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Origin of an Insular Population of the Wood Mouse Based on Parasitological Evidence

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ABSTRACT: Parasitological data were used to test the hypothesis that the wood mouse (Apodemus sylvaticus) population of Fair Isle, Shetland, originated from the British Isles rather than Scandinavia, as is usually argued. This study was based on the assumption that the mice were likely to share most of their parasite fauna with conspecifics from their ancestral home. The ecto- and endo-parasites of wood mice on Fair Isle between 18 June to 10 July 1987 and 17 to 26 August 1991 were identified and compared with those reported from conspecifics in the two putative source areas. All eight species of metazoan parasites that infected A. sylvaticus on Fair Isle were common to mice of the British Isles, whereas just one parasite on Fair Isle, a mite, had been recorded from Scandinavia. This lends support to the hypothesis that the mice originated from Britain rather than Scandinavia.

Key words: Apodemus sylvaticus, mouse, origin, genetics, biological tags, helminths, ectoparasites.

The origin of the wood mouse (Apodemus sylvaticus) on islands north of the British mainland has long been the subject of debate. For many years it was believed that the mice were glacial relicts, but it is now generally accepted that the mice could not have survived the last ice age (Elton, 1947) and, therefore, must have colonized the islands since the end of the Pleistocene (Corbet, 1961; Yalden, 1982). Berry (1969), noting the apparent genetic similarity between mice from Scandinavia and the Hebridean and Shetland islands, suggested that those on the northern isles were carried there by Vikings from the mid-7th century onwards. Conversely, Handford and Pernetta (1974), believed that the islands must have been colonized long before this time and that the mice were probably brought there by Neolithic or Bronze Age migrants from England or Ireland. Based on fossil records, *Apodemus* sp. was present on the neighboring island of Orkney in Neolithic times (Corbet, 1979). However, Berry (1979) argued that Handford and Pernetta misinterpreted his arguments and that his earlier interpretation of the genetic data (Berry, 1969) still holds.

An alternative method of establishing the most likely place of origin of island wood mice populations would be to compare their parasite fauna with that of A. sylvaticus originating from the putative source areas in Scandinavia and the British Isles; Moser (1991) provides a review of the role of parasites as biological tags. This method was previously used by Bengtson et al. (1986) to determine the likely geographical origin of both the wood mouse and the house mouse (Mus musculus) on Iceland. All five species of mites (Acari) found on these animals also were abundant in populations from western Norway, where the first Viking settlers are thought to have originated (Marcus, 1980). Moreover, the mouse flea present in Iceland, Ctenophthalmus agyrtes agyrtes, is commonly found in Nordic countries but is absent from the British Isles, where it is replaced by Ctenophthalmus nobilis (Brinck-Lindroth, 1981). These results provide clear evidence supporting the hypothesis that the Icelandic mice are of Scandinavian rather than British origin.

Our objective was to test the hypothesis that A. sylvaticus on Fair Isle, Shetland, originated from the British Isles rather than Scandinavia. We did this by comparing the endo- and ectoparasites of A. sylvaticus with parasites reported from this host living in Scandinavia and the British Isles; our assumption was that the population would share most of its parasites with mice from its source location.

Fair Isle (59°32'N, 01°37'W) is a small $(3 \text{ km} \times 5 \text{ km})$ island mid-way between Shetland and Orkney, north of the British mainland. The only small mammals on the island are the house mouse (M. domesticus), and the wood mouse (A. sylvaticus), known locally as the hill or red mouse. Currently, this latter species holds the subspecific status (A. sylvaticus fridariensis) given to it by Kinnear (1906), although this will likely change with the next taxonomic revision of this group (Corbet and Harris, 1991). Apodemus sylvaticus is found in all habitat-types throughout the island, whereas the house mouse is mainly found in the southern half of the island where the human population is concentrated (Kinnear, 1906).

Between 18 June and 10 July 1987 (catch 1), and 17 to 26 August 1991 (catch 2), mice were trapped at 23 localities chosen to encompass as much of the island's 500 ha as possible. At each capture, the age, sex, weight, and tarsus length were determined and the fur clipped to allow individual identification. In addition, the pelage was searched thoroughly for ectoparasites. Any mice that died in traps, or were caught at the Bird Observatory at North Harbour, were dissected and examined for helminth parasites. This involved searching the body cavity and all parts of the alimentary canal, from the esophagous to the rectum, under saline and a dissecting microscope. In addition, the liver, spleen, lungs and heart were examined for signs of infection; any infected organs were preserved in 70% alcohol before being sectioned, mounted, and thoroughly examined under a light microscope. Capillaria hepatica was found encysted in the sections of liver, and these were identified by J. M. Behnke. All other parasites were identified by staff at the Natural History Museum (London, UK). Voucher specimens are held there with the following registration numbers: BM(NH) 1988.2.18.5–10 and BM(NH) 1988.356–388.

Over the two catching periods, two (5%)of 44 Fair Isle mice in catch 1 and nine (32%) of 28 in catch 2 had ectoparasites (Table 1); the most common of which was the flea Ctenophthalmus nobilis vulgaris, which infested nine of the mice. Ten of the 11 mice dissected were infected with one or more species of helminth parasite. The most common of these was a nematode of the genus Rictularia; more than 80% of mice were infected with between two and 13 of these parasites. Maritrema apodemicum, Hymenolepis muris sylvatici, Trichuris muris and Capillaria hepatica infected just one, or two of the 11 dissected mice (Table 1).

All the helminth parasites found in A. sylvaticus on Fair Isle also have been reported in wood mice from the British Isles (Table 1): M. apodemicum was first identified by Lewis (1966) on the Welsh island of Skomer; H. muris sylvatici has been recorded from mice in woodlands in southern England (Lewis and Twigg, 1972); T. muris has been reported from County Down, Northern Ireland (Montgomery and Montgomery, 1988) and from southwestern England (Murua, 1978); C. hepatica was found in mice from mid-Wales (Lewis, 1968) and from the Hebridean island group of St. Kilda (Berry and Tricker, 1969); and the only British report of a nematode from the genus Rictularia (Berry and Tricker 1969; identified by Boyd, 1959, as R. cristata) also was from St. Kilda. None of these helminths have been reported from any of the Scandinavian countries (Table 1).

The ectoparasites had a similar division. Although the mite *Eulaelaps stabularis* is found in both Britain and Scandinavia, and hence has low utility for determining the origin of Fair Isle's mice, both the mite *Haemogamasus arvicolarum* and the flea *C. nobilis vulgaris* are found throughout the British Isles (Evans and Till, 1966), including the west of Ireland (Langley and Fairley, 1982) and the Inner Hebrides

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Parasite taxon	Species	Prevalence	Mean inten- sity	Previous records of species	
				British Isles	Scandinavia
Siphonaptera	Ctenophthalmus nobilis vulgaris (Smit 1955)	1987: 2/44 (5%) ^a 1991: 7/28 (25%) ^c	0.05 0.36	Yes (1, 2, 3) ^b	No (1)
Arachnida	Haemogamasus arvico- larum (Berlese 1920)	1987: 0/44 (0%) 1991: 4/28 (14%)	0 0.21	Yes (2, 4)	No (6, 7, 8, 9, 10)
	<i>Eulaelaps stabularis</i> (Koch 1836)	1987: 0/44 (0%) 1991: 1/28 (4%)	0 0.04	Yes (2, 3, 4, 5)	Yes (6, 7, 8, 9, 10)
Digenea	Maritrema apodemicum (Lewis 1966)	1/11 (9%)	0.09	Yes (11)	No
Cestoda	<i>Hymenolepis muris syl-</i> <i>vatici</i> (Rudolphi 1819)	2/11 (18%)	0.18	Yes (12)	No
Nematoda	<i>Trichuris muris</i> (Schrank 1788)	2/11 (18%)	0.64	Yes (13, 14)	No
	<i>Rictularia</i> sp.	9/11 (82%)	4.27	Yes? (15, 16)	No
	Capillaria hepatica (Bancroft 1894)	2/11 (18%)	N/A ^d	Yes (16, 17)	No

TABLE 1. Prevalence and Intensity of Parasite Infections of Apodemus sylvaticus on Fair Isle, Shetland.

"Year sampled: number positive/number evaluated (% positive).

^b Reference sources: 1, Brinck-Lindroth (1981); 2, Langley and Fairley (1982); 3, Corbet (1964); 4, Evans and Till (1966); 5, Elton et al. (1931); 6, Edler (1969); 7, Lundqvist and Edler (1987); 8, Nilsson and Lundqvist (1979); 9, Brinck-Lindroth et al. (1975); 10, Edler and Mehl (1972); 11, Lewis (1966); 12, Lewis and Twigg (1972); 13, Montgomery and Montgomery (1988); 14, Murua (1978); 15, Boyd (1959); 16, Berry and Tricker (1969); 17, Lewis (1968).

^c For the ectoparasites, two prevalences and intensities are given, corresponding to catch 1 and catch 2. Endoparasites were recorded only during catch 1 (1987).

^d Intensity of encysted eggs and worms in the liver was not determined.

(Corbet, 1964). By contrast, in Scandinavia, *H. arvicolarum* is replaced by *H. nidi*, *H. nidiformis*, *H. hirsutus* and *H. ambulans* (e.g., Edler and Mehl, 1972) and *C. nobilis* is replaced by *C. agyrtes*; Brinck-Lindroth (1981) provides a review. Thus, these data provide strong support for the hypothesis that the Fair Isle wood mice originated from the British Isles rather than Scandinavia, as Berry (1969, 1986) in particular has argued.

However, there are at least four alternative explanations that must be considered. First, the absence of any correlation between the mouse parasites of Fair Isle and Scandinavia may be a consequence of a lower sampling effort in Scandinavia compared to the British Isles (Gregory and Blackburn, 1991). We know of only two papers concerned with the helminth fauna of Scandinavian mice (Wiger et al., 1976; Tenora et al., 1977), compared with at least five times this number for British mice. However, despite numerous papers on the fleas and mites of Scandinavian mice, none of these ectoparasite species were found in mice on Fair Isle. Secondly, the parasites may have arrived on the island with mobile intermediate hosts, such as molluscs and arthropods. One species of cestode and one digenean species were found that rely on the food chain for completion of their life-cycles. However, as in other mice populations (Lewis, 1987), the majority of the helminth parasites on Fair Isle are monoxenous nematodes (three species). Moreover, all of the ectoparasites are directly transmitted. Thus, most of the parasites associated with Fair Isle's mice have direct life-cycles and so are unlikely to have arrived there independently of the mice. A third possibility is that the parasites arrived on Fair Isle with M. domesticus from Britain and then cross infected A. sylvaticus. However, only one of the eight parasite species found in wood mice on Fair Isle (T. muris) has been recorded in wild populations of house mice (Murua, 1978; Lewis, 1987). Thus, most A. sylvaticus parasites probably arrived on Fair Isle with wood mice rather than house mice. A fourth possible explanation for the observed trends is that the current parasite fauna is due to more recent invasions, with newer parasites replacing older ones. Clearly, the only way of conclusively excluding this possibility is by performing the same sorts of molecular genetic analyses that also are required for their hosts. To our knowledge, no such analyses have yet been conducted for any host-parasite system.

In conclusion, we propose that the wood mice on Fair Isle may have originated from the British Isles, rather than Scandinavia, although more extensive parasitological and genetic studies are required before this can be verified.

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