of wetland management on species assemblages. Both long term and short term responses to the reprofiling of riverbanks along the River Soar were detected by Lott (1999b). River management probably influences exposed sediment assemblages considerably, but it is important to realise that different types of management can have conflicting effects (Eyre, Luff & Phillips 2001). For example, impoundment and canalisation will reduce the frequency of spates and favour species associated with soft sediments, whereas channel straightening will increase the frequency of spates and may favour species associated with coarse sediments.

Sensitivity to grazing has been detected in assemblages on exposed sediments (Lott 1999b), floodplain wetlands (Lott 1999b), fens (Lott, Proctor & Foster 2002) and Welsh peatland (Holmes, Boyce & Reed 1993). Mowing and grazing have been found to have different effects on the species composition of fenland beetle assemblages (Lott, Proctor & Foster 2002).

Multivariate analyses of coastal wetland beetle assemblages are rare. In a preliminary study on saltmarsh ground beetles in north-east England, Luff & Eyre (2000) found that species assemblages were dominated by generalists. Low species diversity and large within-site variations were other features reported.

Several of the studies referred to above have attempted to classify assemblages and link them to habitat types (see also Coulson & Butterfield 1985, Eyre & Luff 2002). These classifications can rarely be applied outside the context of the original study (Holmes *et al.* 1993) and it is therefore difficult to envisage how they can be useful either in understanding broad ecological principles or in deciding general priorities for nature conservation. Gradient analysis would appear to hold more potential for detecting how wetland beetle communities respond to the hydrological factors and disturbance regimes that characterise wetland ecosystems.

Table 4. Studies of wetland beetle assemblages using multivariate analysis. (ERS = exposed riverine sediments)

Taxonomic group	Wetland habitat structure	Geographical area	Reference
Carabidae	Fen and bog	Wales	Holmes, Boyce & Reed (1993)
Carabidae	ERS	Grensmaas, Belgium	Desender *et al.* (1994)
Carabidae	Floodplain wetlands	Danube, Morava & Dyja rivers, Slovakia	Šustek (1994)
Carabidae, Staphylinidae, Heteroceridae & Elateridae	ERS & floodplain wetlands	River Soar, Leicestershire	Lott (1999b)
Carabidae	Saltmarsh	NE England	Luff & Eyre (2000)
Coleoptera	ERS	England & Wales	Sadler & Petts (2000)
Staphylinidae	ERS	Scotland & N. England	Eyre, Lott & Luff (2001)
Carabidae	ERS	Scotland & N. England	Eyre, Luff & Phillips (2001)
Carabidae & Staphylinidae	Ponds	lowland England	Lott (2001)
Carabidae & Staphylinidae	Fen	East Anglia	Lott, Proctor & Foster (2002)

2.4.2 Species diversity

A number of studies of floodplain ground beetles have compared the species diversities of different assemblages (Holeski & Graves 1978, Jarosik 1983, Rehfeldt 1984, Vitner & Vitner 1986), but the results were not discussed in any theoretical context. Significantly lower species diversities at grazed sites and sites subject to natural flooding were found in the Soar Valley study (Lott 1999b), while species diversity has been found to increase significantly when sedge or reed cutting is introduced to previously unmanaged fens in East Anglia (Lott, Proctor & Foster 2002). These results would appear to fit the intermediate disturbance hypothesis which predicts low species diversities at high and low levels of disturbance. However, because disturbance by grazing and flooding along the Soar has a shorter period than the length of one generation, the first result does not fit the underlying model based on life-history adaptations to disturbance that was proposed for this hypothesis by Huston (1979).

A study of several invertebrate groups in ponds in Leicestershire revealed that on average, each pond had a higher species richness (α-diversity) for water beetles than riparian beetles, but there were greater between-site differences in the riparian beetle fauna (ß-diversity), so the species richness over the whole data set was higher for water-margin beetles than any other single invertebrate group studied (Lott 2001). It was suggested that the differences in species composition between ponds was due to a high habitat specificity among riparian ground beetles and rove beetles, rather than habitat isolation, which was probably more important for molluscs, another group with high ß-diversity.

2.5 Use in site assessment for conservation

2.5.1 Formulation and monitoring of site and landscape management plans

Assemblages of ground beetles and rove beetles have several attributes that make them useful as biotic indicators of environmental change in wetlands. Standard sampling methods will yield a sufficient number of species in mixed assemblages to measure a community response to environmental changes over a wide range of wetland habitat types, with the possible exception of some montane and intertidal wetlands. Ground beetle assemblages are particularly species rich in environments subject to disturbance, because many species are associated with bare ground where they discriminate between different types of substrate. Rove beetle assemblages are species rich in less disturbed wetlands where they appear to be sensitive to hydrological conditions, especially fluctuations in water levels.

Both families have high habitat specificity and, compared to some other wetland groups, there is good variation in species composition of assemblages along environmental gradients (Lott 1999a). They are sensitive to site management operations (see references above, also Foster & Procter 1995) and larger scale changes in land-use (Luff & Woiwod 1995). Together they have the potential to identify important environmental factors operating within a site or landscape, which when linked to successional, fluvial or littoral processes can advise management plans and strategies. Their sensitivity to hydrological change makes them good candidates to monitor the effects of groundwater extraction on fen communities and possibly other subtle changes in hydrology which are difficult to measure directly.

The development of ground beetles and rove beetles assemblages as biotic indicators in wetlands is currently at a preliminary stage. Data from East Anglian fens was used to calculate indicator scores for species of ground and rove beetles relating to sensitivity to grazing, reed-cutting and flooding (Lott, Procter & Foster 2002). Similar analyses in other regions and possibly at a national scale could result in indicator scores that would serve as a robust tool for gauging environmental conditions and measuring environmental change.

A further strategy for applying species habitat requirements to site assessment is suggested by predictive methods developed for aquatic invertebrates (Armitage *et al.* 1986, Moss *et al.* 1987) and hoverflies (Diptera: Syrphidae) (Speight and Castella 2001). Speight and Castella (2001) demonstrated a system based on a consideration of regional species pools and larval microhabitats to identify which guilds are well or poorly represented at a site. However, microhabitat requirements of most wetland beetles are either diffuse, poorly characterised or unknown and it is unlikely that this strategy can be easily transferred to ground and rove beetles. Holmes *et al.* (1993) identified four habitats in 118 Welsh peatland sites, each of which supported ground beetle species that were more or less restricted to that habitat. It was argued that presence or absence of these species could be used to indicate whether the site was being sympathetically managed. Essentially, these indicator species were considered to be stenotopic. While some of these species, such as *Agonum ericeti,* are widely regarded as stenotopic, others, such as *Bembidion lunulatum* are eurytopic species that just happened to be restricted to certain habitats in the sample set and the wider applicability of this set of indicator species is questionable.

2.5.2 Site quality evaluation using habitat fidelity

Site quality evaluations for wetland beetles in Britain have mainly been based on either habitat quality or species rarity, although Good & Butler (1998, 2000, 2001) evaluated saline lagoons and turloughs in Ireland using a hybrid approach that involved indicator species selected on their rarity and fidelity to habitats undisturbed by human activity.

Eyre & Lott (1997) allocated fidelity categories to beetles of exposed riverine sediments and these were further developed by Sadler & Petts (2000). These have not yet been applied to site assessment in a quantitative way and fidelity scores for other wetland habitat types have not been proposed. The main impediment to progress in this area is lack of sufficient baseline data to gauge fidelity accurately. However, it is possible that existing data could be used to investigate whether ecological amplitude along major axes of variation could inform site quality assessments in a similar way.

As previously argued, the assessment of stenotopy and eurytopy using *a priori* defined habitats lacks ecological validity, and the same arguments apply to fidelity scores. However, if a particular habitat structure is identified as a threatened landscape feature and if there is evidence that individual species are restricted in their distribution to these features, then it makes sense to take account of this in site quality assessments. Exposed riverine sediments and slumping cliff seepages are two habitat structures whose value for ground beetles and rove beetles and whose vulnerability to land use changes is recognised (Eyre & Lott 1996, Boyce 2002). There is evidence that late successional wetlands in floodplains and fenland and some coastal features fall into the same category (Hammond 1998, Lott 1999b, Hammond 2000, Lott, Procter & Foster 2002). There is an immediate need to assess the fauna of these habitat structures and also to place them into a wider ecological context that relates to the habitat requirements of the organisms. Such requirements are best described in terms of ecological succession, hydrology and disturbance regimes that can be directly related to landscape management options, so that appropriate conservation or remedial action can be taken.

2.5.3 Site quality evaluation using rarity

Quantitative methods for assessing site quality using the mean of species rarity scores arranged in a geometric progression (Eyre & Rushton 1989) have been used for ground beetles on riverbanks (Eyre, Lott & Garside 1996) and mixed assemblages of ground beetles and rove beetles in floodplain wetlands (Lott 1999b). Individual rarity scores for species were based on their national or regional distributional range expressed as number of 10km, 4km or 1km squares occupied.

In many applications of this method (eg Lott, Proctor & Foster 2002), rarity classes have been mixed with category of threat, expressed as red data book listings and other conservation statuses. Unfortunately, the conservation statuses of some wetland species are based on inaccurate estimates of their distributional range (Eyre, Luff & Lott 2000) and it is clear that better quality base-line data is needed to develop a more authoritative schedule of rarity scores. Gaston (1994) discussed problems in using rarity as a conservation assessment criterion, including the false rarity scores of under-recorded species. Subterranean species in the genera *Thalassophilus, Thinobius* and *Lathrobium* are difficult to sample using normal collecting methods, while rove beetles in the subfamily Aleocharinae have in the past been difficult to identify to species level. As a result, these taxa have often been overlooked by the amateur entomologists, whose work provides much of the basis for our knowledge of species distributions and consequent rarity statuses.

Despite the many problems, rarity probably remains the best currently available criterion to use for site quality evaluations based on beetles, simply because the base-line data is more comprehensive than that used for fidelity scores. However, in the longer term, it may be easier to develop effective base-line data for fidelity, because the necessary research, if properly structured, would not need to be as comprehensive as that needed to identify rarity statuses. Furthermore, the rarity status of an individual species might be expected to vary over time, whereas its fidelity status is more likely to remain constant. Nevertheless, the presence of rare species is an intrinsically popular criterion for site quality evaluation and it is difficult to envisage that it could ever be ignored.

Williams (2000) and Lott, Procter & Foster (2002) identified some undesirable properties of the most commonly used geometric scoring system including its dependency on sampling efficiency. Lott, Butterfield & Jeeves (1999) argued that in selecting sites for conservation, simple threshold criteria are generally preferable to rankings based on complex scoring systems, because they were more comprehensible to a wider range of people and because they are just as effective. There is a danger in devoting too high a proportion of resources to site quality evaluation. In many cases, wetland site quality assessment is of limited value unless it forms part of a strategic approach that recognises the importance of large scale fluvial and littoral processes in shaping individual habitat structures at a site level. High quality sites are often grouped in specific landscape areas or river catchments and at least in the longer term, are probably best viewed as interconnected parts of a larger ecosystem. The main priority for non-aquatic wetland invertebrate conservation is to characterise their habitats in terms related to ecological succession, disturbance and hydrology that can be used to influence management practice.

3. Resources for study

3.1 Sampling methods

Many different sampling techniques have been used for wetland ground beetles and rove beetles. Small-scale sampling methods can be classified into two main types: trapping and hand-collecting. On the landscape scale, Hammond (1998) reviewed and illustrated the use of flood refuse for sampling floodplains. He found that this method can be used to reveal differences in species composition between regions, catchments and stretches of the same river, although samples contain a considerable proportion of non-wetland species.

Surface pitfall trapping has been used extensively for riparian beetles (Lehmann 1965, Meissner 1983, Fowles 1989, Desender *et al.* 1994, Eyre, Lott & Luff 2001), while Dieterich (1996) used sediment baskets and tube traps below the surface. Pitfall traps have also been used in reedswamp (Obrtel 1972), various peatland habitats (Holmes, Boyce & Reed 1993) and fen (Lott, Proctor & Foster 2002). There are several technical difficulties in using pitfall traps in wetlands. They can be vulnerable to human disturbance (Koch 1977), though this is less of a problem than it is for more conspicuous flight interception traps. Pitfall trapping by rivers and in saturated ground is often disrupted by flooding or even physically impossible, while trampling by cattle on damp, soft sediments on grazed marshes and flushes can destroy traps *in situ* (Lott 1999b, Sadler & Petts 2000).

Hand-collecting techniques vary in their applicability from habitat to habitat. Köhler (1996) described a method for collecting beetles on sparsely vegetated, exposed sediments by washing them into a net. Subterranean beetles in exposed sediments can be collected by excavation and immersion of sediments in water, upon which the beetles rise to the surface. Other methods on exposed sediments include turning stones and stamping or tapping the surface of soft sediments, which stimulates the beetles to move on the surface. Beetles in more vegetated habitats can be collected by sieving litter or dissecting tussocks. In saturated habitats, it is productive to immerse emergent vegetation in water and scoop material from the water surface with a fine-meshed strainer. The efficiency of all these methods is increased by extracting specimens from sievings and other material in the laboratory rather than the field. D-vac sampling has also been used in conjunction with other techniques (Good & Butler 1998). Methods of standardising hand-collected samples have involved searching a unit area or quadrat (Krogerus 1948, Andersen 1969, Kurka 1975, Holeski & Graves 1978, Desender & Segers 1985, Landry 1994, Hodge & Jessop 1996) and collecting for a unit length of time (Andersen 1969, Plachter 1986).

Much has been written concerning bias in species composition of riparian samples collected by pitfall trapping and hand-collecting (see eg Andersen 1995, Hammond 1998). Andersen (1969) listed three causes of unwanted variation in hand-collected samples:

1. the subjective collecting error due to the varying efficiency of the collector;
2. the varying activity of the beetles depending upon weather conditions;
3. the fact that more time is used on the collecting itself in proportion to the time used for searching when the abundance is high.

The species composition of pitfall trap samples is sensitive to small changes in trap design (Luff 1975) and so pitfall trapping is also liable to variations in efficiency. However, pitfall trapping reduces problems connected with short-term variations in weather conditions by operating over an extended time period. Andersen (1995) found that nocturnal ground beetles were better represented in riverbank pitfall trap samples than quadrat samples, but these results were not repeated in studies carried out by Lott (unpublished) using timed hand-collected samples. Hand-collecting is also probably biased against small, cryptic species. However, there is also a bias toward larger species in pitfall trap samples of ground beetles, because they are more active and so more likely to meet with traps than smaller species (Greenslade 1964, Luff 1975, Andersen 1995). Because pitfall traps are biased toward more surface-active species, pitfall trap samples contain a higher proportion of low-fidelity species than hand-collected samples (Sadler & Petts 2000).

Pitfall trapping has been recommended as the preferred sampling method for large scale comparative surveys of beetles on exposed riverine sediments (Eyre & Lott 1997), but Sadler & Petts (2000) considered that it is necessary to supplement the trapping programme with timed hand-collected samples. It should be remembered that hand-collecting is less costly and is adequate for many purposes and much less vulnerable to disruption. Hand-collecting by excavation is more efficient at sampling subterranean species in coarse sediments (Sadler & Petts 2000) and probably produces more representative samples on soft sediments. In more saturated environments, where ground water is present at the surface during the sampling period, pitfall trapping is not an effective sampling method. Apart from practical difficulties caused by flooding, ground-living species that are adapted to moving over liquid surfaces are probably adept at avoiding capture in pitfall traps and this can skew rove beetle species composition in pitfall trap samples from fen habitat (Lott, Proctor & Foster 2000).

3.2 Species identification

A lack of expertise in species identification outside a small number of specialists is a major impediment to the study of invertebrates and their use in conservation. Several institutions now run professional courses aimed at increasing proficiency in identification. Although none of these are aimed specifically at wetland ground beetles and Staphylinidae, they could have indirect benefits for the study of these groups by teaching transferable skills. Identification workshops aimed at amateur naturalists are provided by the British Entomological and Natural History Society and the Field Studies Council and these occasionally concern ground beetles and rove beetles. Limited verification of identifications is available through the national recording schemes for ground beetles and Steninae, a subfamily of rove beetles (see below).

Access to reference collections and published works on identification can cause problems for beginners. Publications to aid the identification of ground beetles and rove beetles are confined to the specialist literature and for rove beetles are largely scattered in serial publications, sometimes in languages other than English.

Lindroth (1974) provides keys to British ground beetles. Table 5 contains references to cover wetland species not included by Lindroth (*op. cit.*). The rove beetles are only partially covered by key works specific to the British Isles (Tottenham 1954, Pearce 1957). However, identification keys that cover most British wetland rove beetles are provided by Freude, Harde & Lohse (1964, 1974), though they also key species that have not been recorded in the British Isles. Table 6 contains references to further publications covering British species not included in the standard works as well as particularly useful papers that provide additional characters and illustrations. Further references are provided by Hodge & Jones (1995).

On-line checklists to both the British Carabidae (Luff & Duff 2002) and the British Staphylinidae (Lott & Duff 2002) are periodically updated to incorporate the results of published taxonomic revisions. They provide up to date nomenclature to be used as part of the identification process.

It is a common misconception that keys are the only tool needed to successfully identify species. In fact, workers with experience in a particular invertebrate group will invariably make greater use of reference collections for identification. Moreover, inexperienced workers can easily make mistakes when using keys without checking against reliably named specimens. Access to collections is vital to students early in their career, if they are going to develop adequate identification skills and their lack of use is no doubt an important factor behind the current poor state of such skills in many academic institutions. A strategic review of museum reference collections is needed so that regional gaps in accessibility of study collections can be identified. Comprehensive and accessible study collections of ground beetles and rove beetles, that are known to the author, can be found in museums in Cambridge, Cardiff, Dublin, Edinburgh, Liverpool, Newcastle and Oxford, while the rove beetle collections at the Natural History Museum, London, and in museums in Coventry and Manchester have had their identifications recently revised and serve as particularly useful reference collections for the identification of wetland rove beetles. Useful reference collections of ground beetles are probably more widespread.

Table 5. Key works needed to identify wetland ground beetles (Carabidae).

Taxon	Reference
Carabidae	Lindroth (1974)
Agonum lugens	Anderson (1985)
Asaphidion	Speight et al. (1983)
Bembidion caeruleum	Telfer (2001)
Bembidion humerale	Crossley & Norris (1975)
Bembidion inustum	Levey & Pavett (1999)
Patrobus	Houston & Luff (1983)
Pterostichus rhaeticus	Luff (1990)

Table 6. Key works needed to identify wetland rove beetles (Staphylinidae).

Taxon	Reference
Staphylinidae	Freude *et al.* (1964, 1974), Tottenham (1954)
Staphylinidae (Athetini)	Strand & Vik (1964)
Staphylinidae (Omaliinae)	Zanetti (1987)
Staphylinidae (Pselaphinae)	Pearce (1957)
Acrotona	Brundin (1952).
Actocharis readingi	Joy (1932)
Adota immigrans	Easton (1971).
Aleochara	Welch (1997)
Aloconota	Last (1952), Benick (1954)
Aloconota mihoki	Last (1980)
Aloconota subgrandis	Hammond (1981)
Amischa	Williams (1969), Muona (1990)
Atheta ebenina	Last (1969)
Bledius atricapillus	Lohse & Lucht (1989)

Taxon	Reference
Cafius	Coiffait (1974)
Calodera	Assing (1996)
Carpelimus similis	Lohse & Lucht (1989)
Carpelimus subtilicornis	Steel (1956)
Carpelimus zealandicus	Steel (1969)
Cypha pulicaria	Johnson (1967)
Dasygnypeta	Williams (1980), Palm (1966)
Diglotta	Good (1998)
Erichsonius	Uhlig & Sterrenburg (1990)
Gnypeta	Williams (1980), Palm (1966)
Halobrecta	comprehensive treatment lacking
Hydrosmecta delicatissima	Allen & Eccles (1988)
Ilyobates	Assing (1999)
Medon pocofer	Coiffait (1984)
Meotica	Muona (1991)
Myllaena	Strand (1967)
Myrmecopora	Assing (1997), Owen (1999b)
Neobisnius	Last (1948)
Ochthephilum	Williams (1968)
Ochthephilus	Makranczy (2001)
Ocyusa defecta	Williams (1979)
Olophrum	Hammond (1970)
Oxypoda	Strand & Vik (1966)
Parameotica	Lohse & Lucht (1989)
Philhygra	Brundin (1942).
Philonthus mannerheimi	Last (1974)
Philonthus micantoides	Allen (1971)
Platystethus	Hammond (1971)
Pseudopasilia testacea	Joy (1932)
Quedius balticus	Last (1963)
Schistoglossa aubei	Sinclair & Owen (1998)
Schistoglossa benicki	Lohse & Lucht (1989)
Sepedophilus	Hammond (1973)
Stenus	Wüsthoff (1934)
Stenus butrintensis	Allen (1978)
Stenus europaeus	Puthz (1966)
Stenus glabellus	Lott (1993b)
Stenus glacialis	Johnson (1967)
Thinobius	Lott (1993a)
Thinobius linearis	Makranczy & Schülke (2001)

3.3 Information on distribution, habitats and biology

There is a long-running national recording scheme for British ground beetles which has resulted in the publication of a provisional atlas (Luff 1998). This maps the recorded distribution of each species in Britain on a 10km square basis. National maps showing the distribution of individual species are also published on the web at www.searchnbn.net. Enquiries for up-to-date information as well as the contribution of new records should be addressed to:

Mark Telfer
c/o RSPB
The Lodge
Sandy
Beds SG19 2DL

The national recording scheme for rove beetles is operated by Peter Hammond. Extensive records have been extracted from many museum collections and it is planned to produce an atlas based on 50km squares. Some maps have already appeared in print (Hammond 1998, Hammond 2000). There is also a recording scheme specific to the subfamily Steninae which focuses on modern records contributed by field naturalists. Enquiries to the Steninae recording scheme should be addressed to:

Jonty Denton
2 Sandown Close
Alton
Hants GU34 2TG
e-mail: JontyDenton@aol.com

Anderson, Nash & O'Connor (1997) list Coleoptera that have been recorded from Ireland. There are also summaries of the distribution and habitats of Irish ground beetles (Speight, Anderson & Luff 1982, Anderson, McFerran & Cameron 2000) and two rove beetle subfamilies, Omaliinae (Hammond 1980) and Steninae (Anderson 1984).

Sources of ecological data on wetland ground beetles tend to be more disparate and less organised than those for distributional data. Luff (1998) includes notes on habitats, life history and dispersal for many British species, while Hyman (1992) gives more detailed information for red data book and nationally scarce species. Lindroth (1945) provides extensive information on habitat, life history and dispersal for many species, based on Scandinavian data. Van Huizen (1981) lists species that have been recorded dispersing by flight in Holland.

For rove beetle habitats, it is necessary to consult Horion (1963, 1965, 1967) or Koch (1989, 1990). Horion (*op. cit.*) also gives notes on life history for some species, while Koch (*op. cit.*) includes occasional notes on feeding. However, these works are based on central European data and it should be noted that habitats and life histories of individual species can vary in the British Isles. Ecological information based on British data is provided for red data book and nationally scarce species by Hyman (1994), but it is admitted that much of the information provided is sketchy. Some caution needs to be exercised when using works summarising the habitats of rove beetles. For many species, records are based on a very limited number of largely unsourced, anecdotal observations. There is no attempt to quantify habitat records in any of the publications referred to above and it is possible that some listed habitats originate in single observations that could be based on misidentifications.

Publications dealing with the ecology of individual species in more depth are cited in the annotated list.

4. List of wetland species

This section lists species of ground beetles and rove beetles with a strong association with wetland during part or all of their life cycle. The term 'hygrophilous' is often used for these species, but this term can also be applied to species preferring a humid microenvironment in woodland and rough grassland. The majority of ground beetle and rove beetle species are either evidently associated with wetlands or more or less restricted to terrestrial habitats, but there remain a small proportion of species that are difficult to categorise. It is therefore necessary to draw up criteria for their inclusion in the list. Firstly a more precise and workable definition for wetland habitat is needed.

4.1 Definition of wetland used for list

The Ramsar Convention defines wetlands as *areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water, the depth of which at low tide does not exceed six metres.* This definition, which was designed to describe the habitats of waterfowl, is admirably comprehensive, but does not provide a clear enough boundary between wetland and terrestrial habitats for ground-living beetles.

A manual used in the USA to delineate wetlands for enactment of conservation legislation (Anon 1987) suggests a more practical approach of value for present purposes. This manual defines wetlands as *those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs, and similar areas.* It also includes a definition of non-wetlands. *Nonwetlands include uplands and lowland areas that are neither deepwater aquatic habitats, wetlands, nor other special aquatic sites. They are seldom or never inundated, or if frequently inundated, they have saturated soils for only brief periods during the growing season, and, if vegetated, they normally support a prevalence of vegetation typically adapted for life only in aerobic soil conditions.* This approach has the merit of using easily observable features, namely vegetation, soil and hydrology, but is probably too restrictive for describing beetle habitats. Riparian species in wetlands can occur on well oxygenated coarse-grained substrates. However, it is possible to adapt the above definition of wetland as follows:

Wetlands are those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support , and that under normal circumstances do support a prevalence of vegetation typically adapted for life in saturated soil conditions or in sediments subject to disturbance by flooding. Wetlands generally include swamps, marshes, bogs, flushes and areas of periodically exposed sediment.

This definition includes seasonally inundated floodplain wetlands that support characteristic wetland beetle communities, but excludes many agricultural grasslands on alluvial soils that are dominated by generalist grassland beetles. Consequently, the list omits species such as *Pterostichus macer, Poecilus versicolor, Achenium depressum* and *A. humile,* which are characterised by Hammond (1998) as restricted to alluvial soils. Other species of alluvial soils such as *Pterostichus longicollis,* and several *Lathrobium* species are included because they also regularly occur in marshes or on exposed riverine sediments.

With regard to littoral habitats, the definition includes beaches up to and around the high tide line, but not sand dunes which are only rarely inundated by the sea. Similarly, sea cliffs may be too rarely affected by the sea to be included, although freshwater seepages and trickles on cliffs constitute small-scale wetlands in their own right. It could be argued that montane areas and moorland subject to high annual rates of precipitation are frequently saturated. However, moorland species are only included if they are routinely recorded from wet moss, blanket bog or other mire habitats.

4.2 Criteria for inclusion

There are several rarely recorded species, such as *Anotylus insecatus* or *Ilyobates* spp, whose habitats are poorly understood. Classification of these species as wetland or non-wetland is problematic. However, the majority of rare species are stenotopic and therefore relatively easy to classify either by reference to the literature or field records collected by the author. Species that are abundant in the British Isles present more problems in that some of them are frequently recorded from both wetlands and dryer environments. Some are eurytopic and can breed both in wetlands and outside them. Other species with good dispersive powers are best regarded as vagrants or ephemeral breeders in wetlands. Unfortunately, published data on the wetland affinities of these common species is generally lacking or inadequate.

In order to attempt an objective evaluation of the degree to which common species are associated with wetlands, reference was made to WETCAST, a database of wetland Coleoptera compiled by the author. Since 1985, 870 representative samples of adult ground living beetles were collected by hand from 602 wetland sites in Britain and Ireland. 606 species of ground beetles and rove beetles were recorded in these samples. In early samples, species were simply recorded as present or absent, but since 1991, abundances of individual species have been recorded. In total 95,556 specimens have been identified to species from these later samples. Sampling was also carried out on a more systematic basis from 1991. Sampling area was limited to 100 m of linear habitat and total sampling time was standardised to 30 minutes adjusted to up to two hours at sites such as shingle banks and blanket bogs, which are difficult to sample by hand. It is argued that these samples are broadly comparative in terms of sampling effort.

Two statistics for each species recorded were derived from the database:

1. the number of samples from the whole database, in which the species was present,
2. the mean abundance recorded in samples collected since 1991.

Many species, generally held to be unassociated with wetlands, were recorded from a large number of samples, whereas several rare wetland specialists are unrepresented in the database. The number of samples was therefore found to be poor discriminator between wetland and non-wetland species. However, it was also found that few acknowledged non-wetland species had mean abundances higher than 1.8. About half of these non-wetland species with high abundances had only been recorded from less than five samples. Accordingly, the first criteria for inclusion in the list was presence in five or more samples and a mean abundance of 1.8 or higher.

Many species with an undoubted wetland affinity had mean abundances lower than 1.8. Their low recorded abundances could be due to naturally low population densities or cryptic habits making them difficult to sample. Wetland species additional to those meeting the first criteria were selected by reference to recorded habitats in the literature and the author's own experience of casual collecting in Britain and Ireland. Because a species' habitat in the British Isles can vary from that recorded in continental Europe, continental records, either published or made by the author, have only been used for species, whose habitat has not been adequately recorded in Britain or Ireland.

These criteria are designed to be inclusive rather than exclusive. It is intended that they give a comprehensive list of species that can be expected to complete their life cycles using wetland habitats, because it was considered that this would enable the list to be used for a wider range of purposes. The list can be filtered using the three fidelity atributes assigned to each species if so desired.

If these criteria had been based on a database derived from pitfall trap samples rather than hand-collected samples, it is possible that results would have been slightly different. Some cryptic species such as *Thalassophilus longicornis* and *Trechoblemus micros* are better represented in pitfall trap samples whereas fen species characteristic of permanently saturated ground, such as *Stenus pubescens* and *Erichsonius cinerascens* tend to be under-represented. Pitfall traps in wetlands also pick up more specimens of large ground beetles, such as *Carabus problematicus* and *Pterostichus niger* that wander into wetlands at night from daytime refuges in adjacent habitats, and the wetland affinities of these species may be underestimated in the current list.

4.3 Explanation of column headings

4.3.1 Species

Species names follow Luff & Duff (2002) for Carabidae and Lott & Duff (2002) for Staphylinidae. Species are included according to the criteria given above.

4.3.2 Fidelity

Fidelity is here applied to wetlands as a whole, rather than specific types of wetland habitat. The following fidelity classes are used:

A: Species are routinely recorded from wetlands. They may also be recorded to a greater or lesser degree from artificial habitats such as arable fields or compost heaps, but it is likely that they are mainly dependent on wetlands to sustain viable populations.

B: Species are routinely recorded from wetlands, but also from semi-natural terrestrial habitats over all or part of their geographical area of distribution. Also included here are wetland species that are recorded predominantly from artificial terrestrial habitats in part of their area of distribution.

C: Species frequently recorded in numbers from wetlands, but predominantly terrestrial over all their British area of distribution. Wetland records may be due to vagrants or ephemeral breeding populations.

Question marks have been used to identify poorly understood species, whose wetland affinities require confirmation. The classification of species into fidelity classes is based on literature records and personal experience of the author. It is not based on objective criteria and should be regarded as indicative rather than an authoritative ecological classification.

4.3.3 Habitat

A brief habitat description is given of the main habitat types preferred by each species, but it should be recognised that there is much basic work to be done not only in identifying specific habitats, but also in developing a method and terminology for describing them. Many terms traditionally used to describe habitats have been applied inconsistently. For example, riparian is an adjective normally employed for riverbanks, but is also often extended by ecologists, especially in America, to standing water bodies. Strictly speaking, the riparian zones of standing water bodies should be described as littoral, but this term is normally reserved for the sea shore and the margins of large lakes. In this list, the following loose definitions are used with the justification that they appear to fit the purpose of describing beetle habitats:

bog	acidic mire
carr	wet woodland or scrub on organic substrates
coastal	water margins near the coast
fen	mire fed from groundwater or riverine source containing minerals
marsh	frequently saturated and vegetated mineral sediments
mire	frequently saturated and vegetated peat
riparian	terrestrial margins of both rivers and standing water bodies, including exposed sediments
saltmarsh	marsh with brackish water

4.3.4 Microhabitat

Many wetland species appear to be capable of occupying a wide range of microhabitats. The list of microhabitats given for each species is not comprehensive, but represents the main microhabitats given in the literature or apparent from personal experience of the author.

4.3.5 Status

The national conservation status as listed by Hyman (1992, 1994) is given here. This consists of provisional red data book listings and different categories of national scarcity as explained by Hyman (*op. cit.*) and using the standard symbols used in that work. Eyre, Luff & Lott (2000) pointed out the need for a review of these gradings as applied to species of riverine sediments and some of these gradings may change in the near future as a result of work currently in progress (Adrian Fowles pers. comm.). It is likely that a similar need applies to all wetland ground beetles and rove beetles. Such a review would need to be advised by targeted survey, or, at least, the data collected by a national recording scheme. However the opportunity is taken here to recommend a small number of changes that are particularly obvious in the light of recently published records and the personal experience of the author and colleagues. These recommendations are given in square brackets.

Further symbols used are '-' for no status, 'Ex' for extinct species as listed by Hyman (1994) and Nelson & Anderson (1999) and 'Ir' for species whose modern distribution in the British Isles is restricted to Ireland.

4.3.6 Number of samples

This figure refers to the number of samples in the WETCAST database containing specimens of the species. It should be noted that geographical coverage of the database is uneven, being heavily weighted toward Leicestershire and away from South-west England and coastal localities. Consequently, these figures cannot be used as a reliable measure of national abundance.

Where + appears against a species, it means that there are no records in the database, but that the species has been recorded in wetlands in Britain or Ireland by the author either by casual collecting or in pitfall trap surveys. Where (+) appears against a species, it means that there are no records in the database, but that the species has been recorded in wetlands in continental Europe by the author.

4.3.7 Mean abundance

This figure refers to the mean abundance of the species in WETCAST samples collected since 1991.

4.3.8 Literature references

References used to establish the wetland affinities of species are given here together with other references to detailed treatments of individual species' habitats.

4.3.9 Synonyms

Synonyms used by Pope (1977) and subsequent works are listed.

4.4 Wetland ground beetles (Carabidae)

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature references	Synonym
Acupalpus brunnipes (Sturm)	A	marsh, saltmarsh	moss, litter	Na	0		Luff (1998)	
Acupalpus dubius Schilsky	A	marsh	litter, moss, tussocks		64	5.82		
Acupalpus elegans (Dejean)	A	saltmarsh, coastal cliffs	exposed soft sediments	Ex	0		Luff (1998)	
Acupalpus exiguus Dejean	A	marsh, saltmarsh, sea shore	litter	Nb	3	3.33	Luff (1998)	
Acupalpus flavicollis (Sturm)	A	riparian	exposed sand & silt	Na	(+)		Luff (1998)	
Acupalpus parvulus (Sturm)	A	flushes, mires	exposed peat, tussocks		7	1.86		*Acupalpus dorsalis*
Aepus marinus (Ström)	A	intertidal	under stones on sand & shingle	Nb	1		Luff (1998)	
Aepus robini (Laboulbène)	A	intertidal	rock crevices	Nb	1		King *et al.* (1980)	
Agonum afrum (Duftschmid)	A	marsh	moss		42	1.62	Ribera *et al.* (1996)	*Agonum moestum*
Agonum ericeti (Panzer)	B	wet moorland	*Sphagnum*, exposed peat	Nb	(+)		Eyre *et al.* (1998)	
Agonum fuliginosum (Panzer)	B	marsh, fen	litter, tussocks		271	3.53		
Agonum gracile Sturm	B	marsh, poor fen	moss, tussocks		57	3.1		
Agonum livens (Gyllenhal)	A	marsh, carr	litter, under bark	Nb	26	2.08		
Agonum lugens (Duftschmid)	A	riparian	exposed silt	Ir	1		Anderson (1985)	
Agonum marginatum (Linnaeus)	A	riparian, marsh	exposed sand & silt		75	1.72	Luff (1998)	
Agonum micans Nicolai	A	riparian, marsh	exposed silt, litter, under bark in winter		188	3.57		
Agonum nigrum Dejean	A	marsh, saltmarsh	litter	Nb	3	3	Good & Butler (1998)	
Agonum piceum (Linnaeus)	A	marsh	litter		30	2.46		
Agonum scitulum Dejean	A	marsh, carr	litter	Na	(+)		Luff (1998)	
Agonum sexpunctatum (Linnaeus)	A	wet heath	exposed peat, *Sphagnum*	Na	+		Luff (1998)	
Agonum thoreyi Dejean	A	fen, marsh	litter, emergent veg.		108	5.43		
Agonum versutum Sturm	A	marsh		Nb	1		Luff (1998)	
Agonum viduum (Panzer)	A	marsh			24	1.47	Ribera *et al.* (1996)	
Amara familiaris (Duftschmid)	C				15	1.92		
Amara strenua Zimmermann	A	saltmarsh	litter, under veg.	R3	0		Luff (1998)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature references	Synonym
Anisodactylis binotatus (Fabricius)	B	marsh			1	1	Luff (1998)	
Anisodactylus poeciloides (Stephens)	A	saltmarsh	litter, under stones & veg.	R3	0		Luff (1998)	
Anthracus consputus (Duftschmid)	A	riparian, marsh	litter, under stones	Nb	23	4.95		*Acupalpus consputus*
Asaphidion curtum Heyden	B	riparian	sand & silt		22	1.19	Luff (1998)	
Asaphidion flavipes (Linnaeus)	B	riparian	exposed soft sediments		6	3.6		
Asaphidion pallipes (Duftschmid)	A	riparian, slumping cliffs	exposed sand & silt	Nb	2		Luff (1998)	
Badister anomalus (Perris)	A	riparian		R1 [R3]	(+)		Luff (1998)	
Badister dilatatus Chaudoir	A	marsh	litter	Nb	5	1.6	Luff (1998)	
Badister meridionalis Puel[1]	B	marsh, fen meadow	litter, tussocks	RI	1	2	Hyman (1992)	
Badister peltatus (Panzer)	A	marsh		Na	0		Luff (1998)	
Badister sodalis (Duftschmid)	A	wet woodland	litter		+		Luff (1998)	
Badister unipustulatus Bonelli	A	marsh, fen, carr	litter, under bark	Nb	2	4	Luff (1998)	
Bembidion aeneum Germar	B	riparian inc. estuaries	grass tussocks		167	5.53		
Bembidion andreae (Fabricius)	A	riparian, sea shore	exposed sand & fine gravel		2		Luff (1998)	
Bembidion articulatum (Panzer)	A	riparian	exposed clay & silt		62	3.69		
Bembidion assimile Gyllenhal	A	marsh, saltmarsh	litter		50	3.53		
Bembidion atrocoeruleum (Stephens)	A	riparian, upland	cobbles, moss		14	11.3		
Bembidion biguttatum (Fabricius)	A	marsh, riparian	litter, grass tussocks		314	6.33		
Bembidion bipunctatum (Linnaeus)	A	riparian	exposed sand & gravel	Nb	2		Good & Butler (1998)	
Bembidion bruxellense Wesmael	B	riparian	exposed sand & gravel		9	1.4	Luff (1998)	
Bembidion clarkii (Dawson)	A	marsh, carr, dune slacks	litter, moss	Nb	71	10.9		*Bembidion clarki*
Bembidion coeruleum Serville	A	riparian	exposed sand	[RK]	(+)		Telfer (2001)	
Bembidion decorum (Zenker)	A	riparian	exposed shingle		19	4.62		
Bembidion deletum Serville	B	riparian	exposed soft sediments		12	1.75	Luff (1998)	*Bembidion nitidulum*
Bembidion dentellum (Thunberg)	A	marsh	litter, exposed silt		291	3.52		
Bembidion doris (Panzer)	A	marsh, carr, fen	litter		59	4.69		
Bembidion ephippium (Marsham)	A	saltmarsh	litter, exposed silt	Na	2		Luff (1998)	

[1] The taxonomic status of this species and the related *Badister bullatus* in Britain and Ireland are in need of investigation (Hammond pers. comm.)

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature references	Synonym
Bembidion femoratum Sturm	B	riparian	exposed soft sediments		14	2.33		
Bembidion fluviatile Dejean	A	riparian	eroding river banks	Nb	2	1	Luff (1998)	
Bembidion fumigatum (Duftschmid)	A	marsh, fen	litter	Nb	21	4.76		
Bembidion genei Küster	A	riparian	exposed clay		23	2.2		
Bembidion geniculatum Heer	A	riparian, upland	exposed shingle		2	1.5	Luff (1998)	
Bembidion gilvipes Sturm	A	marsh	grass tussocks	Nb	151	2.97		
Bembidion guttula (Fabricius)	B	riparian	grass tussocks		207	3.22		
Bembidion humerale Sturm	A	bog	exposed peat	RI	0		Luff (1998)	
Bembidion inustum Jacquelin du Val	A	shaded streams		[RK]	0		Levey & Pavett (1999)	
Bembidion iricolor Bedel	A	saltmarsh	litter, tidal refuse		(+)		Luff (1998)	
Bembidion lunatum (Duftschmid)	A	riparian inc. estuaries	under stones, tidal refuse	Nb	1		Luff (1998)	
Bembidion lunulatum (Fourcroy)	A	riparian	exposed silt		216	4.18		
Bembidion mannerheimii Sahlberg	B	bog, damp woods	litter		35	3.15		*Bembidion mannerheimi*
Bembidion maritimum Stephens	A	estuaries, sea shore	exposed sediments		(+)		Luff (1998)	
Bembidion minimum (Fabricius)	A	saltmarsh, also inland	litter, tidal refuse		3	4	Luff (1998)	
Bembidion monticola Sturm	A	riparian	exposed clay	Nb	2	1	Luff (1998)	
Bembidion nigropiceum (Marsham)	A	coastal	exposed sand, under stones, deep in shingle	Na	0		Luff (1998)	
Bembidion normannum Dejean	A	saltmarsh	litter, tidal refuse		+		Luff (1998)	
Bembidion obliquum Sturm	A	riparian	exposed silt	Nb	2	1	Luff (1998)	
Bembidion obtusum Serville	B	riparian	grass tussocks		50	3.42		
Bembidion octomaculatum (Goeze)	A	riparian	exposed soft sediments	Ex [RK]	(+)		Hodge (1997a)	
Bembidion pallidipenne (Illiger)	A	coastal	exposed sand	Nb	4		Luff (1998)	
Bembidion prasinum (Duftschmid)	A	riparian	exposed shingle		4	12	Luff (1998)	
Bembidion punctulatum Drapiez	A	riparian	exposed shingle		43	9.81		
Bembidion quadripustulatum Serville	A	riparian	exposed silt & sand	Nb	0		Luff (1998)	
Bembidion saxatile Gyllenhal	A	riparian, coastal	exposed sand & gravel, under stones	Nb	4	1	Luff (1998)	
Bembidion schuppelii Dejean	A	riparian	exposed soft sediments, litter	Na	1		Reid & Eyre (1985)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature references	Synonym
Bembidion semipunctatum Donovan	A	riparian	exposed sand	Na	3	1	Luff (1998)	
Bembidion stephensii Crotch	A	riparian	exposed soft sediments		1		Luff (1998)	
Bembidion stomoides Dejean	A	riparian	exposed shingle	Nb	+		Luff (1998)	
Bembidion testaceum (Duftschmid)	A	riparian	exposed sand & gravel	Nb [RI]	+		Luff (1998)	
Bembidion tetracolum Say	B	riparian	exposed sand & gravel		203	4.05		
Bembidion tibiale (Duftschmid)	A	riparian	exposed shingle		27	3.89		
Bembidion varium (Olivier)	A	riparian, saltmarsh	exposed silt		8	3.17		
Bembidion virens Gyllenhal	A	riparian	exposed shingle	R3	0		Luff (1998)	
Blethisa multipunctata (Linnaeus)	A	fen, marsh	wet silt with litter	Nb	8	1.5	Luff (1998)	
Bracteon argenteolum Ahrens	A	riparian	exposed sand	RI	0		Luff (1998)	*Bembidion argenteolum*
Bracteon litorale (Olivier)	A	riparian	exposed sand & fine shingle	Nb	3	2	Luff (1998)	*Bembidion litorale*
Carabus arvensis Herbst	B	wet heath			0		Luff (pers. comm.)	
Carabus clathratus Linnaeus	A	bog, riparian		Na	+		Eyre *et al.* (1998)	
Carabus granulatus Linnaeus	A	marshes & fens	under stones & bark		10	1	Luff (1998)	
Carabus nitens Linnaeus	A	wet heath, dune slacks		Nb	0		Luff (1998)	
Chlaenius nigricornis (Fabricius)	A	marsh, mire		Nb	3	1	Luff (1998)	
Chlaenius nitidulus (Schrank)	A	riparian		R1	0		Boyce (2002)	
Chlaenius tristis (Schaller)	A	mire	*Sphagnum*, exposed silt	R1	0		Hodge (1997b)	
Chlaenius vestitus (Paykull)	A	riparian	exposed soft sediments		5	1	Luff (1998)	*Chlaenius vestitus*
Cicindela germanica Linnaeus	A	slumping cliff seepages	exposed soft sediments	R3	+		Else (1993)	
Cillenus lateralis (Samouelle)	A	intertidal saltmarsh	exposed sand & silt		1		Elliot *et al.* (1983a)	*Bembidion lateralis*
Clivina collaris (Herbst)	B	riparian	soft sediments		48	1.6	Luff (1998)	
Clivina fossor (Linnaeus)	C				46	2.19		
Curtonotus convexiusculus (Marsham)	B	saltmarsh			1		Luff (1998)	
Cymindis vaporariorum (Linnaeus)	B	wet moorland		Nb	(+)		Eyre *et al.* (1998)	
Demetrias imperialis (Germar)	A	reedbeds	tall emergent veg.	Nb	1	1	Luff (1998)	
Demetrias monostigma Samouelle	A	fen, dune slacks	litter	Nb	1	1	Luff (1998)	
Dicheirotrichus gustavi Crotch	A	saltmarsh, sea shore	under stones & veg.		4	11	Luff (1998)	

Wetland ground beetles (Carabidae

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature references	Synonym
Dicheirotrichus obsoletus (Dejean)	A	saltmarsh, sea shore	tidal refuse	Nb	0		Luff (1998)	
Dromius longiceps Dejean	A	fen, marsh, reedbeds	tall emergent veg.	R2 [Na]	+		Luff (1998)	
Dromius sigma (Rossi)	A	marsh, fen	grass tussocks	Na	(+)		Luff (1998)	
Drypta dentata (Rossi)	A	coastal flushes	soft sediments	R1	(+)		Boyce (2002)	
Dyschirius aeneus (Dejean)	A	riparian	exposed sand & silt		17	2.4		
Dyschirius angustatus (Ahrens)	A	riparian, coastal	exposed sand	R3	0		Lyszkowski & Owen (2000)	
Dyschirius extensus Putzeys	A	coastal	exposed sand	R1	0		Luff (1998)	
Dyschirius globosus (Herbst)	B	marsh	litter on silt & peat		26	5.57		
Dyschirius impunctipennis Dawson	A	saltmarsh	exposed soft sediments	[Nb]	(+)		Good & Butler (1998)	
Dyschirius luedersi Wagner	A	riparian, saltmarsh	exposed soft sediments		43	2.77		
Dyschirius nitidus (Dejean)	A	saltmarsh	exposed soft sediments	Na	0		Luff (1998)	
Dyschirius obscurus (Gyllenhal)	A	riparian	exposed sand	R2 [RK]	1		Luff (1998)	
Dyschirius politus (Dejean)	B	riparian	exposed sand		1		Luff (1998)	
Dyschirius salinus Schaum	A	saltmarsh	exposed soft sediments		4	1	Luff (1998)	
Dyschirius thoracicus Rossi	A	sea shore	exposed sand		4		Luff (1998)	
Elaphropus parvulus (Dejean)	B	riparian	exposed sediments	Nb	7	1.14	Hyman (1992)	*Tachys parvulus*
Elaphropus walkerianus Sharp	A	mire	*Sphagnum*	R1	1	8	Luff (1998)	*Tachys walkerianus*
Elaphrus cupreus Duftschmid	A	marsh, carr	damp mud with litter		128	1.69	Luff (1998)	
Elaphrus lapponicus Gyllenhal	A	montane bog, riparian	moss	Na	0		Luff (1998)	
Elaphrus riparius (Linnaeus)	A	riparian	exposed soft sediments		128	2.65		
Elaphrus uliginosus Fabricius	A	lowland poor fen and bog		Nb	+		Luff (1998)	
Laemostenus complanatus (Dejean)	A	sea shore	litter	[Nb]	+		Luff (1998)	
Lasiotrechus discus (Fabricius)	A	riparian	in soft sediments	Nb	4	3	Luff (1998)	*Trechus discus*
Lionychus quadrillum (Duftschmid)	A	riparian, coastal	exposed shingle	R3	(+)		Luff (1998)	
Loricera pilicornis (Fabricius)	B	eurytopic	moss, litter, exposed sediments		110	1.27	Luff (1998)	
Nebria brevicollis (Fabricius)	C				27	2.25		
Nebria complanata (Linnaeus)	B	sea shore	litter, exposed sand	Na	+		Luff (1998)	
Nebria livida (Linnaeus)	B	slumping cliff seepages		Na	0		Boyce (2002)	
Nebria rufescens (Ström)	B	stream margins	under stones		11	2		*Nebria gyllenhali*

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature references	Synonym
Odacantha melanura (Linnaeus)	A	fen, reedbeds	tall emergent veg.	Nb	2	1.5	Luff (1998)	
Omophron limbatum (Fabricius)	A	riparian	exposed sand	R1	(+)		Allen (1970)	
Oodes helopioides (Fabricius)	A	fen, marsh	emergent veg., exposed silt	Nb	3	1	Luff (1998)	
Oxypselaphus obscurus (Herbst)	A	marsh, wet woodland	litter		57	3.35		*Agonum obscurum*
Panageus cruxmajor (Linnaeus)	A	marsh, fen	moss, litter	R1	(+)		Luff (1998)	
Paranchus albipes (Fabricius)	A	riparian	under stones & veg.		394	4.57		*Agonum albipes*
Patrobus atrorufus (Ström)	B	wet woodland	litter		23	1.87		
Pelophila borealis (Paykull)	A	riparian, wet flushes	exposed soft sediments	R3	11		Luff (1998)	
Perileptus areolatus (Creutzer)	A	riparian	exposed shingle	Na	1		Luff (1998)	
Platynus assimilis (Paykull)	B	riparian, damp woodland	under stones & bark		36	1.57	Luff (1998)	*Agonum assimile*
Pogonus chalceus (Marsham)	A	saltmarsh, sea shore	litter, under stones		3		Luff (1998)	
Pogonus littoralis (Duftschmid)	A	saltmarsh	exposed clay & silt	Nb	1		Luff (1998)	
Pogonus luridipennis (Germar)	A	saltmarsh	under stones, litter	R3	1		Luff (1998)	
Polistichus connexus (Fourcroy)	B	riparian, coastal cliffs		R2	0		Luff (1998)	
Pterostichus anthracinus (Panzer)	A	fen, carr	litter	Nb	22	1.84		
Pterostichus aterrimus (Herbst)	A	fen		R1	(+)		Nelson & Anderson (199)	
Pterostichus diligens (Sturm)	B	wet heath, mire	moss, grass tussocks		111	4.95		
Pterostichus gracilis (Dejean)	A	marsh, carr	litter	Nb	28	2.23		
Pterostichus longicollis (Duftschmid)	A	riparian	exposed sediments	Nb	0		Luff (1998)	
Pterostichus minor (Gyllenhal)	A	marsh, fen, carr	litter, grass tussocks		151	3.37		
Pterostichus nigrita (Paykull)	B	marsh	litter, exposed silt		210	1.66	Luff (1998)	
Pterostichus rhaeticus Heer	B	wet moorland	moss		47	2.36	Carr & Angus (1992)	*Pterostichus nigrita*
Pterostichus strenuus (Panzer)	B	marsh, wet grassland	grass tussocks		180	2.22		
Pterostichus vernalis (Panzer)	B	marsh, wet grassland	grass tussocks		79	1.63	Luff (1998)	
Stenolophus mixtus (Herbst)	A	marsh	litter		86	2.76		
Stenolophus skrimshiranus Stephens	A	fen, marsh		Na	2	2	Luff (1998)	
Stenolophus teutonus (Schrank)	A	riparian, marsh	exposed soft sediments	Nb	1	1	Luff (1998)	
Tachys bistriatus Duftschmid	A	riparian	exposed soft sediments	Nb	1		Luff (1998)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature references	Synonym
Tachys edmondsi Moore	A	mire	*Sphagnum*	R1	1	5	Luff (1998)	
Tachys micros (Fischer von Waldheim)	A	slumping cliff seepages	exposed soft sediments	Na [RK]	2		Boyce (2002)	
Tachys scutellaris Stephens	A	saltmarsh	exposed soft sediments	Na	1		Luff (1998)	
Thalassophilus longicornis (Sturm)	A	riparian	exposed shingle	Na	1	1	Luff (1998)	
Trechoblemus micros (Herbst)	B	riparian	in soft sediments		1	1	Luff (1998)	*Trechus micros*
Trechus fulvus Dejean	A	seepages on sea shore, caves	under stones	Nb	0		Luff (1998)	
Trechus rivularis (Gyllenhal)	A	ombrotrophic mire, lowland fen	litter, tussocks	R3 [N-]	0		Holmes *et al.* (1990)	
Trechus rubens (Fabricius)	B	riparian, wet grassland	under stones, litter	Nb	1	1	Eyre *et al.* (1998)	
Trechus secalis (Paykull)	B	seasonal pools	litter		8	2.75		
Trechus subnotatus Dejean	B	slumping cliff seepages		R1	1		Lott (1990)	
Trichocellus placidus (Gyllenhal)	A	marsh, fen, wet woodland	grass tussocks, litter		21	2.55		

4.5 Wetland rove beetles (Staphylinidae)

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Acrotona exigua (Erichson)	B?	riparian	exposed sand		1		Lyszkowski & Owen (2000)	*Atheta exigua*
Acrotona obfuscata (Gravenhorst)	A	riparian		N- [-]	9	1.75	Hyman (1994)	*Atheta obfuscata*
Acrotona sylvicola(Kraatz)	A	riparian		RK	+		Koch (1989)	*Atheta sylvicola*
Actocharis readingi Sharp	A	sea shore	exposed sand	RK	0		Hammond (2000)	
Acylophorus glaberrimus (Herbst)	A	mire	*Sphagnum,* exposed peat	R1 [R3]	4	4.25	Shirt (1987)	
Adota immigrans (Easton)	A	sea shore	tidal refuse		0		Hammond (2000)	*Atheta immigrans*
Aleochara brevipennis Gravenhorst	B	marsh, riparian	*Sphagnum,* tussocks	N- [-]	2	1	Welch (1997)	
Aleochara grisea Kraatz	A	sandy sea shore	tidal refuse, carrion		7	5		
Aleochara obscurella Gravenhorst	A	rocky sea shore	tidal refuse, carrion		2	1	Welch (1997)	
Aleochara phycophila Allen	A	sea shore	tidal refuse	RI	0		Welch (1997)	
Aleochara punctatella Motschulsky	A	sandy sea shore	tidal refuse, carrion		4		Welch (1997)	
Alianta incana (Erichson)	A	marsh	*Typha* stems		14	2.57		
Aloconota cambrica (Wollaston)	A	riparian	exposed shingle		14	4		
Aloconota coulsoni (Last)	A	marsh	moss, reed litter	RK	0		Hyman (1994)	
Aloconota currax (Kraatz)	A	riparian	exposed shingle		11	1.86		
Aloconota eichhoffi (Scriba)	A	marsh, riparian	moss, exposed shingle	N-	+		Hyman (1994)	
Aloconota gregaria (Erichson)	C				90	1.85		
Aloconota insecta (Thomson)	A	riparian	exposed sediments		12	1.58	Hammond (1981)	
Aloconota languida (Erichson)	A	marsh, riparian	litter	N-	4	1	Hyman (1994)	
Aloconota longicollis (Mulsant & Rey)	A	marsh	moss, reed litter	N-	0		Hyman (1994)	
Aloconota mihoki Bernhauer	A	riparian	exposed shingle	RI	0		Koch (1989)	
Aloconota planifrons Waterhouse	A	riparian, slumping cliffs	exposed shingle	RK	2	1	Hyman (1994)	
Aloconota subgrandis (Brundin)	A	riparian	exposed sediments	RK	0		Hammond (1981)	
Aloconota sulcifrons (Stephens)	A	riparian	exposed soft sediments		10	1.56	Lott (1995)	
Amischa forcipata Mulsant & Rey	A	marsh	grass tussocks, rotten wood		6	1.17	Lott (unpubl.)	
Amischa nigrofusca (Stephens)	C				6	2.2		
Anotylus insecatus (Gravenhorst)	B?	saltmarsh, riparian	litter, dung		1	1	Hyman (1994)	
Anotylus maritimus (Thomson)	A	sandy sea shore	tidal refuse, dung		1	1	Hammond (2000)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Anotylus rugosus (Fabricius)	B	marsh, riparian	litter		173	2.39		
Arena tabida (Kiesenwetter)	A	sea shore	exposed sand & silt	RK	0		Hammond (2000)	
Astenus immaculatus Stephens	B	marsh	litter	N-	(+)		Hyman (1994)	
Atheta aquatilis (Thomson)	A	flushes, riparian	moss, litter	N-	6	2.2		
Atheta autumnalis (Erichson)	A	wet woodland?	rotten wood	RK	0		Koch (1989)	
Atheta basicornis (Mulsant & Rey)	A	wet woodland	under bark, rotten wood	N-	+		Hyman (1994)	
Atheta ebenina (Mulsant & Rey)	A	marsh	litter	RK	+		Eyre et al. (1998)	
Atheta graminicola (Gravenhorst)	A	marsh	litter, grass tussocks		343	5.62		
Atheta strandiella (Brundin)	A	fen, bog	moss	N-	1	1	Hyman (1994)	
Bibloplectus ambiguus (Reichenbach)	A	bog, marsh	litter, moss		3	2.67	Pearce (1957)	
Bibloplectus delhermi Guillebeau	A	bog, marsh	moss	RK	0		Hyman (1994)	
Bibloplectus minutissimus (Aubé)	A	riparian, coastal	tussocks on shingle	RK	0		Hyman (1994)	
Bibloplectus pusillus (Denny)	A	bog, marsh	grass tussocks	N-	0		Hyman (1994)	
Bibloplectus spinosus Raffray	A	bog, marsh	moss	N-	1	6	Hyman (1994)	
Bibloplectus tenebrosus (Reitter)	A	bog, marsh, fen	moss, tussocks	RK	1	1	Shirt (1987)	
Bledius annae Sharp[2]	A	riparian	exposed soft sediments		3	4.5	Lott (1999a)	
Bledius arcticus Sahlberg	A	riparian	exposed sand & shingle	RI	1	1	Lyszkowski & Owen (2000)	
Bledius atricapillus (Germar)	A	slumping cliffs, estuaries	exposed soft sediments	[RK]	1		Lohse (1982)	
Bledius bicornis (Germar)	A	saltmarsh, coastal flats	exposed soft sediments	Na	1		Hammond (2000)	
Bledius crassicollis Lacordaire	A	slumping cliff seepages	exposed soft sediments	RI	0		Shirt (1987)	
Bledius defensus Fauvel	A	riparian	exposed soft sediments	RK	(+)		Hyman (1994)	
Bledius diota Schiödte	A	saltmarsh, estuaries	exposed soft sediments	RK	+		Hammond (2000)	
Bledius dissimilis Erichson	A	riparian, slumping cliffs	exposed soft sediments	RI	0		Shirt (1987)	
Bledius erraticus Erichson	A	riparian	exposed soft sediments	RK	(+)		Hyman (1994)	
Bledius femoralis (Gyllenhal)	A	riparian	exposed sand	Na	0		Hyman (1994)	
Bledius fergussoni Joy	A	sea shore, dune slacks	exposed soft sediments		5	3		
Bledius filipes Sharp	A	slumping cliff seepages	exposed soft sediments	R1	+		Shirt (1987)	
Bledius furcatus (Olivier)	A	coastal flats	exposed soft sediments	RI	0		Shirt (1987)	

[2] This is a member of the *Bledius pallipes* species group and its specific status needs investigation.

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Bledius fuscipes Rye	A	estuaries, saltmarsh	exposed soft sediments		3	6	Hammond (2000)	
Bledius gallicus (Gravenhorst)	A	riparian	exposed soft sediments		3	2	Lott (1995)	
Bledius limicola Tottenham	A	saltmarsh, estuaries	exposed soft sediments		3		Steel (1955)	*Bledius germanicus*
Bledius longulus Erichson	B	riparian	exposed soft sediments		2	2	Fowler (1888)	
Bledius occidentalis Bondroit	A	dune slacks, sea cliffs	exposed soft sediments	RK	(+)		Boyce (2002)	
Bledius opacus (Block)	B	riparian	exposed soft sediments		+		Koch (1989)	
Bledius pallipes (Gravenhorst)	A	riparian	exposed soft sediments		11	10.3		*Bledius annae*
Bledius praetermissus Williams	A	sea shore, dune slacks	exposed soft sediments		1		Hammond (2000)	
Bledius spectabilis Kraatz	A	saltmarsh	exposed soft sediments		1		Steel (1955)	
Bledius subniger Schneider	A	saltmarsh, estuaries	exposed soft sediments		+		Hammond (2000)	
Bledius subterraneus Erichson	A	riparian	exposed sand		19	7.23		
Bledius terebrans Schiödte	A	riparian	exposed sand	RK	1		Hyman (1994)	
Bledius tricornis (Herbst)	A	saltmarsh, estuaries	exposed soft sediments	Nb	(+)		Steel (1955)	
Bledius unicornis (Germar)	A	saltmarsh, estuaries	exposed soft sediments		+		Steel (1955)	
Boreophilia eremita (Rye)	B	wet moorland	*Sphagnum*		7	1.33	Lott (unpubl.)	
Brachygluta haematica (Reichenbach)	B	marsh	moss, rotten wood		0		Fowler (1889)	
Brachygluta helferi (Schmidt-Göbel)	A	saltmarsh	under veg.		3	1	Hammond (2000)	
Brachygluta pandellei (Saulcy)	A	riparian	exposed sand & shingle, moss	RK	1		Hyman (1994)	
Brachygluta waterhousei (Rye)	A	saltmarsh	litter, under veg.	N-	0		Hammond (2000)	
Brachyusa concolor (Erichson)	A	riparian	exposed soft sediments	N-	18	2.72		
Brundinia marina (Mulsant & Rey)	A	saltmarsh, estuaries	litter		3		Hammond (2000)	
Brundinia meridionalis (Mulsant & Rey)	A	saltmarsh, estuaries	litter		2		Hammond (2000)	
Bryaxis bulbifer (Reichenbach)	B	wet woodland, marsh	litter, moss		26	3.22		
Bryaxis puncticollis (Denny)	B	wet woodland	litter, moss		6	2.2		
Bryoporus cernuus(Gravenhorst)	B?	fen	litter, moss	RK	0		Koch (1989)	
Cafius cicatrosus (Erichson)	A	sandy seashore	tidal refuse	R1	0		Shirt (1987)	
Cafius fucicola Curtis	A	sea shore	tidal refuse		1		Hammond (2000)	
Cafius xantholoma (Gravenhorst)	A	sea shore	tidal refuse		9	8		
Calodera aethiops (Gravenhorst)	A	marsh	litter		14	1.57	Fowler (1888)	
Calodera nigrita Mannerheim	A	marsh	litter	N-	+		Hyman (1994)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Calodera riparia Erichson	A	marsh	litter	N-	5	1.4	Hyman (1994)	
Calodera rufescens Kraatz	A	marsh	litter	RK	1	1	Hyman (1994)	
Calodera uliginosa Erichson	A	seasonal pools	litter	RK	3	4	Lott (1999a)	
Carpelimus bilineatus Stephens[3]	A	riparian, marsh	litter		122	2.21		
Carpelimus corticinus (Gravenhorst)	A	marsh	litter		96	2.19		
Carpelimus despectus (Baudi)	A	coastal flats	exposed soft sediments	[RK]	0		Hammond (2000)	
Carpelimus elongatulus (Erichson)	A	marsh, mire	litter		56	3.54		
Carpelimus foveolatus (Sahlberg)	A	saltmarsh	litter	N-	+		Hammond (2000)	
Carpelimus gracilis (Mannerheim)	A	riparian	exposed sediments, moss		1	1	Fowler (1888)	
Carpelimus halophilus (Kiesenwetter)	A	sea shore, estuaries	exposed soft sediments	N-	0		Hammond (2000)	
Carpelimus impressus (Lacordaire)	A	marsh, carr	litter		98	8.52		
Carpelimus lindrothi Palm	A	riparian	exposed silt	N-	7	2.57		
Carpelimus obesus (Kiesenwetter)	A	riparian	exposed silt	N-	7	1.14	Hyman (1994)	
Carpelimus pusillus (Gravenhorst)	B	riparian	exposed soft sediments		2	1	Hammond (1998)	
Carpelimus rivularis (Motschulsky)	A	marsh, riparian	exposed soft sediments		275	6.34		
Carpelimus schneideri (Ganglbauer)	A	estuaries, saltmarsh	exposed soft sediments	RI	0		Shirt (1987)	
Carpelimus similis (Smetana)	A	riparian	exposed soft sediments	N- [-]	21	2.1		
Carpelimus subtilicornis (Roubal)	A	riparian	exposed soft sediments		114	7.89	Hammond (1998)	
Carpelimus subtilis (Erichson)	A	riparian	exposed sediments	N-	2	1	Hyman (1994)	
Carpelimus zealandicus (Sharp)[4]	A	riparian	exposed sand		3	1	Allen (1979)	
Cousya nigrata (Fairmaire & Laboulbène)	B	marsh		RK	0		Hyman (1994)	*Ocyusa nigrata*
Cypha discoidea (Erichson)	A	fen, marsh, estuaries	litter	Nb	4	1	Hyman (1994)	
Cypha pulicaria (Erichson)	A	bog, marsh	litter	N-	1		Hyman (1994)	
Cypha punctum (Motschulsky)	A	flushes			0		Good & Butler (1998)	
Dacrila fallax (Kraatz)	A	fen	reed litter, moss	N-	8	1.33	Hyman (1994)	
Dasygnypeta velata (Erichson)	A	riparian	exposed silt	N- [-]	45	5.44		*Gnypeta velata*

[3] Two species are currently confused under this name (Lott in prep.)
[4] Two species are currently confused under this name (Hammond pers. comm.)

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Datomicra zosterae (Thomson)	A	fen, marsh	bird nests	N-	2	7	Hyman (1994)	*Atheta zosterae*
Deinopsis erosa (Stephens)	A	riparian	litter		59	1.95		
Deleaster dichrous (Gravenhorst)	A	riparian	exposed sediments	Nb [-]	7	1	Hyman (1994)	
Dianous coerulescens (Gyllenhal)	A	riparian	moss, exposed sediments		5	1.5	Hammond (1998)	
Diglotta mersa (Haliday)	A	intertidal	exposed soft sediments	N-	+		Good (1998)	*Diglotta submarina*
Diglotta sinuaticollis (Mulsant & Rey)	A	intertidal	exposed soft sediments		0		Good (1998)	*Diglotta mersa*
Dilacra luteipes (Erichson)	A	riparian	litter		48	1.62	Fowler (1888)	*Atheta luteipes*
Dilacra vilis (Erichson)	A	marsh, carr	litter		33	3.82		*Atheta vilis*
Dimetrota atramentaria (Gyllenhal)	C				6	2		
Dochmonota clancula (Erichson)	A	marsh, carr	litter	N-	50	3.58		
Drusilla canaliculata (Fabricius)	C				10	2		
Encephalus complicans Stephens	B?	flushes	tussocks, litter		5	1	Lott (unpubl.)	
Erichsonius cinerascens (Gravenhorst)	A	fen	moss		45	3.56		
Erichsonius signaticornis (Mulsant & Rey)	A	riparian, sea cliffs	exposed sediments		2		Hyman (1994)	
Erichsonius ytenensis (Sharp)	A	bog	*Sphagnum*	RI	0		Hyman (1994)	
Euaesthetus bipunctatus (Ljungh)	B	marsh			0		Fowler (1888)	
Euaesthetus laeviusculus Mannerheim	A	mire			7	1.57	Reid (1986)	
Euaesthetus ruficapillus Lacordaire	A	fen	moss, tussocks		22	2.58		
Eucnecosum brachypterum (Gravenhorst)	B	upland mire	moss		2	1	Tottenham (1954)	*Arpedium brachypterum*
Euryporus picipes (Paykull)	B	mire	moss	RK	(+)		Owen (1999a)	
Eusphalerum minutum (Fabricius)	A	mire	flowers		2	1	Tottenham (1954)	
Eusphalerum sorbicola (Kangas)	A	wet moorland	flowers	RI	0		Hyman (1994)	
Falagria sulcatula (Gravenhorst)	A	marsh	moss, exposed sediments	N-	+		Hyman (1994)	
Gabrius appendiculatus Sharp	A	riparian	litter		+		Lott (unpubl.)	*Gabrius subnigritulus*
Gabrius astutoides (Strand)	A	riparian, sea cliffs	exposed sediments	RI	1		Hyman (1994)	
Gabrius bishopi Sharp	A	riparian	exposed sediments	Nb [-]	32	1.81		
Gabrius breviventer (Sperk)	B	marsh	tussocks, litter		80	3.52		*Gabrius pennatus*
Gabrius exiguus (von Nordmann)	A?	riparian		RI	0		Koch (1989)	
Gabrius keysianus Sharp	A	coastal	exposed sand	Nb	2	1	Hyman (1994)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Gabrius nigritulus (Gravenhorst)	A	riparian	exposed sand		3	1.5	Lott (unpubl.)	
Gabrius osseticus (Kolenati)	B	marsh	exposed sand	Nb	+		Hyman (1994)	
Gabrius trossulus (von Nordmann)	A	mire	moss, tussocks		8	2		
Gabrius velox Sharp	A	wet woodland	litter	Nb	2	3	Hyman (1994)	
Geodromicus nigrita (Müller)	A	riparian	exposed shingle, moss		4	1.33	Hammond (1998)	*Psephidonus nigrita*
Geostiba circellaris (Gravenhorst)	C				43	2.85		
Gnypeta caerulea (Sahlberg)	A	riparian	moss	N-	+		Hyman (1994)	
Gnypeta carbonaria (Mannerheim)	A	riparian	exposed silt		112	9.91		
Gnypeta ripicola (Kiesenwetter)	A	riparian	exposed sediments, litter	N- [-]	45	3.25		
Gnypeta rubrior Tottenham	A	riparian	exposed silt		66	4.77		
Gymnusa brevicollis (Paykull)	A	mire	*Sphagnum*		25	2.25		
Gymnusa variegata Kiesenwetter	A	mire	*Sphagnum*	N-	3	2	Fowler (1888)	
Gyrophaena joyi Wendeler	A	wet woodland	fungi	N-	+		Hyman (1994)	
Gyrophaena lucidula Erichson	A	wet woodland	fungi	N-	+		Hyman (1994)	
Habrocerus capillaricornis (Gravenhorst)	C				9	1.89		
Halobrecta algae (Hardy)	A	sea shore	tidal refuse		2		Hammond (2000)	
Halobrecta algophila (Casey)	A	sandy sea shore	tidal refuse		0		Hammond (2000)	
Halobrecta flavipes Thomson	A	sea shore	tidal refuse		1		Hammond (2000)	
Halobrecta princeps (Sharp)	A	sandy sea shore	tidal refuse	RI	0		Hammond (2000)	
Heterota plumbea (Waterhouse)	A	sandy sea shore	tidal refuse	N-	2		Hammond (2000)	
Heterothops binotatus (Gravenhorst)	A	sea shore	tidal refuse		0		Hammond (2000)	
Hydrosmecta delicatissima (Bernhauer)	B?	sea shore	exposed shingle	RK	0		Allen & Eccles (1988)	*Hydrosmectina delicatissima*
Hydrosmecta delicatula (Sharp)	A	riparian	exposed shingle	RK	4	1	Hyman (1994)	
Hydrosmecta eximia (Sharp)	A	riparian	exposed shingle		15	4.86		
Hydrosmecta fragilis (Kraatz)	A	riparian	exposed shingle	N-	5	3.25		
Hydrosmecta longula (Heer)	A	riparian	exposed shingle	N-	10	2.33		*Hydrosmecta thinobioides*
Hydrosmecta septentrionum Benick	A	riparian	exposed sand & shingle	N-	2	3	Hyman (1994)	*Hydrosmectina septentrionum*

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Hygronoma dimidiata (Gravenhorst)	A	marsh	tall emergent veg., litter		68	1.69	Fowler (1888)	
Hygropora cunctans (Erichson)	A	marsh	litter, moss	RK	1		Hyman (1994)	
Ilyobates bennetti Donisthorpe	B	marsh		N-	+		Hyman (1994)	*Ilyobates subopacus*
Ilyobates nigricollis (Paykull)	B	wet heath, wet woodland	*Sphagnum*	RK	1	1	Orton (1989)	
Ilyobates propinquus (Aubé)	B	riparian		N-	+		Hyman (1994)	
Ischnopoda atra (Gravenhorst)	A	riparian	litter		91	2.14		*Tachyusa atra*
Ischnopoda coarctata Erichson	A	riparian	exposed soft sediments	N-	8	1.25	Hyman (1994)	*Tachyusa coarctata*
Ischnopoda constricta (Erichson)	A	riparian	exposed soft sediments		17	10.3		*Tachyusa constricta*
Ischnopoda leucopus (Marsham)	A	riparian	exposed sand		18	3.25		*Tachyusa leucopus*
Ischnopoda scitula Erichson	A	riparian	exposed soft sediments	RK	+		Hyman (1994)	*Tachyusa scitula*
Ischnopoda umbratica (Erichson)	A	riparian	exposed soft sediments		5	4.25		*Tachyusa umbratica*
Ityocara rubens (Erichson)	A	marsh		RI	0		Hyman (1994)	
Lathrobium angustatum Lacordaire	A	riparian, sea cliffs	exposed silt, litter	Nb	1		Hyman (1994)	
Lathrobium angusticolle Lacordaire	A	riparian	exposed shingle	Nb	2	1	Hyman (1994)	
Lathrobium brunnipes (Fabricius)	B	fen	tussocks, moss, litter		218	2.9		
Lathrobium dilutum Erichson	A	riparian	exposed shingle		+		Hyman (1994)	
Lathrobium elongatum (Linnaeus)	B	fen, carr	moss, litter		43	3.93		
Lathrobium fovulum Stephens	A	fen	litter		13	1.77	Fowler (1888)	
Lathrobium fulvipenne (Gravenhorst)	B	riparian	tussocks		68	2.13		
Lathrobium impressum Heer	A	carr	litter		17	1.8		
Lathrobium longulum Gravenhorst	B	marsh	grass tussocks, litter		9	1.33	Fowler (1888)	
Lathrobium multipunctum Gravenhorst	B	riparian, sea cliffs	exposed soft sediments		3	1	Fowler (1888)	*Lobrathium multipunctum*
Lathrobium pallidipenne Hochhuth	B	riparian	exposed sediments	N-	1	1	Hyman (1994)	*Lathrobium ripicola*
Lathrobium pallidum von Nordmann	B	riparian	exposed sediments	RK	1	1	Hyman (1994)	
Lathrobium quadratum (Paykull)	A	marsh, fen	moss, litter		27	1.88		
Lathrobium rufipenne Gyllenhal	A	fen, bog	*Sphagnum*, reed litter	R2	(+)		Shirt (1987)	
Lathrobium rufonitidum Reitter	A	riparian		RI	(+)		Hyman (1994)	*Lathrobium fennicum*
Lathrobium terminatum Gravenhorst	A	fen, bog	moss		89	2.39		
Lathrobium volgense Hochhuth	B?	riparian, marsh	tussocks		30	1.64	Lott (unpubl.)	*Lathrobium geminum*
Lathrobium zetterstedti Rye	A	wet moorland		Nb	(+)		Hyman (1994)	

Wetland rove beetles (Staphylinidae

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Lesteva hanseni Lohse	A	riparian, sea cliffs	moss	N-	1	5	Hyman (1994)	
Lesteva longoelytrata (Goeze)	A	riparian	exposed sediments		208	4.73		
Lesteva monticola Kiesenwetter	A	mire	moss		+		Koch (1989)	
Lesteva pubescens Mannerheim	A	riparian	exposed sediments		14	2.22		
Lesteva punctata Erichson	A	riparian, sea cliffs	exposed sediments, moss		8	3		
Lesteva sicula Erichson	A	fen, riparian	moss, litter		188	3.33		*Lesteva heeri*
Manda mandibularis (Gyllenhal)	A	woodland pools	litter, moss	R1	(+)		Shirt (1987)	
Medon pocofer (Peyron)	A	sea shore	exposed shingle	RI	0		Hyman (1994)	
Medon ripicola (Kraatz)	A	riparian, coastal	exposed sediments	N-	(+)		Hyman (1994)	
Meotica anglica Benick	A	riparian	exposed sediments	N-	0		Hyman (1994)	
Meotica apicalis Benick	A	riparian	litter		+		Muona (1991)	
Meotica exilis (Knoch)	B	eurytopic	soil, litter		0		Muona (1991)	
Meotica exillima Sharp	A	mire	*Sphagnum*	[N-]	5	2.2	Muona (1991)	
Micralymma marina (Ström)	A	intertidal	rock crevices		1		Steel (1958)	
Microdota indubia (Sharp)	C				6	1.83		*Atheta indubia*
Micropeplus caelatus Erichson	A	wet moorland	*Sphagnum*	Ir	0		Koch (1989)	
Mocyta fungi agg (Gravenhorst)[5]	B	marsh	litter, tussocks		258	2.49		*Atheta fungi*
Mycetota laticollis (Stephens)	B	marsh	litter		36	3.86		
Myllaena brevicornis (Matthews)	A	flushes, riparian	moss		26	2.05		
Myllaena dubia (Gravenhorst)	A	fen	litter		58	7.52		
Myllaena elongata (Matthews)	A	riparian	exposed sediments	N- [-]	20	2.45		
Myllaena gracilicornis Fairmaire & Brisout	A?	riparian?		Ex	0		Hyman (1994)	
Myllaena gracilis (Matthews)	A	marsh	litter		9	2.11		
Myllaena infuscata Kraatz	A	fen	litter		30	2.39		
Myllaena intermedia Erichson	A	fen, marsh	litter		77	2.84		
Myllaena kraatzi Sharp	A	mire	moss	N-	15	3.71		
Myllaena masoni Matthews	A		*Molinia*	Ex	0		Hollnaicher & Wunderle (1987)	

[5] This is a complex of species in need of taxonomic revision (Assing & Schülke 2001). Some species within the complex may have wetland habitats.

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Myllaena minuta (Gravenhorst)	A	fen	litter		13	2.33		
Myrmecopora brevipes Butler	A	sandy seashore	tidal refuse	N-	0		Hammond (2000)	
Myrmecopora oweni Assing	A	seashore	tidal refuse, under stones		1		Assing (1997)	
Myrmecopora sulcata (Kiesenwetter)	A	sandy seashore	tidal refuse		3		Assing (1997)	*Myrmecopora simillima*
Myrmecopora uvida (Erichson)	A	seashore	tidal refuse, rock crevices		0		Assing (1997)	
Neobisnius lathrobioides (Baudi)	B?	riparian	exposed soft sediments		(+)		Lott (unpubl.)	
Neobisnius procerulus (Gravenhorst)	A	riparian	exposed soft sediments	RK	(+)		Hyman (1994)	
Neobisnius prolixus (Erichson)	A	riparian	exposed sediments	RK	(+)		Hyman (1994)	
Neobisnius villosulus (Stephens)	A	riparian	exposed soft sediments		22	1.36	Fowler (1888)	
Ocalea latipennis Sharp	A	riparian			0		Koch (1989)	
Ocalea rivularis Miller	A	riparian	exposed soft sediments		+		Hammond (1998)	
Ochthephilum fracticorne (Paykull)	A	fen, bog	moss, litter		18	2.19		
Ochthephilum jacquelini (Boieldieu)	A	saltmarsh	litter	RI	(+)		Hammond (2000)	
Ochthephilus andalusiacus (Fagel)	A	riparian	exposed sediments	N-	3	4	Hyman (1994)	
Ochthephilus angustior (Bernhauer)	A	riparian	exposed sediments	N-	+		Hyman (1994)	*Ochthephilus venustulus*
Ochthephilus aureus (Fauvel)	A	riparian	exposed sediments		7	3.67		
Ochthephilus omalinus (Erichson)	A	riparian	exposed sediments		13	6.44		
Ocyusa defecta Mulsant & Rey	A	marsh		RK	0		Hyman (1994)	
Ocyusa maura (Erichson)	A	marsh, fen	litter		27	4.13		
Ocyusa picina (Aubé)	A	fen, bog	litter		50	5.77		*Ocyusa picina*
Olophrum assimile (Paykull)	A	montane	wet moss, litter	RI	0		Shirt (1987)	
Olophrum consimile (Gyllenhal)	A	fen	moss, litter	Na	(+)		Hyman (1994)	
Olophrum fuscum (Gravenhorst)	A	fen	moss		7	1	Lott (unpubl.)	
Olophrum piceum (Gyllenhal)	B	flushes	moss, tussocks		18	2.47		
Omalium laeviusculum Gyllenhal	A	sea shore	tidal refuse		7	2.33		
Omalium riparium Thomson	A	sea shore	tidal refuse		6	9		
Omalium rugulipenne Rye	A	sandysea shore	tidal refuse	N-	0		Hammond (2000)	
Othius laeviusculus Stephens	C				5	2		
Oxypoda brevicornis (Stephens)	C				14	2.25		*Oxypoda umbrata*
Oxypoda elongatula Aubé	A	fen	moss, tussocks, litter		125	2.88		
Oxypoda exoleta Erichson	B	riparian	exposed soft sediments		11	1.64	Lott (1995)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Oxypoda lentula Erichson	A	marsh, dune slacks	litter, moss		25	5.2		
Oxypoda mutata Sharp	B	riparian		RK	+		Hyman (1994)	*Oxypoda riparia*
Oxypoda nigrocincta Mulsant & Rey	A	floodplain woodland	litter	RI	1	1	Hammond (1998)	
Oxypoda praecox Erichson	A?	riparian	mammal nests	RK	0		Koch (1989)	
Oxypoda procerula Mannerheim	B	mire	tussocks, moss, litter		2	1.5	Lott (unpubl.)	
Oxytelus fulvipes Erichson	A	carr	litter	Na	8	3.5		
Pachnida nigella (Erichson)	A	fen	litter		54	3.68		
Paederidus rubrothoracicus (Goeze)	A	riparian, coastal	exposed sand	Ex	(+)		Hyman (1994)	
Paederus caligatus Erichson	A	fen	moss	R3	16	3.33		
Paederus fuscipes Curtis	A	fen	moss	Nb	10	3.8		
Paederus littoralis Gravenhorst	B	riparian, coastal	exposed soft sediments		3	4	Lott (unpubl.)	
Paederus riparius (Linnaeus)	A	fen	moss		42	10.5		
Parameotica difficilis (Brisout)	A	marsh	litter	N-	4	1	Hyman (1994)	*Atheta difficilis*
Parocyusa longitarsis (Erichson)	A	riparian	exposed soft sediments		166	6.31		*Chiloporata longitarsis*
Parocyusa rubicunda (Erichson)	A	riparian	exposed soft sediments	N-	+		Hyman (1994)	*Chiloporata rubicunda*
Philhygra arctica (Thomson)	A	wet moorland	*Sphagnum*, tussocks		+		Koch (1989)	*Atheta arctica*
Philhygra britteni (Joy)	A	riparian		N-	1	1	Hyman (1994)	*Atheta britteni*
Philhygra debilis (Erichson)	A	riparian	litter		3	1.67	Fowler (1888)	*Atheta debilis*
Philhygra deformis (Kraatz)	B	riparian	moss	N-	1	1	Hyman (1994)	*Atheta deformis*
Philhygra elongatula (Gravenhorst)	A	riparian, marsh	litter		216	7.15		*Atheta elongatula*
Philhygra fallaciosa (Sharp)	A				7	2.29	Anderson (2000)	*Atheta fallaciosa*
Philhygra gyllenhalii (Thomson)	A	carr, marsh	litter		27	1.6	Fowler (1888)	*Atheta gyllenhali*
Philhygra hygrobia (Thomson)	A	carr	litter	N-	23	2.7		*Atheta hygrobia*
Philhygra hygrotopora (Kraatz)	A	riparian	exposed sediments, moss		42	2.08		*Atheta hygrotopora*
Philhygra luridipennis (Mannerheim)	A	riparian	exposed soft sediments		7	1	Koch (1989)	*Atheta luridipennis*
Philhygra malleus (Joy)	A	riparian, marsh	litter		221	2.91		*Atheta malleus*
Philhygra melanocera (Thomson)	A	marsh, riparian	litter		30	2		*Atheta melanocera*
Philhygra obtusangula (Joy)	A	carr	litter, exposed peat		15	1.86		*Atheta obtusangula*
Philhygra palustris (Kiesenwetter)	B	riparian	exposed soft sediments		2	6	Koch (1989)	*Atheta palustris*
Philhygra parca Mulsant & Rey	A	riparian		RK	2	1	Hyman (1994)	*Atheta nannion*

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Philhygra scotica (Elliman)	A	riparian	under stones on sand	N-	0		Lyszkowski & Owen (2000)	*Atheta scotica*
Philhygra terminalis (Gravenhorst)	A	marsh	moss, litter	RK	2	2.5	Hyman (1994)	*Atheta terminalis*
Philhygra volans (Scriba)	A	marsh, riparian	litter		77	1.51	Lott (unpubl.)	*Atheta volans*
Philonthus atratus (Gravenhorst)	A	riparian	exposed soft sediments	Na	3	3.5	Whitehead (1990)	
Philonthus corvinus Erichson	A	fen	moss	Na	5	1	Hyman (1994)	
Philonthus decorus (Gravenhorst)	C				9	2.14		
Philonthus dimidiatipennis Erichson	A	saltmarsh		RI	0		Shirt (1987)	
Philonthus fumarius (Gravenhorst)	A	fen		Nb	17	2.45		
Philonthus furcifer Renkonen	A	marsh		Ir	4		Lott & Bilton (1991)	
Philonthus mannerheimi Fauvel	A	fen, marsh, riparian		Nb	1		Hyman (1994)	
Philonthus micans (Gravenhorst)	A	fen, carr	litter		35	20.2		
Philonthus micantoides Benick & Lohse	A	marsh	litter, tussocks		9	4.25		
Philonthus nigrita (Gravenhorst)	A	fen	*Sphagnum*		30	3.24		
Philonthus punctus (Gravenhorst)	A	riparian	exposed silt		2		Hyman (1994)	
Philonthus quisquiliarius (Gyllenhal)	A	riparian	exposed silt		120	3.15		
Philonthus rotundicollis (Ménétriés)	A	riparian	exposed sediments		+		Cooter (1989)	
Philonthus rubripennis Stephens	A	riparian	exposed shingle		6	2.25		
Philonthus umbratilis (Gravenhorst)	B	flushes	litter		19	1.16	Lott (unpubl.)	
Phytosus balticus Kraatz	A	sandy sea shore	tidal refuse		0		Hammond (2000)	
Phytosus nigriventris (Chevrolat)	A	sandy sea shore	tidal refuse	RK	0		Hammond (2000)	
Phytosus spinifer Curtis	A	sandy sea shore	tidal refuse		0		Hammond (2000)	
Planeustomus flavicollis Fauvel	A?	riparian?	exposed soft sediments?	RI	0		Shirt (1987)	
Planeustomus palpalis (Erichson)	A	riparian	exposed soft sediments	RK	1	1	Hyman (1994)	
Platystethus alutaceus Thomson	A	riparian	exposed silt		0		Hammond (1971)	
Platystethus cornutus (Gravenhorst)	A	riparian	exposed silt		89	5.12		
Platystethus degener Mulsant & Rey	A	riparian	exposed silt		1	4	Hammond (1971)	
Platystethus nitens (Sahlberg)	A	marsh, carr	litter		13	1.08	Hammond (1971)	
Platystethus nodifrons Mannerheim	A	marsh, carr	litter	N-	13	1.15	Hammond (1971)	
Proteinus laevigatus Hochhuth	B	wet woodland	litter, fungi, tussocks		1	1	Lott (unpubl.)	*Proteinus macropterus*
Pselaphaulax dresdensis (Herbst)	A	bog	wet moss	N-	2	1	Hyman (1994)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Pselaphus heisei Herbst	A	bog	moss, tussocks		4	1.5	Pearce (1957)	
Pseudomedon obsoletus (von Nordmann)	A	riparian	litter	RI	(+)		Hyman (1994)	*Lithocharis obsoleta*
Pseudopasilia testacea (Brisout)	A	sandy sea shore	exposed sand	RK	0		Hammond (2000)	
Quedius auricomus Kiesenwetter	A	riparian	moss	Nb	1		Hyman (1994)	
Quedius balticus Korge	A	fen	litter	R1	0		Shirt (1987)	
Quedius boopoides Munster	A	mire	*Sphagnum*		3	1.5	Johnson (1966)	
Quedius cinctus (Paykull)	B	flushes	tussocks		6	2.17		
Quedius fuliginosus (Gravenhorst)	B	fen, marsh, riparian	litter, tussocks, moss		31	1.29	Lott (unpubl.)	
Quedius fulvicollis (Stephens)	B	riparian, marsh	litter, moss	Nb	+		Hyman (1994)	
Quedius maurorufus (Gravenhorst)	A	fen	moss		106	2.17		
Quedius plancus Erichson	B	riparian	exposed soft sediments	Na	2	1.5	Hyman (1994)	
Quedius riparius Kellner	A	riparian	moss	RI	(+)		Hyman (1994)	
Quedius umbrinus Erichson	A	flushes	litter, tussocks		15	1.67	Hammond (1998)	
Reichenbachia juncorum (Leach)	B	flushes	moss, tussocks, litter		5	2.5		
Remus sericeus Holme	A	sea shore	tidal refuse		3		Hammond (2000)	*Cafius sericeus*
Rugilus erichsoni (Fauvel)	B	flushes	tussocks		5	2.75		
Rugilus fragilis (Gravenhorst)	B	marsh, fen	litter	N-	+		Hyman (1994)	
Rybaxis longicornis (Leach)	A	carr	moss, tussocks		37	2.62		*Rybaxis laminata*
Schistoglossa aubei (Brisout)	A	fen	tussocks, *Sphagnum*	RK	3	1	Sinclair & Owen (1998)	
Schistoglossa benicki Lohse	A		moss	RK	0		Hyman (1994)	
Schistoglossa curtipennis (Sharp)	A	mire	tussocks		1	1	Koch (1989)	
Schistoglossa gemina (Erichson)	A	marsh, fen	tussocks, litter, moss	N-	10	1.33	Hyman (1994)	*Schistoglossa gemina*
Schistoglossa viduata (Erichson)	A	fen	tussocks	RK	4	2	Hyman (1994)	
Scopaeus gracilis (Sperk)	A	riparian	exposed shingle	RK	(+)		Hyman (1994)	
Scopaeus laevigatus (Gyllenhal)	A	slumping cliff seepages	exposed sand	RI	(+)		Shirt (1987)	
Scopaeus minutus Erichson	A	slumping cliff seepages	exposed soft sediments	R1	0		Hyman (1994)	
Scopaeus ryei Wollaston	A	riparian, coastal	exposed shingle	RI	0		Shirt (1987)	*Scopaeus minimus*
Scopaeus sulcicollis (Stephens)	B	riparian, slumping cliffs	exposed sediments		2		Allen (1969)	*Scopaeus cognatus*
Sepedophilus pedicularius (Gravenhorst)	A	fen	litter, moss, tussocks	N-	1	1	Hammond (1973)	
Stenus argus Gravenhorst	A	carr	litter	Nb	12	3.42		

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Stenus atratulus Erichson	B?	riparian	exposed sand	Nb	1		Hyman (1994)	
Stenus bifoveolatus Gyllenhal	A	fen	emergent veg.		84	6.23		
Stenus biguttatus (Linnaeus)	A	riparian	exposed soft sediments	[N-]	2	1	Lott (1999a)	
Stenus bimaculatus Gyllenhal	A	carr	litter		124	1.81		
Stenus binotatus Ljungh	A	riparian	tall emergent veg.		30	3.04		
Stenus boops Ljungh	A	eurytopic			350	4.03		
Stenus brevipennis Thomson	A	wet moorland	moss		4	1	Kevan & Allen (1961)	
Stenus brunnipes Stephens	B?	riparian, marsh	moss		17	1.62	Lott (unpubl.)	
Stenus butrintensis Smetana	A	riparian	tussocks, emergent veg.	N-	1	3	Hyman (1994)	
Stenus calcaratus Scriba	A	riparian	litter	RK	0		Hyman (1994)	
Stenus canaliculatus Gyllenhal	A	riparian			19	2		
Stenus canescens Rosenhauer	A	riparian	tussocks, emergent veg.	Nb	(+)		Hyman (1994)	
Stenus carbonarius Gyllenhal	A	carr, fen	litter	Nb	11	2.3		
Stenus cicindeloides (Schaller)	A	fen, marsh	tussocks		104	2.55		
Stenus circularis Gravenhorst	B	fen	litter	Nb	1	1	Hyman (1994)	
Stenus comma LeConte	A	riparian	exposed soft sediments		26	2.04		
Stenus crassus Stephens	B	riparian	exposed soft sediments		1		Anderson (1984)	
Stenus europaeus Puthz	A	fen	litter, moss	Nb	2	2.5	Hyman (1994)	
Stenus flavipes Stephens	A	carr	litter		25	1.95		
Stenus formicetorum Mannerheim	B	fen			8	3.13		
Stenus fornicatus Stephens	A	fen	emergent veg., moss	Nb	6	1	Hyman (1994)	
Stenus fossulatus Erichson	B	riparian	exposed soft sediments	R1	(+)		Shirt (1987)	
Stenus fulvicornis Stephens	B	marsh	moss, litter		23	1.43	Anderson (1984)	
Stenus fuscipes Gravenhorst	A	mire	litter		8	5.5		
Stenus glabellus Thomson	A	fen	emergent veg.	Ir	3	1	Lott (1993b)	
Stenus glacialis Heer	A	montane	wet moss	RK	0		Hyman (1994)	
Stenus guttula Müller	A	riparian, slumping cliffs	moss, exposed sediments		25	1.79	Reid (1984)	
Stenus guynemeri Jacquelin du Val	A	riparian	moss, exposed shingle		3	2	Hammond (1998)	
Stenus impressus Germar	B	mire	moss		39	2.06		
Stenus incanus Erichson	A	riparian	exposed shingle	RK	+		Hyman (1994)	

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Stenus incrassatus Erichson	A	riparian	exposed sand		3	1	Anderson (1984)	
Stenus juno (Paykull)	A	marsh, fen, carr			383	3.64		
Stenus kiesenwetteri Rosenhauer	A	bog	moss	R2 [RK]	7	4		
Stenus latifrons Erichson	A	fen			73	4.55		
Stenus longitarsis Thomson	A?	riparian	exposed sediments	RI	2	1	Lott (2001)	
Stenus ludyi Fauvel	A	wet woodland, riparian		RI	(+)		Koch (1989)	
Stenus lustrator Erichson	A	wet flushes	tussocks		3	1	Reid (1985)	
Stenus melanarius Stephens	A	fen, bog	moss		27	5.93		
Stenus melanopus (Marsham)	B	riparian	exposed soft sediments		28	2.16		
Stenus nigritulus Gyllenhal	A	riparian, saltmarsh	litter, exposed sediments	Nb	(+)		Hyman (1994)	
Stenus nitens Stephens	A	mire			21	7.28		
Stenus nitidiusculus Stephens	A	fen, bog	moss, emergent veg.		96	4.01		
Stenus niveus Fauvel	A	fen	tussocks, moss, litter	Nb	4	1	Hyman (1994)	
Stenus opticus Gravenhorst	A	fen, marsh	litter	Na	1	1	Hyman (1994)	
Stenus oscillator Rye	A	fen		Nb	2	2	Hyman (1994)	
Stenus pallipes Gravenhorst	A	marsh	litter		2	1	Tottenham (1954)	
Stenus pallitarsis Stephens	A	riparian	tall emergent veg.		33	1.85		
Stenus palposus Zetterstedt	A	riparian	exposed sand	Ex, Ir	0		Anderson (1977)	
Stenus palustris Erichson	A	fen	litter, moss, tussocks	Nb	4	1.25	Hyman (1994)	
Stenus picipennis Erichson	A	flushes	tussocks		33	3.03		
*Stenus picipes*Stephens	C				12	2.33		
Stenus proditor Erichson	A	fen, marsh		RI	(+)		Hyman (1994)	
Stenus providus Erichson	B	fen			65	2.55		
Stenus pubescens Stephens	A	riparian	tall emergent veg.		34	3.45		
Stenus pusillus Stephens	A	riparian	exposed soft sediments		26	1.35	Fowler (1888)	
Stenus solutus Erichson	A	fen	emergent veg.		54	2.4		
Stenus tarsalis Ljungh	A	marsh			59	1.89		
Stenus umbratilis Casey	A	mire	emergent veg.		6	1.5	Anderson (1984)	
Sunius bicolor (Olivier)	A	riparian		RK	0		Koch (1989)	
Tachyporus formosus Matthews	A	marsh, sea cliffs	moss	Na	0		Hyman (1994)	
Tachyporus hypnorum (Fabricius)	C				95	2.18		

Species	Fidelity	Habitat	Microhabitats	Status	No samples	Mean abundance	Literature referencess	Synonym
Tachyporus obtusus (Linnaeus)	C				97	2.26		
Tachyporus pallidus Sharp	A	riparian, marsh	tussocks		118	1.83		
Tachyporus transversalis Gravenhorst	B	bog			9	1.5	Reid (1986)	
Teropalpus unicolor (Sharp)	A	sandy sea shore	tidal refuse		1		Hammond (2000)	
Thinobaena vestita (Gravenhorst)	A	sea shore, estuaries	tidal refuse		9	16		*Atheta vestita*
Thinobius brevipennis Kiesenwetter	A	riparian	exposed soft sediments	RK	0		Hyman (1994)	
Thinobius ciliatus Kiesenwetter	A	riparian	exposed shingle	N-	1		Hyman (1994)	*Thinobius praetor*
Thinobius crinifer Smetana	A	riparian	exposed shingle	N-	2	1	Hyman (1994)	*Thinobius strandi*
Thinobius linearis Kraatz	A	riparian	exposed shingle	Na	3	1.5	Hyman (1994)	*Thinobius bicolor*
Thinobius longipennis (Heer)	A	riparian	exposed shingle	[RK]	1		Lott (1993a)	
Thinobius major Kraatz	A	riparian	exposed shingle	RK	0		Hyman (1994)	
Thinobius newberyi Scheerpeltz	A	riparian	exposed shingle	RI	0		Shirt (1987)	
Thinodromus arcuatus (Stephens)	A	riparian	moss		16	2.13		
Trissemus impressus (Panzer)	A	fen	moss		9	2.13		
Zyras collaris (Märkel)	A	marsh	litter	[N-]	2	1.5	Lott (2002)	

4.6 Statistical summary

Of the 606 species recorded in the WETCAST database, 422 qualified for inclusion in the list. An additional 175 species were identified from literature sources and records of casual collecting making a total of 597 wetland species, of which 21 rove beetles are considered to require further work in order to confirm their association with wetlands in Britain, and three ground beetles and 13 rove beetles are regarded as abundant, predominantly terrestrial species that are often found in wetland samples.

The numbers of species in each affinity class is shown in table 7. Approximately 50% of British ground beetle species and nearly 40% of British rove beetle species are here regarded as wetland species. The figures do not contradict estimates that non-aquatic invertebrates in freshwater wetlands have a higher species diversity than aquatic invertebrates. The number of rove beetle species in category A alone exceeds the number of aquatic beetle species (approximately 300 in families listed in table 2, p5). A final assessment of the relative species richness of aquatic and non-aquatic invertebrates would need to take account of the Diptera, an order which probably contains an even greater number of wetland species than the Coleoptera.

The criteria used for compiling the list are inclusive rather than exclusive, but it should be noted that in addition to the listed species, there are several species characteristic of alluvial soils that may be adapted to periodically flooded environments.

Table 7. Numbers of wetland Carabidae and Staphylinidae placed in each affinity class. (For explanation of affinity classes, see p36.)

	A	B	C	total
Carabidae	134	38	3	175
Staphylinidae	345	64	13	422
total	479	102	16	597

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