

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

Kenneth Wilson,^{1,2} Paul Eady,^{1,3} and Adrian J. del Nevo,^{1,4} ¹Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, United Kingdom; ²Present address: Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA, United Kingdom; ³Present address: The Northumbrian Water Ecology Centre, The Science Complex, University of Sunderland, SR1 3SD, United Kingdom; ⁴Present address: Entrix, 590 Ygnacio Valley Road, Suite 200, Walnut Creek, California 94596, USA

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 km × 5 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 sub-specific 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 esophagus 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 registra-

tion 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

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

Parasite taxon	Species	Prevalence	Mean intensity	Previous records of species	
				British Isles	Scandinavia
Siphonaptera	<i>Ctenophthalmus nobilis vulgaris</i> (Smit 1955)	1987: 2/44 (5%) ^a	0.05	Yes (1, 2, 3) ^b	No (1)
		1991: 7/28 (25%) ^c	0.36		
Arachnida	<i>Haemogamasus arvicolarum</i> (Berlese 1920)	1987: 0/44 (0%)	0	Yes (2, 4)	No (6, 7, 8, 9, 10)
		1991: 4/28 (14%)	0.21		
	<i>Eulaelaps stabularis</i> (Koch 1836)	1987: 0/44 (0%)	0	Yes (2, 3, 4, 5)	Yes (6, 7, 8, 9, 10)
		1991: 1/28 (4%)	0.04		
Digenea	<i>Maritrema apodemicum</i> (Lewis 1966)	1/11 (9%)	0.09	Yes (11)	No
Cestoda	<i>Hymenolepis muris sylvatici</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
		9/11 (82%)	4.27		
		2/11 (18%)	N/A ^d		
	<i>Capillaria hepatica</i> (Bancroft 1894)			Yes (16, 17)	No

^a 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.

We gratefully acknowledge the help and support of the following: the people of Fair Isle; The Natural History Museum, London; Sheffield University; A. S. Baker, J. M. Behnke; E. Harris; T. Howard, V. Haukisalmi; W. Landells; A. Lockley; L. Lundqvist; W. Mosely; A. Seccombe; F. Tenora and R. Wiger. K. W. and A.J.dN. were supported by The Mammal Society and P. E. by the Louise Hiom Trust (Sheffield and Glasgow Universities).

LITERATURE CITED

- BENGTSON, S.-A., G. BRINCK-LINDROTH, L. LUNDQVIST, A. NILSSON, AND S. RUNDGREN. 1986. Ectoparasites on small mammals in Iceland: Origin and population characteristics of a species-poor insular community. *Holarctic Ecology* 9: 143-148.
- BERRY, R. J. 1969. History in the evolution of *Apodemus sylvaticus* (Mammalia) at one edge of its range. *Journal of Zoology* 159: 311-328.
- . 1979. On the nature of genetical distance and island races of *Apodemus sylvaticus*. *Journal of Zoology* 169: 292-293.
- . 1986. Genetics of insular populations of mammals, with particular reference to differentiation and founder effects in British small mammals. *Biological Journal of the Linnean Society* 28: 205-230.
- , AND B. J. K. TRICKER. 1969. Competition and extinction: The mice of Foula, with notes on those of Fair Isle and St. Kilda. *Journal of Zoology* 158: 247-265.
- BOYD, J. M. 1959. Observations on the St. Kilda field-mouse *Apodemus sylvaticus hirtensis* Barrett-Hamilton. *Proceedings of the Zoological Society of London* 133: 47-65.
- BRINCK-LINDROTH, G. 1981. Subspeciation of *Ctenophthalmus agyrtus* (Heller, 1896) s.l. (Siphonaptera: Hystrichopsyllidae) in Fennoscandia, Denmark and Iceland. *Entomologica Scandinavica*, Supplement 15: 141-152.
- , A. EDLER, L. LUNDQVIST AND A. NILSSON. 1975. Small mammals and ectoparasites in Scandinavia. In *Biocontrol of rodents*. L. Hansson and B. Nilsson (eds.). Swedish National Science Research Council, Stockholm, Sweden, pp. 73-98.
- CORBET, G. B. 1961. The origin of the British insular races of small mammals and of the "Lusitanian" fauna. *Nature* 191: 1037-1040.
- . 1964. Records of small mammals and their parasites from the islands of Scarba and Luing, Inner Hebrides. *Journal of Zoology* 143: 352-359.
- . 1979. Report of rodent remains. In *Investigations in Orkney*. C. Renfrew (ed.). Society of the Antiquaries, Thames & Hudson, London, United Kingdom, pp. 135-137.
- , AND S. HARRIS (EDITORS). 1991. The handbook of British mammals, 3rd ed. Blackwell Scientific Publications, Oxford, United Kingdom, pp. 220-229.
- EDLER, A. 1969. Ectoparasitic mites (Acarina) from small mammals in Central Sweden. *Entomologisk Tidskrift* 90: 272-284.
- , AND R. MEHL. 1972. Mites (Acari, Gamasina) from small mammals in Norway. *Norwegian Journal of Entomology* 19: 133-147.
- ELTON, C. S. 1947. The survival and extinction of flora and fauna in glacial and post-glacial times. *Nature* 159: 559.
- , E. B. FORD, J. R. BAKER, AND A. D. GARDNER. 1931. The health and parasites of a wild mouse population. *Proceedings of the Zoological Society of London* 1931, 657-721.
- EVANS, G. O., AND W. M. TILL. 1966. Studies on the British Dermanyssidae (Acari: Mesostigmata) Part II. Classification. *Bulletin of the British Museum (Natural History) (Zoology)* 14: 107-370.
- GREGORY, R. D., AND T. M. BLACKBURN. 1991. Parasite prevalence and host sample-size. *Parasitology Today* 7: 316-318.
- HANDFORD, P. T., AND J. C. PERNETTA. 1974. The origin of island races of *Apodemus sylvaticus*: An alternative hypothesis. *Journal of Zoology* 174: 534-537.
- KINNEAR, N. B. 1906. On the mammals of Fair Isle, with a description of a new sub-species of *Mus*

- sylvaticus*. The Annals of Scottish Natural History 1906: 65–68.
- LANGLEY, R., AND J. S. FAIRLEY. 1982. Seasonal variations in infestations of parasites in a wood mouse *Apodemus sylvaticus* population in the west of Ireland. Journal of Zoology 198: 249–261.
- LEWIS, J. W. 1966. *Maritrema apodemum* sp. nov. (Digenea: Microphallidae) from the long-tailed field mouse, *Apodemus sylvaticus* (L.) on Skomer Island. Journal of Helminthology 40: 363–374.
- . 1968. Studies on the helminth parasites of the long-tailed field mouse, *Apodemus sylvaticus sylvaticus* from Wales. Journal of Zoology 154: 287–312.
- . 1987. Helminth parasites of British rodents and insectivores. Mammal Review 17: 81–93.
- , AND G. I. TWIGG. 1972. A study of the internal parasites of small rodents from woodland areas in Surrey. Journal of Zoology 166: 61–77.
- LUNDQVIST, L., AND A. EDLER. 1987. Dispersal in patchy environments: Effect on the prevalence of small mammal ectoparasites. Folia Parasitologica 34: 357–367.
- MARCUS, G. J. 1980. The conquest of the North Atlantic. The Boydell Press, Woodbridge, Suffolk, United Kingdom, 224 pp.
- MONTGOMERY, S. S. J. AND W. I. MONTGOMERY. 1988. Cyclic and non-cyclic dynamics in populations of the helminth parasites of wood mice, *Apodemus sylvaticus*. Journal of Helminthology 62: 78–90.
- MOSER, M. 1991. Parasites as biological tags. Parasitology Today 7: 182–185.
- MURUA, R. E. 1978. Studies on the ecology of parasites of *Apodemus sylvaticus* (L.) and *Clethrionomys glareolus* (Schreb.) (Rodentia): Analysis of the parasite populations and their seasonal variation in the Bristol area. Acta Parasitologica Polonica 25: 149–161.
- NILSSON, A., AND L. LUNDQVIST. 1979. Interspecific relations in small mammal ectoparasites. Recent Advances in Acarology 1: 451–456.
- TENORA, F., F. MESZAROS, AND R. WIGER. 1977. Further records of nematodes in small rodents in Norway. Parasitologica Hungaria 10: 85–89.
- WIGER, R., L. LIEN, AND F. TENORA. 1976. Studies of the helminth fauna of Norway XXXVIII: On the helminths in rodents from Fennoscandia. Norwegian Journal of Zoology 24: 133–135.
- YALDEN, D. W. 1982. When did the mammal fauna of the British Isles arrive? Mammal Review 12: 1–57.

Received for publication 13 February 1996.