When, How, and Whence?

A Tentative Background for the Post-Glacial Immigration of Terrestrial Invertebrates of the Faroes

Pehr H. Enckell

Abstract
An attempt is made to distinguish between different phases in the immigration history of terrestrial invertebrates to the Faroe Islands and to estimate their relative importance. It is shown that a phase of large-scale immigration over the sea occurred some time between 10000 BP and 9000 BP, and that immigration by this means later became less important. Immigration by driftwood has probably occurred now and then; it probably started earlier from the American continent than from the northern parts of Eurasia. Aerial immigration has been important continuously since the islands became available for invasion; this process has increased in importance over time because of increased species richness in the main source areas in NW Europe. Immigration by agency of Man has taken place only during the last 1100 or so years; source areas have been western Norway, Denmark, and the northern part of the British Isles. Chance immigration of species with special habitat requirements has occurred during the human occupancy of the islands; examples are e.g. species that require deep soil layers, and forest-dwelling species in the recently established forest plantations.

The place of the Faroes in the North Atlantic biogeographic context is shown by a comparison between the occurrence of four groups (Coleoptera, Araneae, Lumbricidae, and Gastropoda) in the Faroes and the surrounding areas. Differences in species numbers between the areas are small for anthropochorous groups (Lumbricidae, Gastropoda); they are considerably greater for groups where the main immigration has been by other means than by Man (Coleoptera, Araneae). For these groups isolation, island area, and plant cover are important, in addition to the respective species' dispersal ability.

Introduction
The Faroe Islands is the most isolated island group in the temperate Atlantic. It is situated 320 km from Scotland (the nearest mainland), while, e.g. Shetland is only

about 100 km distant from the mainland. The degree of isolation is mirrored in the depauperate insect fauna: only about 950 insect species are known from the islands, while the number in the British Isles is about 20000, in Norway at least 12000, and in Denmark more than 13000 (Bengtson 1982).

The terrestrial invertebrates in the Faroes have immigrated after the last glaciation (see below). The immigration process can be divided into stages, implying that taxa with different dispersal abilities and/or different habitat requirements have colonized the islands during different time periods (or at least have started to do so). To take just one example: anthropochorous species have been able to invade the islands later than, e.g., anemochorous species.

The Post-Glacial period

The Faroes were completely ice-covered during the last Pleistocene glaciation (the Weichselian). The islands were covered by a local ice sheet (or at times isolated ice sheets covering the single islands) - the striae are directed from the centre of the island group (Rasmussen 1982). The ice cover reached far outside the present outline of the islands and (based on geological evidence) no floral or faunal refugium can have existed (Rasmussen 1982). Nor is there any evidence of a land-bridge connection between the Faroes and the British Isles. The geology of the Faroes is summarized in Rasmussen (1982).

The polar front (or convergence) separating arctic and subarctic waters from subtropical waters passed rapidly (on a geological timescale) from its position west of Portugal northwards past the west coast of the British Isles at about 13500 BP (Ruddiman et al. 1977) (Fig. 1). This caused (or was caused by) a rapid expansion of the currents bringing subtropical waters to the seas of western Europe. This current, in contrast to conditions today, was a restricted, anticlockwise gyre (Jansen et al. 1983, Buckland 1988). Coope (1979) has argued that during this period the North Atlantic islands and part of Scandinavia were invaded by certain taxa but this does not seem likely (Buckland 1988, see also below).

During the Younger Dryas Stadial the polar front advanced southwards, reaching the SW coast of Ireland at about 10200 BP (Fig. 1), and the circulation of the ocean current in the North Atlantic returned to glacial conditions. The subsequent retreat northwards of the polar front seems to have been just as sudden (Ruddiman et al. 1977: Tab. 6), and the front reached a position just south of Greenland by 9300 BP (Fig. 1). The North Atlantic gyre then returned to its former anticlockwise pattern and was still at that time restricted to the seas off northwestern Europe (Fig. 2).

Fossil finds from Iceland indicate that the pre-Landnám fauna was a cool temperate rather than an arctic fauna (Buckland 1988). The few subfossil finds from the Faroes indicate that similar conditions obtained there; the single taxon of the 11 taxa reported by Jessen and Rasmussen (1922) that does not occur in the Faroes today, the carabid beetle *Calathus micropterus* Duft. is not an arctic species but a forest-dwelling one, wich occurs both in Scotland and western Norway today.

The oldest known flora in the Faroes is of Preboreal age, although in composition

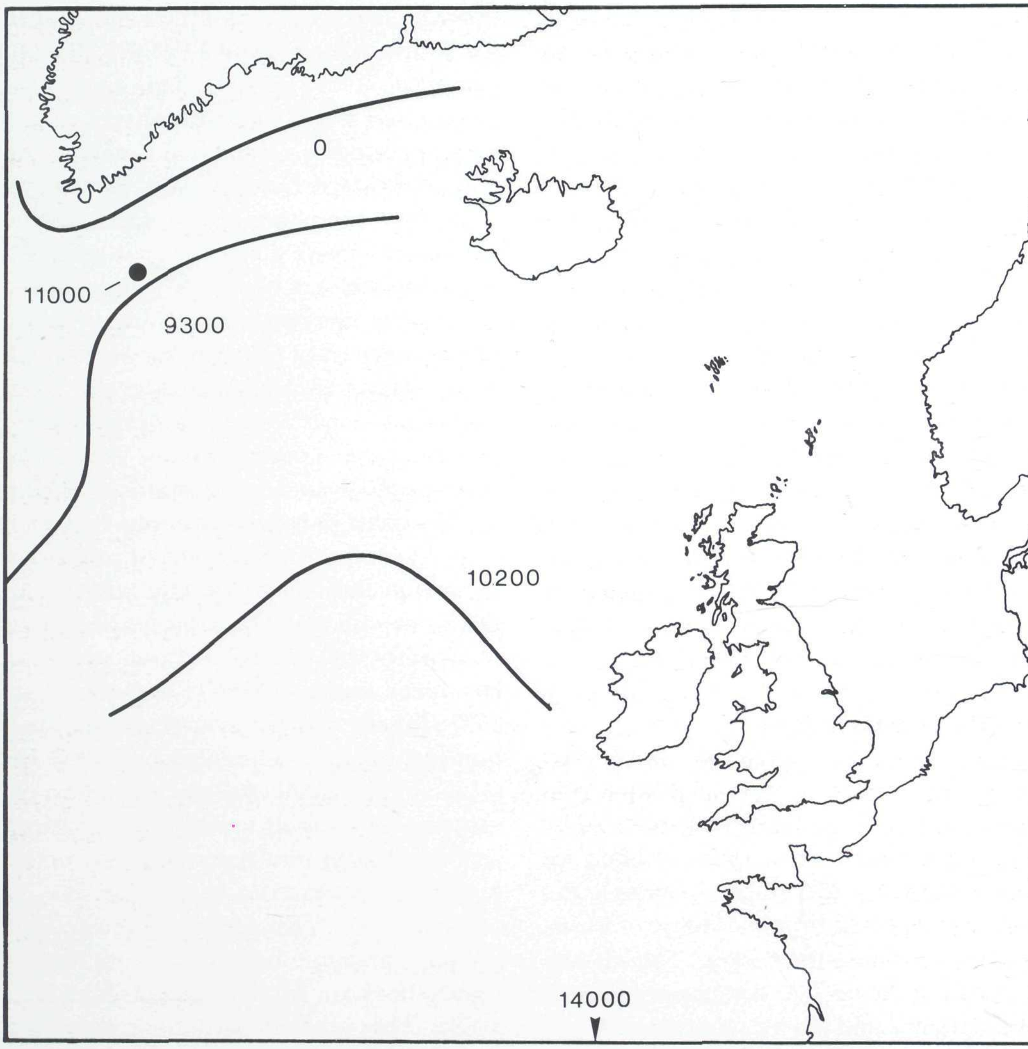

Fig. 1. The movements of the polar front from 14000 BP to the present. Figures given are years BP. The front retreated northwards after its extreme position in the south and has been recorded off southern Greenland at 11000 BP (filled circle). During the Younger Dryas it advanced southwards again and reached its southern limit at 10200 BP, when the North Atlantic for a short period returned to glacial conditions. A warming then occurred and at 9300 BP the front was again situated off southern Greenland. The extreme interglacial position of the front is also shown (0 BP). The arrow indicates that the polar front was situated off Cape Finisterre at about 14000 BP. Note that the coast lines are the current ones. (Redrawn after Ruddiman et al. 1977).
The North Atlantic Drift probably penetrated between the British Isles and Iceland during its first retreat, but was again shut off from the North Atlantic during the Younger Dryas. After this short glacial spell the Drift returned northwards again, but was turned back on itself at about the level of Iceland (see Fig. 2).

similar to the Late Weichselian flora further to the south (in the British Isles, Jóhansen 1982). For instance, *Betula nana* L. immigrated to Scotland around 10400 BP, to the Faroes around 9500 BP, and to eastern Greenland around 8000 BP. An immigration of *B. nana* to the Faroes from Scotland (or possibly Scandinavia) therefore seems likely (Jóhansen 1982). It is also notable that the first immigration to the Faroes occurred shortly after the polar front had reached Greenland, following its southward advance in the Younger Dryas.

That the earliest faunas in Iceland and the Faroes were apparently cool temperate rather than arctic is interesting when compared with the Late Pleistocene climatic record. Coope (1969, 1979) has discussed the possibility of taxa emigrating from the British Isles to Scandinavia during the retreat northwards of the polar front at about 13500 BP. In view of the fact that the front advanced southwards a few thousand years later, and that Midland England immediately south of the ice front appears to have been devoid of invertebrates between about 18000 BP and 14500 BP (Ruddiman and McIntyre 1981), it is difficult to perceive of a dispersal to the Faroes during the breakup of the Weichselian ice sheets at around 13500 BP. The climatic tolerance of the known pre-Landnám fossil insects in Iceland and the Faroes (Jessen and Rasmussen 1922, Buckland 1988) seems rather to indicate an immigration during the *second* retreat northwards of the polar front (at about 9500 BP in the case of the Faroes), or, alternatively, that species that had invaded earlier went extinct during the Younger Dryas and left no (up to now recovered) traces in the fossil record.

Apparently, then, there were two (geologically) sudden changes in climate, both possible to explain by the retreat of the polar front northwards. Summer temperatures in the sea north of the polar front were probably not above 6°C and a temperature gradient across the front in summer in Late Glacial times of about 7°C has been proposed (Ruddiman et al. 1977). This may perhaps explain the sudden terrestrial faunal changes in the British Isles, which independently suggest an increase in July temperatures of about 7°C (Coope and Brophy 1972).

A rapid warming occurred in the British Isles around 10000 BP (indicating a similar warming in the Faroes at about 9500 BP when the polar front had passed still further northwards); this is evidenced both by fossil insect remains and deep-sea core data (Ruddiman et al. 1977, Coope 1979, Osborne 1980). Apparently deglaciation was rapid (Andersen 1980). At about 9500 BP a temperate insect fauna had been established in SW Scotland and replaced the previous aboreal fauna (Ashworth 1973). Such an amelioration of climate had previously been suggested by paleobotanical data (Iversen 1954).

Even *if* arctic species immigrated to the northern islands during the first retreat northwards of the polar front, as suggested by Coope (1979), the rapid response of the fauna to climatic change would have resulted in an extinction of the arctic elements (data from Midland England indicate such an extinction; see above; Ruddiman and McIntyre 1981). Ashworth (1973) gives similar examples of rapid faunal changes with changing climate.

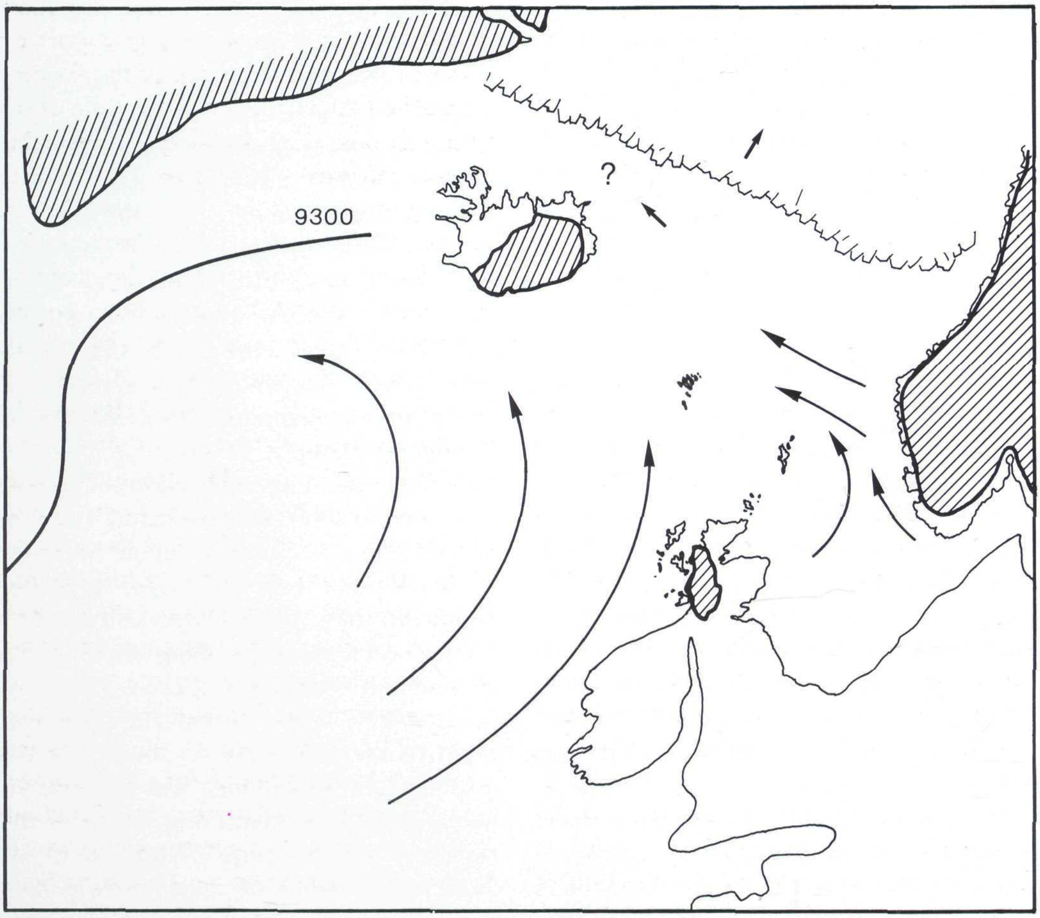

Fig. 2. The first immigration phase to the Faroes occurred at about 9500 BP when the polar front had retreated northwards and thus enabled the North Atlantic Drift to push against the North Atlantic islands. The circulation was still not the typical interglacial one and the Drift was turned back on itself. The melting Scandinavian and Loch Lomond ice sheets assisted in sweeping taxa to the sea from the coastal regions that were bare of ice, and rafting could occur further out to the sea. The rafts were transported N- and NW-wards by the currents off the western coasts of Scotland and Norway. The first immigration of species to the Faroes and Iceland probably occurred during this rather short phase in the return to interglacial conditions. When the polar front had reached its interglacial position just off Greenland (see Fig. 1) the North Atlantic Drift could advance northwards beyond the Faroes and Iceland along the Norwegian coast and the current pattern depicted ceased. (Redrawn and modified after Buckland 1988).

The process of the first immigration

»It is suggested that the creatures are likely to be carried by currents while hiding in chinks of drift-timber, and more rarely with icebergs, ...; thus situated they may sometimes be protected, or partially protected, for a time from contact with sea-water, and may possibly be safely carried during calm weather to great distances, so that arrival of shells, still alive, on the shores of a foreign country or distant island may not be a very rare event.«

Harry Wallis Kew 1893

How, then, did the immigration to the northern islands occur? Let us return to the scenario at that time. The Scandinavian and Loch Lomond ice sheets were rapidly melting. The lowering of the sea level meant that a large part of the present North Sea was dry (e.g., Coope 1979). Thus, distances across water where much shorter than today. Moreover, the shortened course of the North Atlantic Drift, which in addition ran anti-clockwise, would have facilitated dispersal across the water (Fig. 2).

If we assume that species invading the western part of the Scandinavian peninsula at least partly originated from the British Isles as suggested by Coope (1979), the obstacles that had to be overcome can not have been great (Fig. 2). The deep trench off the southern coast of Norway probably had a surface layer of fresh (or brackish) water from the melting Scandinavian ice sheet. For species capable of flight its crossing cannot have posed any great problem. For flightless taxa this freshwater trench was probably not an insurmountable barrier, although the northwards progress was in all probability slower than for the flying ones [as has been discussed by, e.g., Coope (1969, 1979)].

The migration process for flightless species probably involved a transport on flood debris on the surface of the floating ice washed out to the sea at the time of the spring floods. Such floods were probably immense in areas where the ice sheets were melting and freshwater could have floated on the denser marine water for considerable distances. The species dispersing in this manner would then have been protected from the seawater both by debris layers, ice rafts, and a layer of fresh (or brackish) water (Coope 1979). It could be mentioned here that, e.g., certain carabid beetles are able to endure for surprisingly long times even when drifting or swimming in seawater (Thiele 1977). The short course of the then anticlockwise North Atlantic Drift would then have assisted the dispersing species in reaching habitable areas before their transport disintegrated.

Species from the British Isles could have reached the west coast of Norway in this way. The North Atlantic islands, however, were probably invaded from two directions during this period - from the west coast of Norway and from the west coast of Scotland (including the Hebrides); in both cases rafting on ice carried by the fresh water from the melting Scandinavian and Loch Lomond ice sheets (Fig. 2). In the case of Scotland and the Hebrides the seaborne flood debris was problably swept northwards by the North Atlantic Drift (for a different view see Buckland 1988).

In this way we would have a passive dispersal, with increasing losses of species, from both western Norway and the western Scotland/Hebrides area, over Shetland, the Faroes, Iceland and on to Greenland (Fig. 2). This was, in Simpson's (1940) terms, a sweepstake; see also the discussion in Diamond and Gilpin (1983) about the origin of the Philippine avifauna, which shows certain essential similarities to this scenario.

During such a dispersal process island size probably played a small role, if any. The magnitude of this passive dispersal would have ensured that a species sooner or later would have reached all areas available for colonization regardless of their size (provided, of course, that it took part in the dispersal process; see below). That a successful dispersal resulted in a waif colonization was, of course, not given. And even when it did, persistence in such areas was partly a result of later climatic changes. Periods like the Small Ice Age, for example, probably meant floral and faunal impoverishment [see also the discussion in Lindroth et al. (1973) on the difference between dispersal and colonization].

It must be remembered that the conditions outlined above do not prevail today. They did exist for a (geologically) short period at the end of the Weichselian (probably somewhere between 500 and 1000 years, Ruddiman et al. 1977) before the Fennoscandian ice sheet had melted away far from the coasts (when the meltwater would be distributed over land instead of running directly to the sea via fjords and bays) and before the retreat of the polar front northwards had enabled the North Atlantic Drift to establish its »normal« interglacial pattern.

It should also be noted that the source areas for such a large-scale passive dispersal as envisaged here are not only low-lying lands like Jaeren in Norway (Andersen 1980: Fig.1) and parts of the Hebrides, but also fjord landscapes like the stretches north and south of Bergen in Norway and the mountainous region of western Scotland. Much of the meltwater entered the sea in such mountainous regions for purely topographic reasons, but the low-lying lands (which had perhaps been colonized earlier - for example Jaeren from the British Isles) were probably flooded by the meltwater, with the result that many species were rafted to the sea.

This, however, also meant that species with special habitat requirements (for example those requiring deep soil layers or luxuriant vegetation) could not have immigrated to the North Atlantic islands during this period. A terminal date for this passive colonization can be set at about 9000 BP (Buckland 1988) but probably the process was more rapid (see above).

After the re-establishment of the interglacial ocean current pattern immigration by this means ceased altogether (or nearly so). Instead other possibilities opened up for species immigrating over water (although on a much smaller scale). The reestablished North Atlantic Drift brought considerable amounts of driftwood to the Faroes and Iceland, especially from the American continent. Certain amounts of driftwood from the east (notably originating from the rivers Ob and Yenisej, Bjørk 1985) later started to run ashore. Driftwood has been (and still is) abundant in the Faroes as indicated by, e.g., place names like *Viðareiði* and the island name of *Viðoy (»viður«* is Faroese for wood). It has been reported (Bjørk 1985) that tree trunks of Siberian origin which had run ashore at Kirkjubøur (at the southern tip of Streymoy) still had soil attached to the roots. The report of Jessen and Rasmussen (1922) mentioned above also included a find of a piece of *Picea* (or *Larix* in a subfossil layer, which was interpreted as originating from Siberia. That driftwood is common and has been of economic importance is clear; it was included as an asset in the Taxation report of 1873 (Anon. 1973) and for example Kirkjubøur, mentioned above, was taxed with 25 *Rigsdaler* annually for the value of driftwood regularly running ashore.

Just as with the drifting ice floes, the driftwood could have brought only certain kinds of species to the Faroes. These may have included a number that survived for a time but later went extinct (perhaps species like *C. micropterus* mentioned above, which is a forest-dwelling species, or wood-boring species of various kinds).

Aerial dispersal

In addition to this short waterborne immigration an aerial sweepstake has influenced the fauna during the whole of the Holocene (Gíslason 1981, Buckland 1988) and is still going on. It seems probable that this aerial dispersal mainly stems from NW Europe, although the winds over the Faroes are mainly westerly. However, winds from the south, southeast and east are not uncommon; according to Sestoft (in Trap 1968) they amount to 27.6% of prevailing winds (S 9.3%, SE 9.8%, E 8.5%). Among the species that may have immigrated by air is a considerable number of spiders. It is perhaps significant that reports on the spider founa of the Faroes from two collecting periods 50 years apart (Braendegaard 1928, later added to in Ashmole 1979, and Bengtson and Hauge 1979) yielded about the same number of species, but that overlap of the species lists was only about 50%. This might indicate that spiders are constantly immigrating to the islands by aerial dispersal (ballooning) and that a number of the immigrants after a time go extinct.

Other taxa that have been reported to disperse by air are, e.g., freshwater sponges (Porifera); the gemmulae attach to the feathers of birds. There is only one species of Porifera on the Faroes, the amphiatlantic *Heteromeyenia ryderi* Potts. In addition to its American distribution it has been found in Ireland, on the island of Mull, in the Outer Hebrides, and in the Faroes (Arndt 1928, Waterston 1981) (see the discussion above of the transport along the western coast of Scotland, including the Hebrides, northwards by the North Atlantic Drift).

Other anecdotic evidence exists. During our investigation in the Faroes (see Bengtson and Hauge 1979) we found, on the island of Sandoy, the sand-dune living lepidopteran *Photedes stigmatica* Ev. This species was found in Iceland for the first time in 1937 (a single record); in the 1970's a population was found in SE Iceland (Ólafsson and Björnsson 1976). The nearest known occurrence of the species is in the Ural area in Siberia; in the Faroes it was found in the only sand dune in the islands.

Dispersal by birds is perhaps not uncommon. Pedersen (1971), intrigued by the occurrence of same nearctic species of Diptera in Iceland, fed robins *(Erithacus rubecula)* egg-bearing females of *Tipula autumnalis*. About a third of the eggs that were collected from the faeces were still viable.

Dispersal by wind is probably on a scale not generally appreciated. Two modern examples might illustrate the rapidity and the large scale of such a process:

1) The volcanic island of Surtsey appeared in 1963 off the southern coast of Iceland. In 1965 investigations started on the island and already by 1968, 70 species of arthropods, mainly Diptera (43 species) had been caught there. By 1970 the number had risen to 158 (of which 105 were Diptera) (Lindroth 1971, Lindroth et al. 1973). By 1981 the number was 197 (121 Diptera) (Ólafsson 1978, 1982).

2) It has been established that roughly 4.5 billions of insects per day are lost by wind drift at the height of summer on the North Sea coast of Germany from a coastal strip 30 km wide (Heydemann 1967). Several similar examples could be given.

Thus, for a long time (on an ecological scale) immigration to the North Atlantic islands was by wind (and exceptionally by other means mentioned above). The increasing diversity and species richness of the source areas in NW Europe probably led to this process having increased its importance for the immigration to the islands over time.

Man's influence on the immigration process

A new dimension in the immigration process was introduced with the advent of Man, as discussed in detail for Scandinavia by Brinck (1966a, b).

During the last 1100 years man has played an increasing role in changing the biota of the North Atlantic islands by bringing anthropochorous species to - in the first place - the inhabited parts of the islands, and by habitat perturbations. To identify possible source areas for these species a brief account will be given of the communication pattern between the Faroes and the surrounding areas; this is because the Faroes may be considered a representative case in the North Atlantic.

The first inhabitants in the islands might have been Irish monks (Dicuil 825). They possibly cultivated cereals (*Avena sativa;* Jóhansen 1979). It is thought that the monks lived in Mykines (old fields have been found there); a few other sites are also probable. It is also not known whether there was any communication between the monks and Ireland. They were (probably) ousted by Norsemen in the 9th century. It is not known from where the immigrating Norsemen arrived; recent opinion has it that they came from Shetland (this at that time occupied area forming a stepping-stone during the expansion of the Norse to the Faroes and Iceland; Nielung 1967-69). From then until about AD 1050-1100 most contacts (they were probably few) were with Norway, although also Shetland, the Hebrides, possibly Ireland, and on a small scale Iceland were involved. Most communications, however, were with Bergen in Norway (the Faroes were at that time under Norwegian jurisdiction), where the tribute to the Norwegian King, which consisted of wool, was landed. This was a more or less irregular communication, which became regulated in the 12th century. There is no record of what was brought back to the Faroes but one can be reasonably sure ballast was a minor part (scattered reports indicate that beer, wine, cereals and sometimes perhaps cattle - with the necessary fodder and water - was imported at the time).

A second stage in the inner colonization of the islands seems to have started in about AD 1200 when the remote parts of the islands were colonized. When the pressure on the land became too great this practice was curtailed in 1298 by the *Seyðabrævið* (Sheep Letter).

In 1271 a royal decree promised that two ships should ply between Norway and the Faroes (perhaps indicating that communications had been too irregular in the past).

In 1294, and again in 1302, the Hanseatic merchants were prohibited by Norway from trading with the Faroes; this was apparently an attempt to set up a trading monopoly between Norway and the Faroes; communications were thus kept restricted between these two areas.

The *Sheep Letter* of 1298 partly dealt with the setting up of new farms. Persons were prohibited from establishing new farms unless they owned three cows.

This prohibition remained in force until 1637.

That connections with Shetland existed at that time is shown by the fact that the *Sheep Letter* was drawn up on the advice of, i.a., the Lawman of Shetland, who had been sent to the Faroes to consider the deficiencies in the agricultural law.

The Black Death reached the islands probably around AD 1350. It is thought that perhaps one third of the population may have perished. At least Húsavík on Sandoy and Saksun on Streymoy seem to have been laid desolate. Probably connections with other countries, as well as communications within and between the islands, diminished. Trade with Norway decreased, which is shown by the fact that the Hanseatic League in 1361 obtained the same right to trade with the Faroes as the Norwegian merchants in Bergen had. Apparently the trade was not very profitable, which implies that contacts between Norway and the Faroes were scarce.

In 1468/69 trading with the Orkneys and Shetland might have increased, since those areas then left the Union of Denmark and Norway to become parts of Scotland; in 1490 the Dutch were granted the same trading rights with the Faroes as the Hanseatics had.

In 1536 a trade monopoly came into being and the first monopoly grant was given to a Hamburg merchant. This restricted other trade channels with the Faroes (or closed them altogether, except for a possibly increasing smuggling trade). The monopoly lasted until 1856, when the islands were opened to international commerce.

Between (and within) the islands a certain communication pattern prevailed. During this whole period the Faroese *Løgting* was situated in Tórshavn which became the meeting-place for the inhabitants of the islands. Communications between the islands were undoubtedly more common than with outside countries.

Tórshavn was the only place where trade could legally be conducted. This, of course, increased communications between Tórshavn and the peripheral islands, and probably (secondarily) decreased contacts between the peripheral islands. Out-stations of the monopoly were opened in 1836 in Tvøroyri (Suðuroy), in 1838 in Klaksvík (Borðoy), and in 1839 in Vestmanna (Streymoy). In 1867 the Sheep Letter was replaced by a taxation law (»Outfield Law«). In 1873 a taxation survey was carried out (Anon. 1973) which changed the value of some of the in- and outfields.

The latest impact on the Faroese biota was made when plantations were started to be established around 1900. Cuttings were brought in, mainly from Denmark, but also from other countries (Ødum 1979). In addition to foreign elements in the soil fauna which were possibly brought to the islands in this way, the plantations have become sites for forest species (mainly birds, Bengtson and Bloch 1983, aphids, Heie

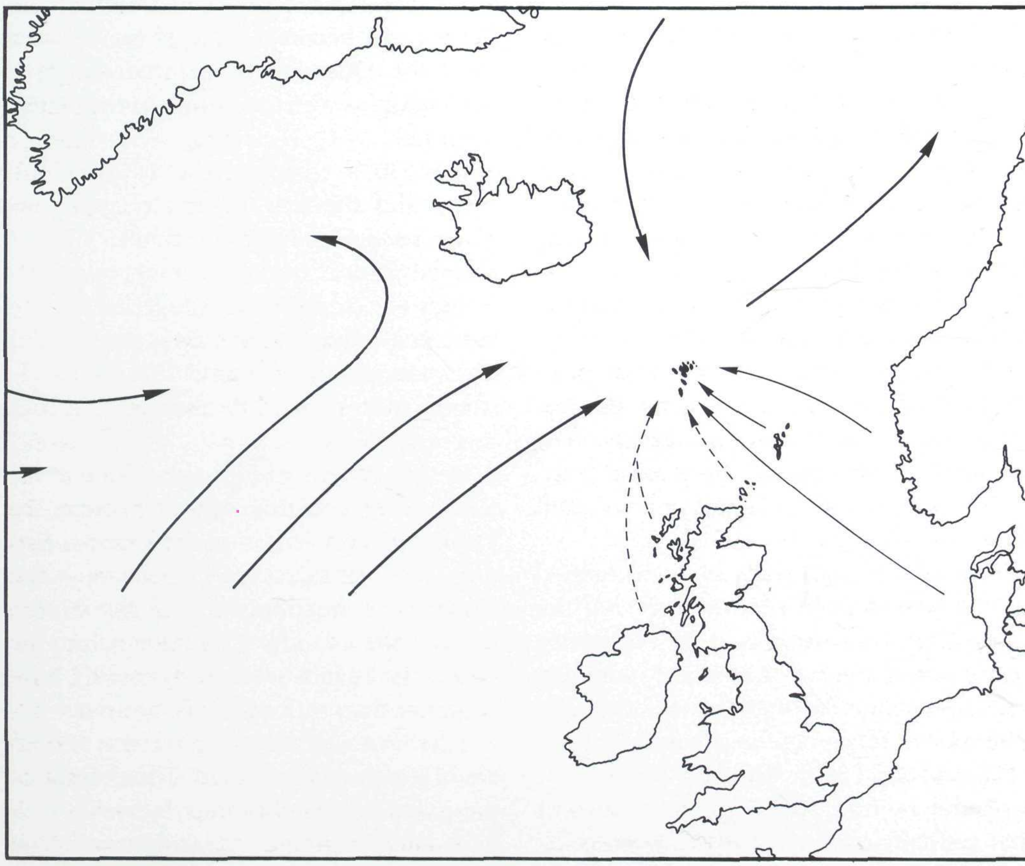

Fig. 3. Immigration paths of terrestrial invertebrate taxa to the Faroe Islands during different periods after the first immigration phase. Driftwood arrived from the American continent and the northern part of Eurasia and still does (thick arrow = ocean currents). Human communications (thin arrows) existed from about AD 850 onwards; first with Shetland and western Norway, and later (especially during the trade monopoly) with Danish areas. Intermittent contacts occurred with the Orkney Island, the Hebrides, perheps Ireland (and occasionally with Iceland). In addition, immigration by aerial dispersal (mostly from a S-SE-E direction) has occurred continously.

1972, other insects, Koponen 1985). Twenty-three plantations, most of them between 1 and 5 ha (some less successful) have been established.

The above historical account relies on West (1972) and Young (1979).

Summary of the immigration to and colonization of the Faroes

The foregoing account can be conveniently summarized as follows:

1) A large-scale immigration event (but not necessarily colonization to the same degree) occurred some time between 10000 and 9000 BP from coastal areas in western Scandinavia and western Scotland with the Hebrides (Fig. 2).

2) An immigration trickle occurred with driftwood from the American continent and the northern part of Eurasia; the former probably starting earlier than the latter (on account of ice conditions in arctic areas and forest development in northern Eurasia).

3) Aerial immigration probably occurred continuously from the moment the Faroes became available to immigrants. This kind of dispersal has probably increased in intensity, and with a succession of species, as a consequence of the increasing species richness and changing faunal composition in the source areas in NW Europe.

4) Immigration with Man has occurred during approximately the last 1100 years (if one disregards the earliest contacts with Ireland as having had a negligible effect). The main periods and directions have been (Fig. 3):

a) From Shetland and western Norway from about AD 850, with small additions from Ireland, the Orkney Islands, and Iceland, up to about AD 1550.

b) From Denmark and surrounding areas during the period of the trade monopoly (AD 1529 - 1536 to 1856)

c) From indeterminable directions during the last 100 years, although probably still with a preponderance of NW European contacts.

5) In addition to this immigration of species to the Faroes (1-4) a dispersal between and within the separate islands in the group has occurred continuously but possibly more intensively during the second period of inner colonization (AD 1200 - 1300); during the period of the trade monopoly, and in recent times.

The biogeographical position of the present-day terrestrial invertebrate fauna of the Faroes

Any qualitative assessment of the faunal diversity and taxonomic composition of the present terrestrial invertebrate fauna of the Faroes rests on how complete species lists are (reflecting the degree of coverage and collecting effort). To illustrate the position of the Faroes as concerns faunal richness, and similarity to neighbouring areas, I have chosen to summarize the information available on four taxonomic groups (Coleoptera, Araneae, Lumbricidae and Gastropoda) which are believed to be rather well known in most of the areas concerned. The literature sources are given in the legend of Fig. 4; it should be noted that information from the Orkney Islands is more incomplete than for the other areas.

Some salient features emerge from the numbers in Fig. 4.

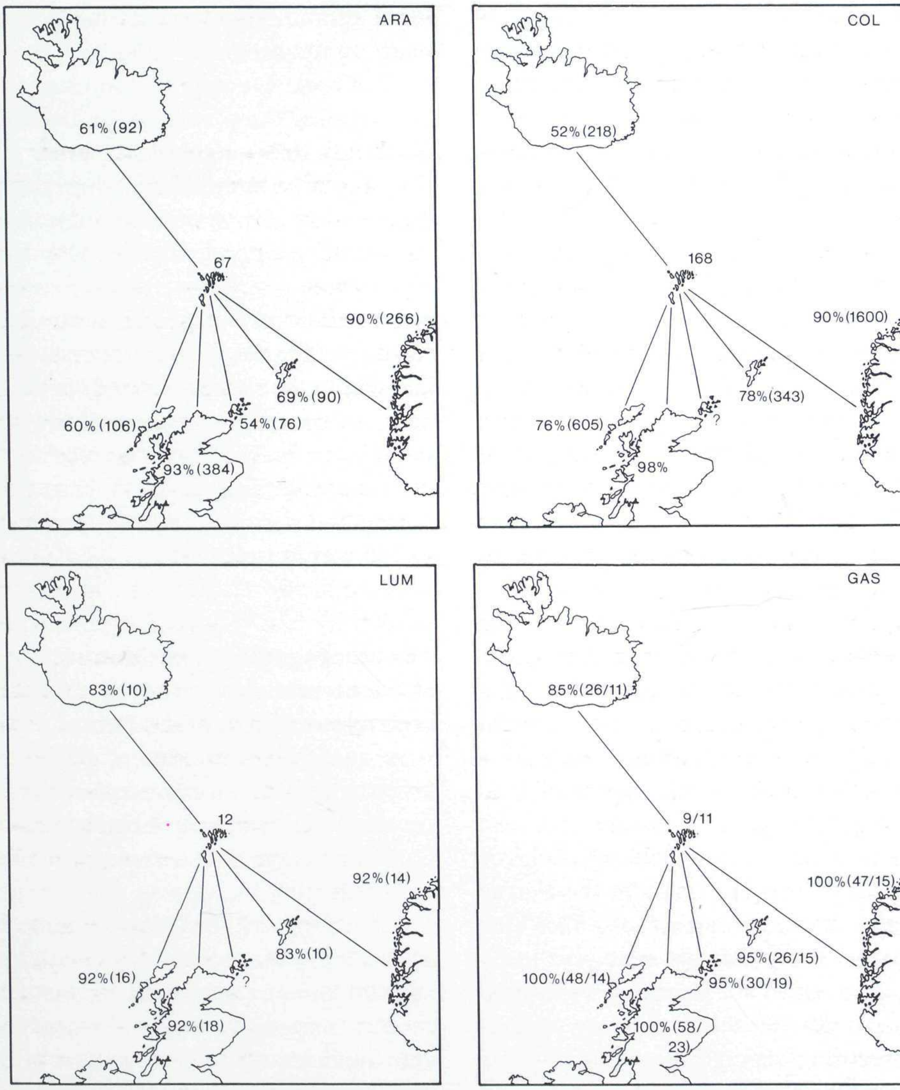

Fig. 4. The percentage of the Faroese fauna of Coleoptera (COL), Araneae (ARA), Lumbricidae (LUM) and Gastropoda (GAS, slugs/snails) found in the neighbouring areas. Figures in parenthese indicate the known number of species of the respective groups in these areas. Areas included are the Outer Hebrides, the Scottish Mainland, the Orkney Islands, Shetland, western Norway (the counties Sogn og Fjordane, Hordaland, and Rogaland, i.e. approximately the stretch between Ålesund in the north to Stavanger in the south), and Iceland. Data on the groups from: *Coleoptera:* Bengtson 1981 and references therein, Waterston 1981, *Araneae:* Ashmole 1979, Bengtson and Hauge 1979 and references therein, Waterston 1981; *Lumbricidae:* Enckell and Rundgren 1983 and references therein, Gerard 1964, Waterston 1981; *Gastropoda:* Solhøy 1981 and references therein, Waterston 1981. For Coleoptera, the total species number in the British Isles is about 3800; the Faroese species have been checked as to their occurrence in Scotland.

Species richness

It is immediately apparent that the Faroes is the most species-poor area in the temperate North Atlantic. There is a decrease in the number of species in all groups from the Scottish mainland northwards and particularly between Shetland and the Faroes as concerns beetles and molluscs (it is less pronounced in spiders). A number of factors contribute to make the Faroes so depauperate: 1) It is the most isolated area in the North Atlantic; the distance to the nearest mainland is 320 km (as compared with Shetland's 100 km). 2) The area of the Faroes is small; it is about equal to Shetland. Iceland, for example, is 75 times larger. 3) It has been available for colonization a shorter time than both the Hebrides, Orkney, and Shetland, and it is probable that its biota are not yet saturated. 4) The plant cover of the islands is relatively homogeneous (in itself partly a result of the low species number of plants, but also of the intensive grazing over practically the whole vegetated area). Thus the structural diversity of the plant cover is also low. 5) Man reached the Faroes only about 1300 years ago, while for example Orkney and Shetland were inhabited already in Neolithic times, about 3000 BP. Human communications with the Faroes have also been rather restricted for a large part of this period as compared with e.g. the Outer Hebrides (Waterston 1981). Thus, the anthropochorous species are proportionally fewer than for these areas. 6) The climate of the Faroes is distinctly more oceanic than for the other areas (perhaps excepting Shetland), which means that continental species immigrating to the islands may survive less well even if they establish themselves for a short period (one example is *Betula nana,* see above).

Similarity with neighbouring areas

The majority of the Faroese species are to be found in most of the neighbouring areas. However, this similarity (expressed in Fig. 4 as the percentage of the Faroese species found in the respective area) is higher towards the south and towards western Norway than between the Faroes and Iceland. Among the areas included Iceland contains by far the largest numbers of high-boreal and arctic species (including a number of Nearctic species) and exerts a double-filter effect on the composition of the Faroese fauna. Several species do not extend their distribution ranges northwards beyond the Faroes, while some northern species occur, e.g., in higher mountainous regions in the British isles. Thus, while there is a drop in the number of species between Shetland and the Faroes there is a more pronounced change in the taxonomic composition as one proceeds from the Faroes to Iceland.

As to the most likely source areas for the Faroese fauna, present-day faunal lists are of limited use. The source species pools in Fennoscandia and Scotland do not simply represent a numerical measure from which a certain fixed percentage of species has dispersed to the Faroes (or even, to the more close-lying Orkney and the Hebrides), according to some popular statistical formula in current use. The source pools are made up of assemblages of species with different habitat requirements and different dispersal abilities. A statistical approach to the numerical data is thus not feasible; the biological properties of the individual species must form the background for an estimate whether the occurrence of these species on distant islands is probable or improbable. This is, of course, not true only for these four invertebrate groups; biological common sense argues that such basic data must be taken into account when dealing with any animal (or for that matter plant) group.

Differences between groups

As discussed above, different species (in some cases higher taxa) probably experienced peaks during different times in their colonization of the Faroes, depending upon a number of factors. This ought to be reflected (at least to some extent) in their present distribution in the North Atlantic area. The four groups used here to illustrate the present pattern (Fig. 4) have different dispersal abilities. The spiders, for example, include a large proportion of species which readily disperse by air (ballooning, and in the case of small-sized species also drifting by currents). (For differences between families of spiders in this respect, see Ashmole 1979: Tab. 6.) This is true also for beetles, where many species are capable of dispersal by flight, though a number of them are also readily transported over the sea (salinity tolerant) or with man (anthropochorous). In contrast, earthworms and terrestrial gastropods are not able to cross water without aid. It is striking, therefore, that the last two groups are qualitatively very alike on the island groups compared. In fact, the few lacking records of Faroese snails and slugs on the other island groups in the area only refer to *Deroceras agreste* not having been recorded from Shetland and Orkney (and three small species of snails not recorded in Iceland). In the case of earthworms the discrepancies between the island groups can be explained by the find of one species in the Faroes *(Allolobophora similis* Friend, previously only found in Kew), and a few other species not recorded in one or two of the other areas (see Enckell and Rundgren 1983). In summary, then, the groups depending on Man for their dispersal show a more homogeneous distribution pattern in this area than groups with better dispersal abilities (Enckell et al. 1986).

The general high degree of similarity in faunal composition between the Faroes and the surrounding areas permits various interpretations as to the source areas of the different species. A purely taxonomic comparison leads nowhere; it is possible, however, that comparisons of genetic variation in species occurring in the Faroes and in other areas could give some clues to the origin of these species.

Last, it should be pointed out that a static or equilibrium state has probably not been reached as concerns the invertebrate fauna of the Faroes. Certain species have no doubt reached the islands only recently and have still not colonized all the sites (or islands) where they would be able to exist. It is not known how rapid the colonization of an island group is, once a species has obtained a beach-head. In view of the fact that the inner colonization often takes place from a source of individuals which is rather scarce (the population of another island in the island group) it seems intuitively true that invasion of an island group may initially be rapid (large-scale invasion from a large species pool), but that the subsequent inner colonization may be rather slow, if immigration from the source pool ceases and the further colonization of the island group becomes (mainly) dependent on dispersal from the populations which have established themselves in (perhaps a few) beach-heads.

My belief is that this is what happened for a number of species after the initial large-scale immigration during the first Post-Glacial dispersal event. This large-scale immigration ceased after some time and left the further spread of the taxa over the islands to the already established populations. Some of the species distribution patterns we have found in the Faroes indicate that the dispersal process within the islands is still not completed.

This general overview is, however, not the place to discuss individual species, or differences within larger taxonomical groups when it comes to colonizing the Faroe Islands. Some such patterns are treated in fuller detail in Enchell et al. 1986.

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Pehr H. Enckell
Department of Animal Ecology
Ecology Building
University of Lund
S-223 62 Lund, Sweden.

Úrtak

Roynt verður at greina ímillum ymisk skeið í innflytningarsøguni til Føroya hjá rygg-loysingum, ið liva á landi, og at meta um tilmunarliga týdningin hjá hesum søgu-skeiðum. Víst verður á skeið við ovurstórari innflyting eftir sjónum onkuntíð millum 10.000 og 9.000 fyri Krist, og at innflyting tann vegin seinni hevur minni upp á seg. Innflyting við rekaviði hevur trúliga verið av og á; hon tók seg helst fyrr upp av amerikanska meginlandinum enn av norðaru leiðunum í Europa og Ásia. Innflyting gjøgnum luftina hevur verið týðandi alla tíðina, síðan oyggjarnar gjørdust førar fyri at taka *ímóti tílíkum lívverum*; *henda* gongd hevur so líðandi vundið upp á seg, so hvørt sum sløgini eru nørd í tali í útnyrðingsparti Europa. Innflyting við fólki er farin fram tey seinastu 1100 árini; upphavsstaðir hava verið Vestur-Noreg, Danmørk og Bretlandsoyggjar norðantil. Tilfallandi innflyting av sløgum við serstøkum lívlendiskrøvum er komin ta tíð, sum fólk hevur búð í landinum; dømi eru eitt nú sløg, ið krevja djúpa mold, og skógarsløg í nýliga gróðursettum viðarlundum.

Lega Føroya í norðuratlanskum lívlandafrøðiligum høpi verður víst við at bera saman fyrikomingar av fýra bólkum (Coleoptera, Aranese, Lumbticidae og Gastropoda). Týdning fyri hesar bólkar hava avbyrging, oyggjalendi og gróður, umframt útbreiðsluevnini hjá teimum ymisku sløgunum.