THE BIOGEOGRAPHY OF THE COLEOPTERA OF THE ORKNEY ISLES OF BRITAIN

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With 4 figures and 8 tables

ABSTRACT. The Coleopteran (beetle) fauna of Orkney is described on the basis of recent collecting and palaeoentomological studies (1988-91), and earlier published and unpublished research. The number of species recorded on the islands has risen by 7, from 357 and 364, although it is apparent that several habitats, particularly synanthropic ones, remain undercollected. An additional eighteen species are known only as Holocene fossils. Despite an increase in the amount of entomological work, there are no studies examining the ecology of the fauna. Collections from Westray, an island in the north of the group, provides a preliminary classification of heath and grassland communities. Further work is needed to expand the classification, notably from islands such as Hoy and Rousay that have markedly contrasting environments. The zoogeography of the beetles is discussed in comparison with the Shetlandic fauna. Both island groups have many of the features that characterise other oceanic islands in the North Atlantic region. The insect faunas have no endemics, are depauperate in species and disharmonic, with a disproportionately large number of predators and a dearth of phytophages. Faunistically Orkney and Shetland belong to the British Isles, having more species in common with this area than Scandinavia. The origins of the fauna are not well known and immigration from the mainland is assumed to be an important mechanism, but when and how this might have taken place is poorly documented. A possible Lateglacial landbridge has been hypothesised between Orkney and Caithness on the mainland. Later colonisation is complicated by the early settlement of the islands by prehistoric peoples, who greatly modified the environment and may have introduced a substantive element of the faunas. Orkney probably received most of its colonists from mainland Scotland, although there is a possibility that, along with Shetland, some species arrived from Scandinavia.

KEY WORDS: Orkney, Shetland, Biogeography, Zoogeography, Coleoptera, Fossils

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INTRODUCTION

The Orkney islands are situated at the far north east of the British Isles. The islands are separated from mainland Scotland by the Pentland Firth which narrows to 16 km between north Caithness and South Ronaldsay, the most southerly inhabitated island of the Orkney group. Although pollen and charcoal evidence has been invoked to suggest early Holocene occupation, the earliest archaeological remains belong to the Neolithic period (c. 5000BP), and there are a large number of monuments dating to this and later periods (RENFREW 1979; 1985). The palynological literature clearly indicates that humans have had a great impact on the landscapes of the islands. The profiles of MOAR (1969), KEATINGE & DICKSON (1979) and BUNTING (1994) highlight the level of landscape modification by early agriculturalists, and they have been implicated in the disappearance of woodland and the increase in heathland development (but cf. BUNTING 1996). This pattern of vegetational change is similar to that experienced at various times on other Atlantic islands, on Shetland (BENNETT et al. 1992; KEITH-LUCUS 1986), Faroe (JÓHANSEN 1975; 1985), Iceland (HALLSDÓTTIR 1987), and Greenland (FREDSKILD 1983; 1988).

The distinctive Orcadian landscape has a unique ecology that has interested naturalists for many years (see BERRY 1985). Its best known inhabitant, the Orkney vole, *Microtus orcadensis*, is now regarded as a subspecies of *Microtus arvalis* (BERRY & ROSE 1975). Elsewhere in the British Isles, *M. arvalis* is known only from Guernsey, although the species is widely distributed on the continent. The origins of the vole populations of Orkney are summarised by BERRY (1985) who suggests that the species may have been introducted to Orkney with colonists from the continent. In contrast, the invertebrate fauna, is comparatively under-researched and this lack of data has hampered biogeographic studies. It is apparent that the Coleoptera (beetles) of Orkney exhibit many of the characteristics of the faunas of other Atlantic islands, such as Shetland, Faroe, Iceland and Greenland. The origins and zoogeography of the North Atlantic islands beetle fauna has been the subject of considerable debate (BUCKLAND 1988; DOWNES 1988; LINDROTH 1931; 1957). Notwithstanding their faunal similarities, Orkney and Shetland have tended to be ignored in this general discussion. In part, this is due to the paucity of research, but more important is the geographical proximity of the islands to Britain which has led workers to treat them as part of the mainland. This paper, (i) considers the ecology of the beetles of Westray, north Orkney, and uses this survey and additional published and unpublished sources to, (ii) examine the zoogeography of the Orkney Coleoptera (beetle) fauna. The aim is to establish whether the fauna it is truly British, and to consider aspects of the islands' faunal history in comparison with that of Shetland and the other islands of the North Atlantic region.

Background

The Orkney Islands

Orkney lies between 58° 41'N and 59° 24'N and 2° 22'W and 4° 25'W making it approximately equidistant between Reykjavík, Stockholm, Berlin, Brussels, and Paris (BERRY 1985; Fig 1). The 70 islands, islets and skerries of the group are distributed over 90 km north to south and 37 km west to east. In the main, the larger islands of the group are low-lying, fertile and biologically diverse. Much of the land is cultivated, and has maximum elevation of less than 273m OD, although the peat covered island of Hoy rises to 477m at its highest point.

Westray

Westray (Fig. 1) is one of the most northerly of the Orkney islands and, in common with the neighbouring isles of Sanday and Papa Westray, it is relatively low-lying and devoid of blanket peat and woodland. The island has several freshwater lochans and adjacent fen vegetation, many small seasonal pools on the higher ground and a small area of salt marsh at Tuquoy Bay to the south. Westray is intensely cultivated and grassland communities cover much of the island. Most of the land is used for pasturing cattle and sheep, although some barley is grown in the north of island. At the Links of Noltland in the north, machair vegetation can be found, similar to that on the Western Isles of Lewis, Harris and the Uists (CURRIE 1979; RICHIE 1979). On the higher ground, particularly Fitty Hill, there are small areas of *Calluna*, *Empetrum* and *Erica* heath (BERRY 1985: 82).

METHODS

The entomological surveys were carried out on Westray in the summer (July and August) of 1988, and these form the basis of an assessment of the ecology of elements of the Orcadian fauna. Sampling was undertaken in as many habitat types as was possible in the six week field season. Weather conditions during this period were changeable, although generally fair. Four separate phases of pitfall trapping was carried out, each one a week in duration. In total, 39 species of Coleoptera were recorded from the 33 sites in the pitfall survey (Table 1). The data were classified using Two-way Indicator Species Analysis (TWINSPAN; HILL 1979). The pitfall data were augmented by timed searching (40 mins) of aquatic, synanthropous (mainly barns), coprophilic (dung), and fucicolic (littoral) habitats (Table 2). The total number of species recorded as a result of the survey was 70.

The zoogeographic analyses for Orkney are based upon the list in BERRY (1985), which was compiled by Mr V. Lorimer of Orphir (Orkney) and Mr M. Bacchus of the British Natural History Museum, with recent additions to the list by SADLER (1993). Holocene fossil insect analyses are based on the data from three sites: a medieval (Norse) ditch section at Tuquoy on Westray, deposits from a Neolithic midden at Skara Brae on mainland Orkney (SADLER 1991b; Fig 1), and a peat succession sealed by tephra from a mid-Holocene eruption (H_4) of the volcano Hekla in Iceland (DUGMORE *et al.* 1995) at Helldalewater on Hoy. Data for the other North Atlantic islands comes from the following sources: Shetland (Bacchus in BERRY & JOHNSTON 1980; Buckland in press); Iceland (includes the review of LARSSON & GÍGJA (1959), updated by recent collecting (DUGMORE & BUCKLAND 1984; INGÓLFSSON 1976; LINDROTH 1965, LINDROTH *et al.* 1973; 1988, ÓLAFSSON 1979) and subfossil analyses (BUCKLAND 1988; BUCKLAND *et al* 1992; AMOROSI *et al* 1992)), Faroe (BENGSTON 1981; DINNIN unpubl; ENCKELL 1985, SADLER unpubl), Greenland (BÖCHER 1988; SADLER 1991a).

The beetle fauna

The published list of Orkney Coleoptera (in BERRY 1985) incorporates the work of POPPIUS (1904-5) and a survey of water beetles by BALFOUR-BROWNE (1948). BERRY's species list put the number of species on Orkney at a mere 358. Treatment of *Philonthus varius* (Gyll.) and *Philonthus varius var. shetlandicus* Poppius as records of one species (*contra* POPPIUS 1905) reduces the number to 357. Limited collecting was undertaken by SINCLAIR (1984; 1988), and a larger scale study of the modern and fossil Coleoptera of the islands (SADLER 1991b; 1993) has added a further seven species to the island list which now totals 364. A total of eighteen species are only recorded as Holocene fossils on the islands (Table 3) and only one site, that on Hoy, records an essentially natural Coleopterous fauna. The spatial coverage is thus patchy and more work remains to be completed, particularly on the southern islands, such as Hoy and Rousay, that have markedly contrasting environments.

Notes on species not recorded by Berry

CARABIDAE

Dyschirius globosus (Herbst). One individual recovered from a pitfall trap in an area of wet meadow on the silty soils of the drained Loch of Tuquoy (NGR HY 454433) on Westray. The species is widely distributed in the British Isles (LINDROTH 1974) and in continental Europe (LINDROTH 1985).

Laemostenus terricola (Herbst). Many individuals were captured in pitfall traps from heavily grazed pasture at Tuquoy (HY 454431) and the Links of Noltland. Although this troglophilous species is predominantly synanthropous in the north (LINDROTH 1986), it is occasionally taken remote from human habitations from birds' nests and the burrows of rabbits and other mammals. In common with the records from the Outer Hebrides (WELCH 1979), on Westray, the species is probably a resident in rabbit burrows, which were extremely common in the area of pitfall trapping.

STAPHYLINIDAE

Anotylus maritimus Thomson. One individual was shaken from seaweed on the strandline at the Bay of Tafts (HY 498417), on Westray. This species is widely distributed around the western coast of the British Isles and is a common inhabitat of the littoral of the Western Isles of Scotland (WELCH 1979).

A. sculpturatus (Gravenhorst). Many individuals taken in cow dung at various localities on Westray. The species occurs also as a fossil on the medieval site of Tuquoy.

T*achyporus dispar* (Paykull). Two individuals taken in pasture (HY 498417) on Westray. This species is a recent addition to the British list and was previously confused with *T. chrysomelinus* (L.). It is probable that some of the specimens listed by BERRY (1985) are in fact *T. dispar*. The species is widely distributed in the British Isles, where it is common on well drained soils (BOOTH 1988).

CRYPTOPHAGIDAE

Atomaria apicalis Erichson. Many individuals from pitfall traps in pastureland and shaken from hay residues in barns and hay ricks on Westray.

LATHRIDIIDAE

Lathridius pseudominutus (Strand). Many individuals taken in barns and hay stores and similar synanthropous habitats. The specimens were differentiated from *L. minutus* with recourse to the key characters outlined by TOZER (1972). The species is thought to be widely distributed throughout the British Isles (*op cit.*).

Beetle habitats on Westray

Grassland and heath grassland

The classification of Coleopteran habitats on Westray as interpreted from the TWINSPAN end groups is given in Figure 2. A total of 6 grassland habitat types are indicated and the frequency of species in the groups is shown in Table 1.

Habitat 1. Higher ground with thin mineral soils. Mainly heath grassland, characterized by *Olisthopus rotundatus* (Paykull) and *Tachinus marginellus* (F.). This mainly relates to the higher ground of Fitty Hill, in areas of what has been classified as Fell Field by BERRY (1985, p.76).

Habitat 2. Rough and rarely grazed grassland associated with the surroundings of buildings. Characteristic species include *Nebria spp.* and *Patrobus atrorufus* (Strom). This relates to perhaps the most abundant habitat on the island. It is highly modified and has a limited species diversity of plants and invertebrates.

Habitat 3. Wet meadow with some wetland vegetation, areas of exposed mud and a silty substrate. Light grazing by sheep. Characteristic species include *Loricera pilicornis* (F.) and *Helophorus grandis* Ill.

Habitat 4. Dry short pasture. Intensively grazed with an abundance of rabbit burrows. Characteristic species include *Nebria brevicollis* (F.), *Megasternum obscurum* (Marsh.) and *Tachyporus spp.*

Habitat 5. Lush coastal grassland on well-drained sandy soils. Rarely grazed by stock, but much damage by rabbits. Characteristic species include *Serica brunnea* (L.) and *Amara bifrons* (Gyllenhal). These sites were almost solely restricted to the Links of Noltland and have degraded machair communities analagous to those found in the Western Isles (WELCH 1979).

Habitat 6. Heavily grazed coastal grassland. Characteristic species include *Calathus spp.*, *Amara spp.* and *Leiodes dubia* (Kug.). A rather degraded Maritime grassland community where the dominant factor shaping community ecology is the intensity of grazing.

Other habitats

Table 2 shows the data resulting from timed searches of discrete habitats including, the littoral, culture-favoured or synanthropous habitats (mainly barns, byres and hay ricks), aquatic habitats (ditches, lochans and peaty pools) and coprophilic habitats (sheep, cattle and rabbit dung and manure). The littoral fauna is dominated by the hydrophilid, *Cercyon littoralis* (Gyll.) and the staphylinids, *Omalium riparium* Thoms. and *Cafius xantholoma* (Grav.). An absentee from this community is the small rove beetle, *Micralymma marina* (Strom). The species has an amphiatlantic distribution and is widely distributed in Iceland (LARSSON & GIGJA 1959), the Western Isles (WATERSTON 1981), Shetland (BACCHUS in BERRY & JOHNSTON 1980) and on the western coast of the British Isles (TOTTENHAM 1954). Why it has not been recorded from Orkney is not clear. Although it may relate to the dearth of work in littoral habitats, collecting in eastern Iceland indicates a preference for the upper tidal and supratidal zones of rocky shores, which are less frequent on Westray.

The dung faunas are similarly depauperate in species and typified by four species of *Aphodius* (*A. ater* (DeG.), *A. depressus* (Kug.), *A. rufipes* (L.), *A. rufus* (Moll)), the hydrophilid *Cercyon melanocephalus* (L.) and two species of staphylinid, *Megarthus depressus* (Payk.) and *Anotylus sculpturatus* (Grav.). As SKIDMORE (1991) has shown, coprophilic habitats often support a large and diverse community. The paucity of species on Westray is curious, particularly as species that occupy this habitat are effective and active dispersers, distributed in Caithness on the Scottish mainland.

The synanthropous habitats are characterised by mould feeders, such species of *Lathridius, Atomaria apicalis* Erich. and *Enicmus transversus* (Ol.), predators, including *Calathus melanocephalus* (L.), and staphylinids, *Omalium excavatum* Steph., *Tachinus signatus* Grav. and *Quedius spp.*, and occasional phytophages, such as, *Sitona lepidus* Gyll.. Similar assemblages are common in such situations elsewhere in the United Kingdom, Faroe (BENGSTON 1981), and Iceland (LARSSON & GÍGJA 1959). Bacchus notes that synanthropous species are not well-studied in Shetland (in BERRY & JOHNSTON 1980), an assertion that is supported by the zoogeographic analyses (below; Table 6).

Aquatic habitats on Westray are very limited. Most are very small bodies of standing water inhabited by species with high dispersal potential. Small and seasonal peaty pools at Noup Head are characterised by *Hydoporus pubescens* (Gyll.) and species of *Agabus*. The Haliplids, *Haliplus ruficollis* (DeG.) and *H. lineaticollis* (Marsh.), and the dytiscids *Hydroporus palustris* (L.) and *H. striola* (Gyll.) are common in the littoral zone of hill lochans. More eutrophic water bodies, primarily ditches, were dominated by *H. palustris.* Elsewhere on Orkney larger lochs, such as those at Harray and Stenness, have considerably more diverse faunas (BALFOUR-BROWNE 1948; BERRY 1985).

Zoogeography

For the purposes of this discussion the following definitions are used: Palaearctic species have distributions in Europe and Asia, whereas nearctic species are found only in the Americas; holarctic species are common to both areas. Circumpolar species are restricted to high latitude 'polar' regions in the palaearctic or nearctic regions. The term amphiatlantic refers to a distributional pattern which is restricted to the coastal regions on either side of the Atlantic Ocean.

In comparison to the European Continental fauna, the Orkney fauna is essentially disharmonic. Several families of Coleoptera are not recorded from the islands and the majority of the species (including introduced species) belong to four families, the ground beetles (Carabidae = 52 spp: 15%), the predatory water beetles (Dytiscidae = 34: 10%), the rove beetles (Staphylinidae = 89: 26%) and the weevils (Curculionidae = 32: 9%). The remaining

130 species (40% of the total) are dispersed through a further 29 beetle families. The zoogeographical characteristics of this fauna are summarized in Table 4. Data from the other North Atlantic islands are provided for comparative purposes.

DOWNES (1988) outlines the main characteristics of the faunas of the North Atlantic region and the Orcadian beetles are best considered within his framework. Orkney has no endemics, although POPPIUS (1904-5) described *Philonthus varius* var. *Shetlandicus*, a variant of *Philonthus varius* (Gyllenhal), as occurring only on Orkney and Shetland. The lack of endemics is a characteristic of the North Atlantic islands as a whole, a point emphasised by Lindroth as early as 1931, and this favours a hypothesis of Lateglacial or Early Holocene colonisation, rather than survival of the biota in refugia, areas free from ice cover during glaciation (BUCKLAND & DUGMORE 1991). The overwhelming majority of Orcadian beetle species are exclusively palaearctic (326; 89.6%), a pattern mirrored on the other Atlantic islands. The percentage of palaeartic species drops as one moves from east to west across the islands and even in Greenland they account for 41% of the fauna, a surprisingly high figure for an island so close to America. Smaller proportions of the Orcadian fauna are holarctic (23; 6.3%), circumpolar (8; 2.2%) and cosmopolitan (7; 1.9%). Fifteen of the holarctic species are members of the Haliplidae, Dytiscidae and Hydrophilidae families of water beetles. Despite the relatively high numbers of circumpolar and holarctic species, the fauna of Orkney can be described as boreal or cool temperate. The northerners in the Orcadian community, such as the carabids, *Nebria rufescens* (Strom.) (= *gyllenhali* (Schon.)) and *Pelophila borealis* (Payk.), and the dytiscid *Hydroporus morio* (Aúbe), reach the subarctic zone in Greenland and Scandinavia, and have a restricted southern distribution in Europe and United Kingdom (LINDROTH 1985; BALFOUR-BROWNE 1940). A modest proportion of Orcadian beetles are brachypterous (flightless), including several of the large ground beetles (eg. *Carabus problematicus* (Herbst)), weevils (eg. *Otiorhynchus arcticus* (F.)) and dytiscids (eg. *Dytiscus lapponicus* (Gyll.)) (JACKSON 1956). The numbers of flightless and wing dimorphic species increases as one moves west out across the North Atlantic (Fig. 3)

All of the species found on the islands are common to the British mainland and 314 (93.4%) species from Orkney are present in Scandinavia (Table 5). Of the fourteen species from Orkney that are not recorded from Scandinavia, thirteen have a markedly Central and Southern European distribution and one, *Apion reyi* Blackburn, is restricted to Orkney, Shetland and the Outer Hebrides. Morris (1990: 64) notes, however, that "the slight and comparative characters which distinguish this taxon from *A. assimile* reflect considerable doubt as to its specific distinctness. It may fall within the range of variation of *A. assimile sensu lato*, and be part of a roughly north-south geographical cline". *Apion assimile* Kirby is present in Scandinavia. There is therefore a clear division between the Northern Islands (i.e. Orkney and Shetland) and the other islands in the region. The former has faunal affinities linking them to mainland Britain and the latter have more in common with Scandinavia. The characteristics of the Orcadian fauna and its relationships to the other islands of the North

Atlantic is of some biological significance, and it is inextricably linked to the colonisation history of the region. An important question that must be addressed is whether or not the beetles survived the last (Devensian) glaciation in Refugia.

Glacial Refugia

It was the contention of LINDROTH (1931; 1957; 1965; 1972) and others (LARSSON 1959) that the present day fauna of the North Atlantic islands survived the Pleistocene glaciations in ice-free foreland Refugia in Iceland and Scandinavia from which repopulation took place as the glaciation receded. This hypothesis, strongly restated by DAHL (1987), has found support among botanists (eg. LÖVE 1963; LÖVE and LÖVE 1963; 1979) and some geologists (EINARSSON 1977; 1985). No evidence has been forwarded to suggest the existence of Refugia on the Orkney islands, although questions still remain concerning the existence of ice cover during the Late Devensian. Examination of erratics in the shelly till and glacial striae indicate an initial northeast movement of ice and a northwest movement out of the Moray Firth across Orkney due to deflection by the Scandinavian ice sheet (MYKURA 1976). SISSONS (1981) has noted, however, that there is no evidence to indicate that this was the *last* ice sheet. In recent review papers, SUTHERLAND (1984; 1991) and SUTHERLAND and GORDON (1993) classify this advance as 'pre-Late Devensian', but dating evidence is needed before a firm conclusion can be reached. These papers and further data available as a result of offshore surveys in the central North Sea basin (THOMPSON and EDEN 1977; NESJE and SEJRUP 1988) seem to indicate that during the Late Devensian parts of Caithness were ice-free as were the Orkneys and that deglaciation might have taken place before *c.* 13,000 BP (SUTHERLAND 1984). The Scottish ice sheet seems to have been rather restricted reaching only a short distance offshore in northwest Scotland (THOMPSON and EDEN 1977). Using all available evidence, SISSONS (1981) has speculated that from the glacial maxima (*c.* 18,000 BP) much of the Scottish ice sheet wasted away due to a snowfall deficiency, while the British Isles were surrounded by polar water. This interpretation raises the possibility of retreat of ice in northern Britain while further south the ice was still advancing (BALLANTYNE and GRAY 1984). To the northeast, suggestions that the Scottish and Scandinavian ice sheets coalesced in the Fladen ground of the North Sea now appear untenable and the evidence indicates large areas of dry land to the south of a marine embayment (NESJE and SEJRUP 1988; PEACOCK and HARKNESS 1990: Fig. 4).

Despite the strength of evidence indicating ice-free conditions in Orkney, several factors mitigate against the survival of insects in Refugia here and elsewhere in the North Atlantic. The evidence accruing from Quaternary insect fossils indicates that the Coleoptera responded to the selective pressures of climatic cooling by massive changes in geographical range and localized extinction of warm temperate elements of the fauna (COOPE 1995). During the periods of arctic severity in climate in the last (Devensian) glaciation, species preferring cold continental conditions were present in Britain (COOPE 1977) and during interglacials and interstadials thermophilous species extended their ranges northwards, including several species now restricted to the Mediterranean region (COOPE 1990). The intensity of the glacial maxima was such that most of the North Atlantic was locked in ice. Summer temperatures were below 10°C and some winter months were down to -16°C (ATKINSON *et al.* 1987). Under such conditions biological activity must have been minimized with perhaps a few lichens inhabiting bare rock. It is probably relevant that there seems to be a significant gap in the biological record of lowland Britain between *c.* 18,000-15,000 B.P. (the last glacial maximum) in the varve sediments of proglacial Lake Humber.

The Refugia hypothesis can also be criticized on biological grounds because the species that are purported to have inhabited the islands throughout the glaciations are essentially cool temperate or boreal rather than cold-adapted arctic species. In the rigorous climate of the Devensian, it is hard to reconcile the existence of boreal forms, and, had survival actually occurred, one would expect to find a predominance of arctic species on the North Atlantic islands. This is clearly not the case. The transition from high arctic conditions as far south as southern England (COOPE 1981) to conditions probably warmer than today (OSBORNE 1980) lead to the rapid extinction of high arctic forms in the tundra south of the Scandinavian ice sheet. A similar pattern has been noted in the development of the North American insect fauna (SCHWERT and ASHWORTH 1988). In contrast, ASHMOLE (1979) considers that the Boreo-montane spiders of Shetland may have survived the glaciation near the ice edge in Britain or the nearby 'North Sea Land' (Fig. 4). When the ice retreated these species followed the ice north and colonised the newly exposed land. Such as process would establish populations on mountain tops, where they might persist when conditions began to warm. The zoogeographical characteristics of the beetles in Shetland (Table 4) offer no support for such a theory.

These arguments point in one direction - that, even if ice-free areas existed, at the height of the glacial cycles the north Atlantic islands would have had an extreme arctic climate in which no boreal species could have survived (BUCKLAND & DUGMORE 1991). There can be little doubt that the characteristics of the modern fauna and the accumulating fossil insect and geological data (BUCKLAND 1988; BUCKLAND et al. 1986; COOPE 1986; DOWNES 1988) offer a wealth of corroborating evidence supporting an hypothesis of Late- or post-glacial colonization of the North Atlantic islands.

Colonisation mechanisms

The means of insect dispersal to Orkney fall into five main groups; i) Late glacial/ early Holocene land connections, ii) aerial dispersal, iii) zoochorous dispersal, iv) hydrochorous dispersal, and v) anthropochorous dispersal.

Late Devensian/Early Holocene Land connections

Given the lowering of sea levels (MERRIT et al. 1995), and the existence of ice-free areas in Caithness, Orkney and the Fladen ground of the North Sea (SUTHERLAND 1993; SUTHERLAND & GORDON 1993; NESJE & SEJRUP 1988; Fig. 4), the possibility of a Late Devensian land connection between mainland Scotland and Orkney (and Shetland) must be considered. The admiralty chart gives a depth of the Pentland Firth as 53 fathoms (105m) (BERRY 1985). It is just possible that the generally accepted estimates for a Late Glacial reduction in sea level of -100 to -130m O.D. (DAWSON 1984; FLINT 1971; SYNGE 1977) created an area of dry land between Orkney and Scotland. If not, the remaining stretch of water would have been small indeed and not provided much of a barrier to macropterous species. It must be stressed, however, that any insects crossing the Pentland Firth to Orkney and moving onto Shetland before, during, or immediately after the Late Glacial interstadial would have probably become locally extinct when high arctic conditions returned during the Loch Lomond stadial (*c.* 11,000 BP). Given the ice core record indicating the rapidity of climate change at the end of the glaciation (TAYLOR et al. 1993), the subsequent speed of deglaciation in Norway, and elsewhere (ANDERSEN 1980) and rise in sea level at around 10,000 B.P., a landbridge cannot have existed long in a condition favourable for the immigration of large numbers of plants and animals. This would, however, provide a mechanism that explains the presence of larger flightless beetles on Orkney, such the Otiorhynchine weevils. Deer may also have immigrated in the early Holocene (MCCORMICK & BUCKLAND, in press).

Aerial dispersal

Orkney lies only 16km away from mainland Britain across the Pentland Firth. It could be suggested, therefore, that aerial immigration may have played a more important role in the colonization of the islands. A significant proportion of the fauna is brachypterous, however, and many of these species are common to the other North Atlantic islands (Fig 3). Assessing which species actively flew to the islands is difficult because of the dearth of data relating to flight in Coleoptera. Empirical data are scarce but suggest that flight and flight duration has a physiological basis and depends upon several factors such as the age of the insect, the temperature, and the time of year. It has been recognized that many insects have a post-teneral, pre-reproductive propensity to fly (JOHNSON 1969), following which wing muscles atrophy. DAVIS (1980) suggests that most insects are short fliers and implies that this may have adaptative significance in that short fliers maintain a centre of dispersal in an area of favourable habitat, while long fliers colonize new habitats. DEN BOER (1970) notes that carabids inhabiting 'unstable' habitats invest heavily in flight. Both admit, however, that data pertaining to dispersal and migration are too scarce for the formation of concrete conclusions.

ASHMOLE & ASHMOLE (1988) examined insect dispersal to Tenerife, Canary Islands, by sampling the biological fallout on mountain snowfields and captures from neuston and kite nets. Their data indicate that a wide variety of species are involved in aerial dispersal (cf. HARDY & CHENG 1986). Although, the Coleoptera involved were only identified to the family level, it is clear that they belong to readily dispersing taxa, such as species of Coccinellidae, Staphylinidae and Anobiidae. It is likely, therefore, that some of the able dispersers in the Orcadian fauna (eg. Staphylinidae, some water beetles, Scarabaeidae), immigrated in the aerial plankton during the Post-glacial period. This process is probably still going on today (cf. GÍSLASON 1981). Documented instances of aerial dispersal in the North Atlantic are scarce and the only record of aerial dispersal of Coleoptera to Iceland refers to the coccinellid, *Coccinella septempunctata* L. (ÓLAFSSON and BJÖRNSSON 1976). Large numbers of this species were, however, noted on an Atlantic ferry in 1984 (PCB) and dispersal may have been largely anthropochorous.

The limited success of aerial dispersal in the Coleoptera is perhaps best illustrated by the colonization of Surtsey, which lies 30km south of Iceland. Surtsey was formed by volcanic activity during 1963 and in 1973 only four species of Coleoptera had been captured alive on the island. One of these *Lathridius minutus* (L.) is synanthropous and is restricted to a survey hut. *Atheta atramentaria* Gyll (flying actively) and *Amara quenseli* (Schon.) (two macropterous individuals) presumably arrived by flight. The other, *Otiorhynchus arcticus* (F.) (one alive, the other dead) was found in shore drift (LINDROTH et al. 1973).

Zoochorous dispersal

Birds are commonly cited as being responsible for dispersal of this kind. Small animals are easily attached to the feet and feathers of birds when they are resting on the ground or swimming in freshwater. When migrating, birds are able to produce spectacular long-range transport (eg. REES 1965). Very few Coleoptera, however, are phoretic in habit (CROWSON 1981) and thus immigration by this means is likely to be of little importance.

Hydrochorous dispersal

It was noted at an early stage that stretches of water form effective barriers to many Coleoptera. LINDROTH (1957) highlights the effectiveness of the Davis Strait in reducing the numbers of Nearctic species in Greenland. It is well documented that increasing salinity reduces the tolerance of many insect species to exposure in water. Prolonged exposure to sea water leads to desiccation through osmosis (LINDROTH *et al.* 1973). Some species, most notably the flightless littoral beetle, *Micralymma marina* (Strom), are able to withstand saline conditions. The amphiatlantic nature of this species distribution led LINDROTH (1931) to suggest it was passively distributed by the Gulf Stream. If this is the case, its absence from Orkney is not easy to reconcile when it is widely distributed elsewhere. Dispersal by the Gulf Stream is unlikely because of the distances and time it would take to cross the Atlantic and as LARSSON and GÍGJA (1959: 68) note, the distribution in Newfoundland and New England is in agreement with the description given by LINDROTH (1957) of the importance of ballast movement in distributing insects (see below).

Movement on rafts of floating debris offers another alternative means of immigration. Indeed, LINDROTH and others (1973) make reference to the find of a piece of driftwood on a beach on Surtsey, under which eight specimens of *O. arcticus* were observed. Four individuals were half concealed in holes in the wood. Similarly, a tuft of grass was found washed ashore from which live specimens of Collembola and Acari were extracted. Experiments with other floating grass tussocks suggested that some species of Coleoptera can survive exposure to saline conditions for several days, although Collembola and Oribatid mites are better suited to such a method of transport (LINDROTH et al. 1973: 256-259). Before deforestation, driftwood would have been plentiful around the shores of Scotland and the Northern Isles and would have provided a further mechanism for dispersal (cf. WARREN & KEY 1991)

Ice rafting

Immigration on sediment in ice floes had been independently proposed by LINDROTH (1963) to account for elements in the biota of Newfoundland and by FRIDRIKSSON (1969) and COOPE (1969; 1979) with respect to the faunas of Scandinavia and the North Atlantic islands. Examination of the fossil insect record has modified and extended this hypothesis (BUCKLAND 1988; BUCKLAND *et al.* 1986; COOPE 1986). The withdrawal of Atlantic sea ice to about 66-68°N consequent upon the rapid warming at the end of the last glaciation seems to have had a dramatic impact upon the ocean circulation patterns. For a short period during the Late Devensian, the North Atlantic Drift became an anticlockwise gyre carrying an inflow of meltwater from the North Sea, the Norwegian fjords and the Baltic with ice and sediment from the adjacent lands. The contained and predominantly warm temperate insect fauna would have been insulated from the ice by sediments and buffered from the adverse effects of sea water by a massive fresh (melt) water slick. The ice floes were transported westwards across the ocean, and were beached along the sweepstake route of the North Atlantic islands of Orkney, Shetland, Faroe, Iceland, and south Greenland.

DOWNES (1988) highlights some of the difficulties of the ice rafting mechanism, noting that the time taken to cross the Atlantic is a journey reckoned in weeks rather than days. He states that given problems such as changing weather, the onset of emergence from dormancy, absence of food and exposure to rain and spray, the potential for insect survival might have been severely reduced. Additionally, problems occur with respect to the main source areas of the fauna. COOPE (1986) favours both Scotland and Scandinavia, whereas (BUCKLAND, 1988; BUCKLAND *et al.* 1986) suggests south Scandinavia, more specifically the fjords of southwest Norway. The analysis of the modern faunas marginally favours the former (Tables 4-5), and indicates a strong link between Faroe and the Northern Scottish islands, as well as Scandinavia. Iceland has more in common with Scandinavia than the British Isles, although only two Icelandic species are not found in Britain. The limited nature of the last Scottish ice sheet is also relevant since it must have considerably reduced the faunas possibilities of finding a suitable 'raft' for export across the Atlantic. On balance, there is insufficient data to support one argument to the total exclusion of the other. It is plausible that the some elements in the fauna of Shetland originate from Scandinavia, and there remains a possibility that the northern islands in Orkney were involved in such a movement of species.

Anthropochorous dispersal

It has long been recognised that humans have had a major effect on the distribution of many species of plants and animals (SAUNDERS 1883), either by direct transportation, or indirectly through an association with habitats created by humans (eg. houses, cultivated land and so on). In this respect, the global impact of European expansionism is pronounced and very well documented (CROSBY 1986). Insects make excellent colonists and the fossil record shows quite clearly that they have been moved around by humans throughout prehistory (BUCKLAND 1981). LINDROTH (1957) provides an excellent biohistorical study of the mechanisms of species dispersal in the North Atlantic and he emphasises the importance of the movement of ballast and the Newfoundland stock fish trade in disseminating Coleoptera, particularly Carabidae, Staphylinidae and Curculionidae. In an earlier study, OSTENFELD (1926) suggested that the entire European element of the flora of Greenland had been introduced with the Norse (Viking) settlers. This was obviously an over-estimate but subsequent research into the fossil record of the region has indicated that, (i) many species of beetles made their first appearance on the islands of Faroe, Iceland and Greenland along with Norse colonists, having been transported in ballast and dunnage (BUCKLAND 1988; SADLER 1991a,b), and (ii) European species were introduced to America early in the contact period (BUCKLAND *et al.* 1995; SCHWERT 1996). In fact, it is possible that almost half the species of Greenland and Iceland are introduced, although on Orkney and Shetland the figure drops to 9.9% and 14.5% respectively (Table 6). This pattern of a relatively small number of introduced species is mirrored in the spider fauna of the region. ASHMOLE (1979) records only one potential introduction to Orkney, *Tegenaria domestica*, and only three on Shetland.

One could argue, however, that the low numbers of introduced species is surprising, given that both Orkney and Shetland were settled by Europeans some 6000 years earlier than Faroe, Iceland and Greenland. This apparent contradiction is largely a result of both defining introduced species on their degree of synanthropy and the lack of research into farm and other wholly man-made habitats. A synanthropous species can be described as one which is *unable* to maintain *breeding* populations on an island *without* the ameliorated conditions provided by *human* buildings and aspects of human activity (cf. TISCHLER 1973). The definition, however, varies according to the latitude of the island populations. It is well-documented that species on the edge of the distributional range are often synanthropous. Thus, a species of synanthropous habit in Greenland and Iceland need not be so constrained in Orkney or Shetland. It is probable that the numbers of synanthropous on the more southern islands of Faroe, Shetland and Orkney are underestimated. Further analyses of the fossil record are needed to confirm this hypothesis.

Early faunal development

The fossil insect fauna from Skara Brae on mainland Orkney (Fig. 1) offers an insight into the faunal development of the islands, after the arrival of the first agriculturalists. The assemblage is biogeographically important because it indicates that the synanthropous elements of the present day fauna coalesced into recognizable assemblages at least as early as the Late Neolithic period. HUNTER and OTHERS (1973) have considered the groups of outdoor insects that are of importance in the infestation of stored products (Table 7). Reversing the logic of this argument allows one to gain an insight into the probable 'natural' habitats of some of the synanthropous species noted in the fossil record.

The great majority of the synanthropous species belong to groups 2 and 3 of the classification in HUNTER and OTHERS (1973) (Table 7). The mould feeders (lathridiids, cryptophagids) and predators (staphylinids) now associated with decomposing material might have initially been residents of the community which lived under bark on rotting trees. Mouldy and decomposing leaf and vegetable litter would also have provided similar micro-habitats. As WOODROFFE's (1953) classic study illustrated, many synanthropes are common inhabitants of birds' nests. Indeed, the staphylinids, *Xylodromus sp.* and the lathriidids, *Corticarina fuscula* (Gyll.) and *Lathridius minutus* grp. have also been noted in decayed trees and birds nests (PALM 1951; 1959), and may have arrived in Orkney with the first boats of the settlers, in the dunnage or fodder associated with introduced domestic animals.

One can envisage, therefore, a situation wherein pre- to early agricultural activity, which initially destroyed and modified the broad habitats of many species of the primary forest (cf. BUCKLAND 1979), created new micro-habitats which mimiced the primary habitats (cf. GIRLING and GREIG 1977). This would have allowed many species to make the transition from 'natural' to synanthropous habitats with little problem. Thereafter, these species would have been transported around the world as stowaways or serfs (SADLER 1991b; ENCKELL *et al.* 1987). It should be stressed that the habitat preferences of these species do not seem to have changed; rather they have found a similar micro-habitat or niche in the heavily modified post-settlement landscape.

The Skara Brae fauna, from a midden close to the stone-built houses, also includes the earliest record of the human flea, *Pulex irritans* L. BUCKLAND and SADLER (1989) have argued that this flea was initially a New World animal, which tranferred it attentions to humans during the Lateglacial / early Holocene, and rapidly spread across North America and Eurasia as a consequence of 'trade' in furs. The flea is particularly common on Norse sites in Greenland (SADLER 1990), and it is also present on the similarly dated site at Tuquoy on Westray, where it is supplemented by the human louse, *Pediculus humanus* (L.). The wingless ectoparasite of sheep, the fly *Melophagus ovinus* (L.) is also present at Tuquoy.

The Tuquoy faunas, more extensive that the Skara Brae ones, include a number of other species which are strongly synanthropic in the northern part of their range. The spider beetle *Ptinus fur* (L.) is known from natural prehistoric deposits in England (BUCKLAND 1979), but the earliest records of *Tipnus unicolor* (Pill. & Mitt.) are Roman (cf. HALL & KENWARD 1990) and the beetle was probably introduced.

Faunal change

Elements of landscape change in Orkney are reasonably well-documented, although it must be stressed that the data are patchy both in terms of spatial spread and temporal continuity. Associated changes in the fauna have yet to be documented. Much of the evidence comes from palynological studies at or close to archaeological sites on mainland Orkney. Pollen profiles were studied by MOAR (1969), KEATINGE and DICKSON (1979) and these provide a useful environmental framework that has recently been updated by BUNTING (1994; 1996). Further data are available from smaller mainland regional profiles and samples associated with Maes Howe, the Ring of Brogar (JONES 1979) and the stones of Stenness (CASELDINE and WHITTINGTON 1976).

The pollen profiles indicate a mid-Flandrian, pre-settlement vegetation of birch and hazel scrub woodland, with a rich ground flora of tall herbs and ferns. There is no evidence that oak, alder and pine were indigenous species. The reduction in woodland is commensurate with the appearance of the first settlers (*c.* 5000 BP). The remaining herb and fern vegetation was replaced by grassland and pasture and in the Late Neolithic period the landscape was one of open herbaceous and dwarf-shrub heath vegetation. A possible climatic deterioration is suggested, thereafter, and this coupled with the intensive grazing, is implicated in the growth of blanket peat on the hills. During the Bronze Age (c. 3000 BP) the vegetation seems to have began to resemble that found today.

The fossil insect faunas from north of Heldalewater on Hoy provide some idea of the nature of the fauna of the areas of blanket bog and include several of the species noted in the faunal classification of this habitat on Westray. The samples come from beneath a tephra (=volcanic ash) horizon dated to 3840 ± 15 BP (DUGMORE *et al.* 1995). Although this is later than the earliest evidence for settlement, the fauna, with the exception of the lathridiid *Cortinicara gibbosa* (Hbst.), not currently recorded from Orkney, are unlikely to be anthropochorous (Table 8), and the assemblage suggests that acid mire habitats are likely to have existed on Hoy since the early postglacial. Several other taxa in the samples are not presently recorded. *Olophrum fuscum* (Grav.) is usually the more northerly of the two species, *O. fuscum* and *O. piceum* (Gyll.) (TOTTENHAM 1954), and its absence from the modern Orkney list is surprising.

The palynological and archaeological evidence indicate that farming continued through prehistory into the Norse period, although the amount of available agricultural land appears the have been progressively reduced by soil exhaustion and bog growth. As DAVIDSON and JONES (1985) have noted, major changes have also taken place during the last 200 years. The enclosure movement in the early nineteenth century, the introduction of new seeds, the drainage of wetlands and the application of nitrate based fertilizers have all had an impact on the Orcadian landscape and its insect fauna.

Conclusions

10,000 years of isolation and extensive human modification have moulded the distinctive Orcadian landscape. Situated at the far north east of the British Isles, the islands are biologically interesting, although under-researched. The examination of a number of sites on the island of Westray is the first systematic study of Orkney's beetle fauna and provides a preliminary classification of grassland habitats. It is clear, however, that further research is needed before the classification adequately describes the variation in across the numerous islands of the group.

There can be little doubt that Orkney faunistically belongs to the British Isles. This must be a reflection of its proximity to the mainland which severely reduces the impact of the aerial sweepstake. Similarly, the putative late land connection (c. 10,000 BP) might have had an important part to play in producing the islands faunal characteristics. Ice rafted immigration is possible very early in the Holocene, particularly on the more northern island of the group such as Westray, Papa Westray, North Ronaldsay and Sanday. It might prove instructive to examine the faunas of these islands and contrast the data with mainland Orkney and the southern islands.

A number of Coleoptera from Orkney have been introduced. The problems in defining synanthropous species, coupled with the paucity of fossil records, makes predictions about the timing and nature of their dispersal problematic. Several species, however, are present in Neolithic deposits and they offer an indication as to the early development of the synanthropous fauna.

ACKNOWLEDGEMENTS

This research forms part of an on-going project examining the biogeography of the insects of the North Atlantic region, part funded through the NSF (USA) Office of Polar Programs NABO research project. The fieldwork in Orkney was funded by the Archaeological Conservation and Operations Unit (AOC) of the Scottish Development Department and, without the full support of OLWYN OWEN and JOHN BARBER (AOC), it could not have been undertaken. Thanks are also due to the landowners of Westray, Orkney, who permitted access to their land, in particular, to Mr TOM POTTINGER of Tuquoy farm. Sampling on Hoy was carried out in association with KEVIN EDWARDS, KEITH DOBANEY, JEFF BLACKFORD and ALEX WOLF, as part of a Leverhulme-funded project examining the impact of Icelandic eruptions in the North Atlantic region.

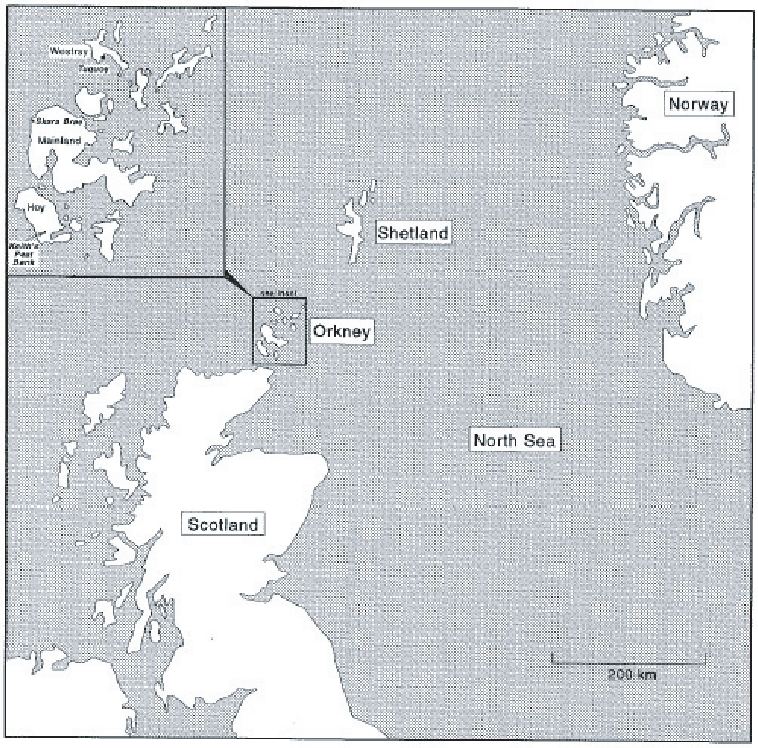

Fig. 1 - The location of the Northern Isles of Orkney and the island of Westray. The sites where fossil studies have been undertaken are indicated in italics.

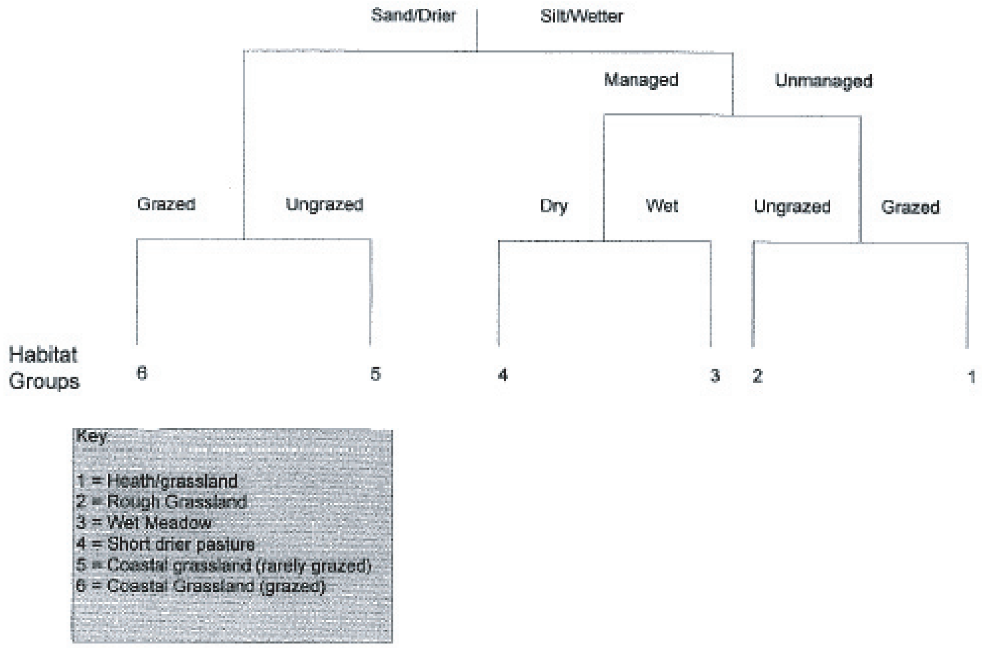

Fig 2 - TWINSPAN dendrogram showing beetles grassland beetle habitats on Westray. The indicator species are shown at each level (the numbers refer to the listing shown in Table 2).

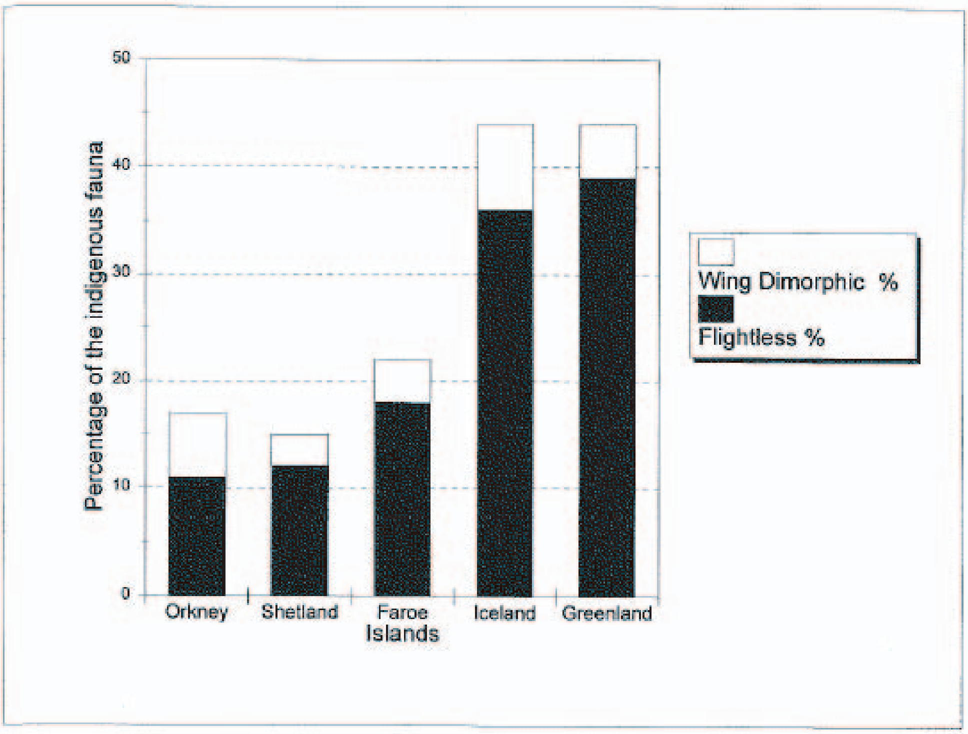

Fig 3 - The percentage of flightless and wing dimorphic Coleoptera on the North Atlantic islands. Populations of wing dimorphic species have both flighted and non-flighted individuals (Sources: see Table 4).

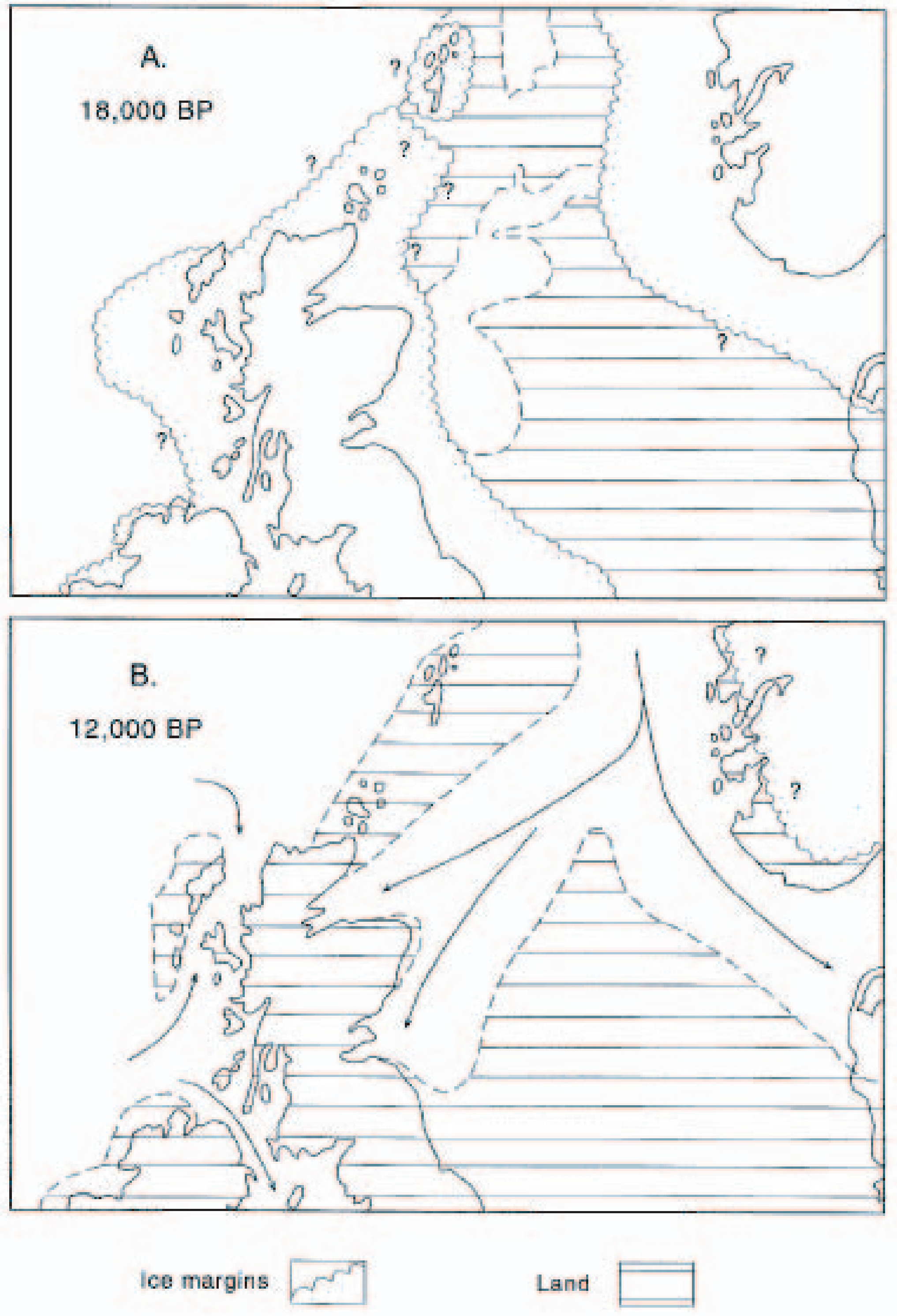

Fig. 4 - The configuration of land, sea and ice at 18,000 and 12,000 BP. The arrows indicate the influx of sea water into the shallow seas around Orkney and Shetland and the question marks areas where ice limits are poorly documented (after PEACOCK & HARKNESS 1990).

TABLE 1 - The frequency of species in the habitat groups as interpreted from the TWINSPAN end groups. (. = absent, 1 = 1-20%, 2 = 21-40, 3 = 41-60, 4 = 61-80, 5 = 81-100). The species are listed in the order generated by TWINSPAN and the numbers refer to the indicator species given in Figure 2. Species not recorded in BERRY (1985) are denoted with the plus (+) character.

	Habitat Groups					
Taxa	1	2	3	4	5	6
1. Trechus obtusus Erich.	.	.	.	1	.	.
2. Cercyon haemorrhoidalis (F.)	.	.	.	1	.	.
3. Philonthus sordidus (Graven.)	.	.	.	1	.	.
4. Philonthus spp.	.	.	.	1	.	.
5. Tachyporus dispar (Paykull) +	.	.	.	2	.	.
6. Tachyporus pallidus Sharp	.	.	.	1	.	.
7. Clivina fossor (L.)	.	.	.	1	.	.
8. Xantholinus glabratus (Graven.)	.	.	1	2	.	.
9. Loricera pilicornis (F.)	.	.	4	2	.	.
10. Dyschirius globosus (Herbst) +	.	.	1	.	.	.
11. Ochthebius dilatatus Steph.	.	.	1	.	.	.
12. Stenus brunnipes	.	.	1	.	.	.
13. Helophorus grandis Ill.	3	.	2	1	.	.
14. Tachinus signatus Graven.	.	2	1	3	.	.
15. Nebria brevicollis (F.)	3	4	2	5	2	.
16. Nebria salina Fair. & Lab.	3	4	4	1	.	.
17. Trechus quadristriatus (Schr.)	.	1	.	.	.	.
18. Patrobus atrorufus (Strom)	3	3	.	.	.	.
19. Olisthopus rotundatus (Payk.)	3	.	.	.	.	.
20. Tachinus marginellus (F.)	5	.	.	.	.	.
21. Megasternum obscurum (Marsh.)	5	4	2	4	5	3
22. Tachinus latticolis Graven.	3	.	.	2	2	.
23. Atomaria apicalis Erich. +	.	.	.	3	2	1
24. Helophorus brevipalpis Bedel	.	.	2	4	4	4
25. Sitona lepidus Gyll.	.	.	.	2	.	1
26. Calathus fuscipes (Goeze)	.	.	.	2	.	2
27. Laemostenus terricola (Herbst.) +	.	.	.	1	2	.
28. Tachyporus pusillus Graven.	.	.	.	2	5	1
29. Atomaria atricapilla Steph.	.	.	.	1	.	1
30. Amara bifrons (Gyll.)	.	.	.	2	5	2
31. Calathus melanocephalus (L.)	.	.	.	.	.	2
32. Helophorus minutus F.	.	.	.	.	.	1
33. Leiodes dubia (Kuge.)	.	1	.	.	4	5
34. Cryptophagus scanicus (L.)	.	.	.	.	.	1
35. Crepidodera ferruginea (Scopoli)	.	.	.	.	.	2
36. Notiophilus biguttatus (F.)	.	.	.	.	2	.
37. Corticarina fuscula (Gyll.)	.	.	.	.	2	.
38. Serica brunnea (L.)	.	.	.	.	4	.
39. Notiophilus palustris (Duft.)	.	1	.	.	.	.

TABLE 2 - Westray search data (Col. J. SADLER July-Aug 1988). * Indicates a single capture and ** 2 or more individuals. Species which are not recorded in BERRY (1985) are denoted by a plus (+) character in the table. Taxonomy after Lucht (1987).

Taxa	Hay Barns/ricks	Littoral	Aquatic	Dung
Calathus melanocephalus (L.)	**			
Haliplus lineatocollis (Marsh.)			*	
Haliplus ruficollis (Deg.)			**	
Hydroporus palustris (L.)			**	
Hydroporus striola (Gyll.)			*	
Hydroporus pubescens (Gyll.)			**	
Agabus bipustulatus (L.)			**	
Limnebius truncatellus (Thun.)			**	
Helophorus aequalis Thomson			**	
Helophorus brevipalpis Bedal			*	
Helophorus flavipes (F.)			*	
Helophorus minutus F.			**	
Cercyon littoralis (Gyll.)		**		
Cercyon haemorrhoidalis (F.)				**
Cercyon melanocephalus (L.)		**		**
Megasternum obscurum (Marsh.)	*			*
Megarthrus depressus (Payk.)				**
Omalium riparium Thom.		**		
Omalium excavatum Steph.	*			
Anotylus maritimus Thom. +		*		
Anotylus sculpturatus (Graven.) +				**
Platystethus arenarius (Four.)	**			
Cafius xantholoma (Graven.)				
Philonthus marginatus (Strom)				**
Quedius mesomelinus (Marsh.)	*			
Quedius umbrinus Erich.	*			
Tachinus signatus Graven.	*			
Simplocaria semistriata (F.)	*			
Cryptophagus dentatus (Herbst)	*			
Cryptophagus pilosus Gyll.	*			
Atomaria apicalis Erich.+	**			
Lathridius pseudominutus (Stran)+	**			
Enicmus transversus (Oliv.)	**			
Aphodius rufipes (L.)				**
Aphodius depressus (Kuge.)				**
Aphodius ater (Deg.)				*
Aphodius rufus (Moll)				**
Barynotus squamosus Germar				
Sitona lepidus Gyll.				

TABLE 3 - Species known only as fossils from the North Atlantic islands (Sources: BENGSTON, 1981; BUCKLAND, 1988; unpubl; DINNIN, unpubl; SADLER 1991b; 1993; SKIDMORE, unpubl.).

Island	Taxa
Orkney	*Bembidion unicolor* Chaud.
	Acritus nigricornis (Hoff.)
	Thanatophilus dispar (Herbst)
	Micropeplus fulvus Erich.
	Xylodromus concinnus (Marsh.)
	X. depressus (Graven.)
	Carpelimus bilineatus Steph.
	Tachinus corticinus Graven.
	Aphodius fimetarius (L.)
	Dascillus cervinus (L.)
	Calyptomerus dubius (Marsh.)
	Tipnus unicolor (Pill. & Mitt.)
	Alophus triguttatus (F.)
	Phytobius quadrituberculatus F.
Shetland	*Cryptophagus scutellatus* Newm.
	Aglenus brunneus (Gyll.)
	Mycetaea hirta (Marsh.)
	Tipnus unicolor (Pill. & Mitt.)
Faroe	*Calathus micropterus* Dufts.
	Ochthephilus omalinus (Erich.)
Iceland	*Hydraena britteni* Joy.
	Aphodius firmetarius (L.)
	A. cf. prodromus (Brahm)
	Oxyomus sylvestris (Scopoli)
Greenland	*Othius angustus* Steph.
	Philonthus politus (L.)
	Philonthus cephalotes (Graven.)
	Ocalea picata (Steph.)
	Atomaria sp.

TABLE 4 - The Zoogeography of the Coleoptera (beetles) of the North Atlantic islands. (Sources: Greenland, (BÖCHER, 1988; SADLER, 1991b), Iceland (BUCKLAND, 1988; *et al.*, 1986; DUGMORE and BUCKLAND, 1984; INGÓLFSSON, 1976; LARSSON and GÍGJA, 1959; LINDROTH, 1931; 1957; 1965; et al., 1973; 1988; ÓLAFSSON, 1979; SADLER and BUCKLAND unpubl.), Faroe (BENGSTON, 1981; DINNIN, unpubl; ENCKELL,1985), Shetland (BERRY and JOHNSTON, 1980), Orkney (BERRY, 1985; SADLER, 1993)).

	Orkney	*Shetland*	*Faroe*	*Iceland*	*Greenland*
Cosmopolitan	7(1.9)	9(2.7)	12(7.1)	20(13.3)	16(22.5)
Circumpolar	8(2.2)	10(3.0)	6(3.6)	15(10.0)	15(19.7)
Holarctic	23(6.3)	16(4.7)	5(3.0)	9(6.0)	7(9.9)
Amphiatlantic	-	1(0.3)	1(0.6)	1(0.7)	1(1.4)
Nearctic	-	-	-	1(0.7)	2(2.8)
Palaearctic	326(89.6)	302(89.3)	145(85.8)	104(69.3)	29(40.8)
Endemic	-	-	-	-	1(1.4)
Arctic species	-	-	-	-	1(1.4)
TOTAL	364	338	169	150	71

TABLE 5 - Numbers of North Atlantic Coleoptera common to the British Isles and Scandinavia. (Sources: see table 4)

Island	*British Isles*	*Scandinavia*	*Totals*
Orkney	364 (100)	350 (96.1)	364
Shetland	338 (100)	330 (97.6)	338
Faroe	165 (97.6)	166 (98.2)	169
Iceland	82 (97.6)	84 (100)	150
Greenland	19 (68.7)	24 (85.7)	71

TABLE 6 - Indigenous and introduced Coleoptera of the North Atlantic islands. Species only recorded as fossils are excluded from the totals. Percentage figures are in parentheses (Sources: see Table 4).

Island	*Indigenous*	*Introduced*	*Total*
Orkney	328 (90.1)	36 (9.9)	364
Shetland	289 (85.5)	49 (14.5)	338
Faroe	140 (82.8)	29 (17.2)	169
Iceland	84 (56)	66 (44)	150
Greenland	28 (39.4)	43 (60.6)	71

TABLE 7 - Important groups of outdoor insects as sources of infestation of stored products (Source: HUNTER et al. 1973).

Groupings	
I	Feeders in the field on seeds of grain and pulses (eg. grain fauna).
II	Fungal feeders (eg. Lathridiids, Cryptophagids and so on).
III	General feeders living in accumulations of animal and vegetable waste in a variety of situations, such as, animal nests, flood refuse, leaf and stick litter, decaying wood and carrion (eg. Staphylinids, Scarabaeids and Dermestids).
IV	Sub-cortical timber feeders (eg. Anobiids and Cerambycids).

TABLE 8 - Fossil beetle fauna from beneath a tephra horizon dated to 3840 ± 15 BP at Keith's Peat Bank, Heldalewater, Hoy, Orkney.

Taxon	KPB2	KPB3
Nebria salina Fair. & Lab.		1
Pterostichus diligens (Strm.)	4	
Pterostichus nigrita (Payk.)/rhaeticus Heer	1	
Olisthopus rotundatus (Payk.)		1
Hydroporus nigrita (F.)	2	1
Anacaena globulus (Payk.)	1	
Agathidium sp.	1	
Olophrum fuscum (Grav.)	3	1
Stenus sp.	2	1
Lathrobium sp.	5	1
Othius angustus Steph.	1	2
Philonthus sp.	1	
Quedius sp.	1	
Aleocharinae gen. indet.	3	1
Bryaxis sp.	4	
Agriotes sp.	1	
Cortinicara gibbosa (Hbst.)		1
Geotrupes sp.	1	
Otiorhynchus nodosus (Müll.)	1	
Micrelus ericae (Gyll.)		2

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