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THE MYSTERY OF THE ORKNEY VOLE

Julian Branscombe and Keith Dobney

An Orkney Vole moves through its run.
Peter Reynolds/FLPA

The Orkney Vole offers a window into 130 years of British natural history and an island mystery that involves ecologists, archaeologists and geneticists. These interdisciplinary endeavours are providing striking insights into the potential pace of evolution and the role of human history in shaping our wildlife today. Here, the authors tell a tale of ecological and cultural history.

'…one of the most interesting and unexpected discoveries ever made in British mammalogy. … This animal presents a most interesting problem, both zoological and geographical.'

Oldfield Thomas (NHM Zoological Dept, 1878–1929) – Postscript to Millais (1904)

The Orkney Vole *Microtus arvalis orcadensis* has an enigmatic history. A subspecies of the continental Common Vole *M. arvalis*, it is twice the size of its continental relatives, and it is also the reason why Orkney has an edge over Shetland in one aspect of wildlife interest. Both archipelagos have their seabirds, a wealth of marine habitat, rare plants and vagrant birds, but Shetland – without voles – has a deeply impoverished raptor fauna. In contrast, just about every day in Orkney is enlivened by the sight of a Short-eared Owl *Asio flammeus* or a Hen Harrier *Circus cyaneus*.

The Orkney Vole today

A PhD study by Reynolds (1992) found high vole densities in Orkney's old peat cuttings and rough grassland (including strips along ditches and fence lines) and lower numbers in moorland. The population was estimated at one million at the start of each breeding season, but it was clear that there had been a large decline over the twentieth century as a result of agricultural intensification, the vole no longer occurring in arable or improved grassland. It used to be common in hay meadows, but silage-cutting is now the norm.

Reynolds confirmed the vole as the most important prey item for Short-eared Owls (Reynolds & Gorman 1994, 1999), although he found that, for Hen Harriers, voles were a complementary dietary item rather than their principal prey. The harrier has its UK stronghold in Orkney; 103 females reared 101 young in the recent peak year of 2011 (Williams 2012).

It had been considered that Orkney Vole population levels were stable from year to year, in contrast to Common Voles on the Continent. The cold winters of 2009/10 and 2010/11, however, gave an unusual lasting blanket of snow over much of Orkney. This protected the voles from aerial predation through these winters, leading to a boom in numbers. Short-eared Owls responded dramatically, the population peaking at at least 109 occupied territories in 2012 (Williams 2013).

Discovery of the Orkney Vole

When John Guille Millais (seventh child of the founding member of the Pre-Raphaelite Brotherhood) walked back from a fishing trip at the Loch of Stenness, Mainland Orkney, in August 1886, he spotted what he took momentarily to be a melanistic Water Vole *Arvicola terrestris*. With his interest piqued, he had specimens sent to him in the following year, and these convinced him that this animal was neither Water Vole nor Field Vole *Microtus agrestis*.

For Hen Harriers, Orkney Voles are a secondary dietary item. Morris Rendall

He waited until 1904 before publishing what he described as a new species (Millais 1904). The reasons for the delay are unclear – perhaps he was spurred into doing so by his momentous project to write and illustrate *The Mammals of Great Britain and Ireland*, which included the Orkney Vole in Vol. II (Millais 1905). A further inspiration may have been the discovery of the Skomer Vole *Myodes glareolus skomerensis*, which Major G. E. H. Barrett-Hamilton (1903) described as a new species but which Millais (1905) treated as a subspecies of Bank Vole *M. glareolus*.

The excitement over the July 1904 description of the Orkney Vole in *The Zoologist* ('A Monthly Journal of Natural History') is clear from the postscript by the eminent Oldfield Thomas, quoted above, while the preface to the index to the volume confidently states:

> 'The present volume more than maintains its interest and importance in the details of British Zoology. This is particularly the case with the Mammalia, and we cannot but allude to the description by Mr. Millais of a new species of Vole from the Orkney Islands. To discover a mammal new to Britain, and that an undescribed species, is at the present day more extraordinary than unearthing the remains of some extinct monster hitherto unknown to Palaeontology.'

The explosion of interest was something which latter-day Visit Orkney would have been proud of. The famed Eagle Clarke undertook a pilgrimage to see the vole in Orkney, adding this to a trip to the Flannan Isles (Eagle Clarke 1905), while other notes resulting from vole tourism included Godfrey (1905 and Kinnear (1905). Ellison (1906) produced a beautiful pamphlet which was 'read before the Warrington Field Club, March 1906' – although Ellison added little beyond a measured drawing of an Orkney Vole nest from his visit,

The Common Vole, a close relative, is only about half the size of the Orkney Vole. Jelger Herder/Minden Pictures/FLPA

otherwise shamelessly plagiarising various chunks of Millais' paper with which he obviously hoped that WFC members were unfamiliar!

Small-mammal mania was now afoot. Gerrit Miller, of the US National Museum, began describing island subspecies of Orkney Vole in 1905, deciding later that the Orkney Voles on Sanday merited full species status in the paper *Eighteen new European voles* (Miller 1908), before going on to describe the Guernsey Vole (now *Microtus arvalis sarnius*) (Miller 1909). On joining the London Natural History Museum staff, Martin Hinton threw himself heavily into the subject (Hinton 1910a, 1910b, 1913), although the posthumous attention he now receives is as one of the prime suspects in the infamous 'Piltdown Man' hoax.

The frenzy of Edwardian taxonomic naming and 'splitting' reached its zenith with every island population of Orkney Voles afforded at least subspecies status. Affinities with the Common Vole began, however, to be noted. Finally, chromosome-based genetic studies by Matthey (1951), followed by the breeding experiments of Zimmermann (1959), confirmed that all Orkney Voles should be considered a subspecies of the Common Vole.

Endemic or recent arrivals?

Hinton (1910a) assumed the Orkney Vole to be a late-glacial relic. A consensus has emerged, however, that this cannot have been the case. Common Voles have never been found in Arctic conditions, while no small mammals are now considered to have been capable of surviving the last glacial maximum (some 20,000 years ago) in Orkney.

It is now clear that there was no land-bridge between mainland Scotland and Orkney during the late glacial period or since, ruling out overland arrival. Furthermore, there is no credible evidence for the past presence of Common Voles in the UK (Yalden 1999). The reported finds of *M. arvalis* or potential ancestor species during or since the last glaciation have been explained by the misidentification of Root Voles *M. oeconomus* (now long extinct in Britain) and Field Voles (Sutcliffe & Kowalski 1976; Hall & Yalden 1978; Yalden 1982).

So, Orkney Voles must have arrived by sea. Corbet (1961) postulated that the first voles could have reached Orkney 'at any time since the Viking era'. The advent of radiocarbon dating, however, has shown that vole bones from various

archaeological sites in Orkney are up to 5,500 years old (Martínková *et al.* 2013).

How did they get to Orkney?

The heart of the mystery of the Orkney Vole is that it arrived from continental Europe while apparently bypassing the entirety of mainland Britain.

Corbet (1961) makes the perceptive comment that 'Establishment would be easier in Orkney than Mainland Britain, because of the absence of competitors and ground predators'. This is borne out by the vole's 1980s introduction to Eday. A farmer on another Orkney island (Westray) had been conducting Longworth-trapping to assist with an academic study of mouse genetics, voles turning up as by-catch in his live-traps. Mike Cockram, an Eday farmer, thought that voles would be a valuable addition to his island's fauna, so he had his friend send three consignments of voles, totalling around 15 animals, over three years. A fishing boat conveyed the voles across the Westray Sound, Mike rowing out to collect them. They were released at two locations on Eday, and three years later they had spread throughout this island of 27 km^2 (M. Cockram, pers. comm.).

Returning to prehistory, there is a possibility of voles arriving on rafts of floating vegetation, washed down the large dynamic rivers of continental Europe. River mouths and coastlines now deep under the southern half of the North Sea were dry land as late as 8,000 years ago (possibly later), so that possible sources of Continental *M. arvalis* populations were closer than they are today. Modern flood-management measures and the scarcity of natural vegetation on the floodplains of today prevent us from witnessing the full potential for rivers to spit a mass of vegetation out into the sea. Even so, the chances of a founder population arriving by a long sea voyage of this type still do not seem likely.

The work of Martínková *et al.* (2013) found surprisingly large genetic diversity in modern and ancient Orkney Voles. This suggests a single large introduction from a genetically varied population or multiple introductions from diverse places. This is not what would be expected if chance rafting events had brought the voles to Orkney.

So, this leaves us with the remaining possibility that Common Voles arrived with humans, either deliberately or as unintended stowaways. It seems more than a coincidence that voles appeared in Orkney around the same time as, or soon after, the arrival of the first farmers. This Neolithic period saw Orkney's early farming society developing a distinctive (and now world-famous) culture characterised by stone-built houses and chambered tombs – excavation of which has produced copious vole remains. Trade and exchange networks using boats existed throughout western Europe at the time.

Humans have been the main vector for the spread of rodent pests to islands around the world. Voles, however, are much less 'synanthropic' than rats and mice, not favouring grain stores or buildings. Perhaps Common Voles were inadvertently transported in livestock bedding, leaf fodder or hay. The Sibling Vole *Microtus laevis* is thought to have arrived in Svalbard with a shipment of hay from Leningrad (Fredga *et al.* 1990), while the arrival of the Bank Vole in south-west Ireland around 1950 (Smal & Fairley 1978) may have been by a similar mode of transport.

Why are they found on archaeological sites?

Inadvertent transport is not the only way in which people could bring the Common Vole to Orkney, especially when consideration is given to the complexity of past human cultures. There is good evidence for deliberate prehistoric introduction of mammals to the islands of the Mediterranean, for instance. Furthermore, the presence of Hedgehog

Excavation work at the Ness of Brodgar has revealed Orkney Vole bones. markferguson2/Alamy

Erinaceus europaeus remains in Neolithic human burials on the Baltic island of Gotland attest to the 'special' status of a small mammal which seems to have been introduced with the people who settled that island.

Since Millais' discovery, Orkney Voles have proved to be obliging in captivity, breeding freely and biting seldom. Their amenable traits have even been their downfall, as they have been used as 'lab rats' in an unpleasant-sounding experiment (Chitty *et al.* 1956). Could they have been pets? Alternatively, were they 'fast-food snacks' (much like the Pacific Rat *Rattus exulans* was to the New Zealand Maori) or did they have some ritual purpose for the people who settled Neolithic Orkney?

Much has been written too about the possible totemic status of animals in Orcadian prehistory. Hedges (1984) discusses the remains of White-tailed Eagles *Haliaeetus albicilla* found in the famed early Neolithic site of Tomb of the Eagles, and mentions the concentrations of remains of domestic dogs, Red Deer *Cervus elaphus* and songbirds in other Orkney chambered cairns. A concentration of vole remains was found at the Quanterness Tomb, and numerous Orkney Vole bones were found in an alcove near the entrance to Structure 10 at the Ness of Brodgar (a stunning Neolithic temple complex currently under excavation). Could this indicate that voles had a ritual use or a totem quality?

This possibility cannot be ruled out, but their presence in large numbers at different archaeological sites is generally considered to reflect accumulations of owl pellets, rather than ritual or subsistence behaviour by humans. Whereas Short-eared Owls are common in Orkney, Barn Owls *Tyto alba* are a rarity today, albeit an increasing visitor now that they breed in Caithness. Short-eared Owls actively avoid buildings, and, as it seems unlikely that this species will have had different habitat preferences in the past, perhaps Barn Owls were present in Orkney in prehistory.

Some of our voles are missing

When discovered, the vole was found to be present on most of Orkney's larger islands (Westray, Sanday, Rousay, South Ronaldsay and Mainland Orkney), but not on the others – reports from Shapinsay and Stronsay being considered to have been erroneous. Since then, it has spread from South Ronaldsay to Burray, after construction of the Churchill Barriers led to a dramatic sand-dune build-up, creating a vegetated land-bridge between the two islands.

Vole remains were found in 1982 and 1983 from the early-Neolithic tomb on Holm of Papay (Ritchie 2009). Today, Orkney Voles are absent from the Holm, and from nearby Papa Westray, although they are found three miles away on Westray.

Recent excavations on South Walls (a separate island which is joined to Hoy by a largely natural causeway) have recovered remains of Orkney Voles from the upper layers of Neolithic and Bronze Age funerary monuments. There are no voles on Hoy and Walls today. Radiocarbon dating of several of the remains from the Neolithic chambered tomb were puzzling, placing these voles firmly in the Norse era, around the twelfth century AD.

Could this mean that voles were present across all of the archipelago during early prehistory? Did they arrive and disperse when sea levels were much lower and Orkney itself was one large island? With rising sea levels, populations of voles could have

Current distribution of the Orkney Vole

Short-eared Owls (top) and Long-eared Owls have been recorded disgorging pellets containing vole bones on vole-free islands. Morris Rendall

become isolated on individual islands, where a range of factors perhaps led to local extinction – hence their absence on some islands today.

Having said that, we cannot be certain that voles were ever wild on South Walls, the Holm of Papay and Papa Westray. The presence of archaeological vole remains on islands without voles today could equally be explained by the voles having been captive, or by owls from one island commuting to adjacent islands to hunt, as Short-eared Owls have been observed returning to vole-free islands to disgorge pellets (Eric Meek & Jim Williams, pers. comm.). In addition, Long-eared Owls *Asio otus*, although scarce on Orkney, have been recorded producing pellets containing Orkney Vole on the vole-free island of Hoy.

Where did Orkney Voles come from?

The search for the continental origins of Orkney Voles goes back to Berry & Rose (1975). They analysed features of the skull, coming up with the surprising finding that the closest similarity was with Common Voles in the Balkans. This is the story that most naturalists will have come across, thanks to the classic *The Natural History of Orkney* (Berry 1985). The likelihood of these conclusions, however, was convincingly questioned by Corbet (1986).

Since then, studies by Haynes *et al.* (2003) and Martínková *et al.* (2013), using cutting-edge DNA techniques, have thrown more definitive light on the subject. The earlier Haynes study focused on the mitochondrial cytochrome *b* gene in Common Voles, identifying four lineages of Common Vole living across Europe today, each assumed to correspond to populations from different glacial refugia. Modern Orkney Vole populations sat with the so-called 'western lineage' along with Common Voles from Spain and France, indicating a western European origin for the Orkney Vole.

The most recent study, which included many more samples from northern France and the Low Countries, along with numerous ancient DNA sequences from a range of Orcadian archaeological vole specimens, shows them to be clearly associated with a northern group of the western lineage. Analyses of nuclear DNA and a single archaeological specimen from Belgium finally revealed the closest match with modern and ancient Orkney Voles to be from the vicinity of Bruges (not far from the mouth of the Rhine). These findings caused some consternation in the archaeological community, not least because most models had favoured Neolithic colonisation from farther west. New ideas regarding the later inundation of Doggerland and the possibility of a separate introduction of Neolithic culture to Scotland, however, mean that nothing can be ruled out.

Even in the face of this apparent clear genetic evidence, the Orkney Vole continues to confuse and perplex. Both DNA studies noted that the genetic diversity found in modern and ancient vole populations from Orkney far exceeded that found in the whole of the rest of their current continental cousins. This scenario completely contradicts the predicted model of island colonisation by a small (genetically restricted) sub-sample of individuals from a much more genetically diverse continental population, giving rise to a founder effect limiting the genetic diversity on the islands.

The only explanation for this unexpected pattern is the combination of a large and/or diverse founding population in Orkney, compared

Orkney Vole at the Ring of Brodgar. Paul Wilson

with a drastic reduction of Common Vole genetic diversity (the result of boom-and-bust cycles recorded for the species during historical times) across the Continent. These boom-and-bust cycles have never been recorded in Orkney.

This means that the broad genetic diversity found in Orkney Vole populations today represents a unique relic of at least some of the wider genetic diversity once present in continental Common Voles but which has long since disappeared. That makes living Orkney Voles true time-travellers from the past.

While their genetic diversity stayed much the same in Orkney for 5,500 years, the size and shape of the Orkney Vole followed the well-understood diverging trajectory of island isolation. The mitochondrial and nuclear DNA evidence is consistent with a Neolithic colonisation, but the archaeological remains dating from this period show that the increase in size of Orkney Voles had already occurred 5,500 years ago. This provides further evidence of the speed of evolutionary change possible on islands (Millien 2011). With such an excellent and long-term record of the voles' existence on Orkney, it is no surprise that they have been the subject of one of the most detailed studies ever carried out on an island rodent's evolutionary history (Cucchi *et al.* 2014).

The genetic and morphological work takes us right up to our current understanding of the Orkney Vole story, but is this all that that detective work can tell us? Almost certainly not. Watch this space!

A new and unwelcome threat

In 2010, there were sightings of Stoat *Mustela erminea* reported from South Ronaldsay and mainland Orkney. After initial disbelief, these sightings were confirmed. A volunteer trapping effort coordinated by Scottish Natural Heritage caught several individuals, which were relocated to Fife, but the efforts proved insufficient to stem a rapid increase in sightings over subsequent years. Eradication is an objective which is being actively pursued again, although it seems unlikely that sufficient resources can now be found to achieve this.

There is no consensus over how the Stoats got to Orkney. Some assume that they arrived by accident, perhaps in one of the regular imports of lorry-loads of straw or animal feed. Others are certain that there must have been a deliberate introduction. Their simultaneous appearance in well-separated parts of the county perhaps suggests the latter.

Wetland landscapes such as this, at the Loons RSPB reserve, Mainland, are ideal Orkney Vole habitat.
Peter Reynolds/FLPA

Previously, cats (feral and domestic) were the only terrestrial predator of Orkney Voles. Stoats have long been present in Shetland, where, in the absence of voles, they are not considered a serious problem. The Orkney Vole is an ideal food item for Stoats and there is great concern that this mustelid could cause a crash in vole numbers, in turn affecting Short-eared Owls and other raptors. It may be purely coincidental as Stoat numbers are still building, but Short-eared Owl numbers have decreased markedly since Stoats arrived – only 43 territories were occupied in 2015 (Branscombe 2016). Furthermore, if high numbers of Stoats can survive the winter by preying on voles, there is the clear potential for abundant Stoats to switch to preying on ground-nesting birds in spring.

If predation by Stoats becomes a principal cause of Orkney Vole mortality, a significant reduction in the latter's size is likely, thereby reversing the 'Island Effect' which leads to size increase in small mammals on islands with abundant resources and limited predation pressure. If high Stoat numbers cause a crash in vole numbers, this genetic bottleneck could significantly reduce the voles' unique genetic diversity. Behavioural changes are also likely, affecting the activity patterns studied by Reynolds, and the frequency of above-ground nests.

Conclusion

The Orkney Vole is slow to give up its secrets. As scientists, we adhere to the principle of Occam's Razor – the simplest explanation is the most likely – but there is nothing simple about the Orkney Vole story. Each new discovery leads to further twists and turns worthy of a John Le Carré thriller. Its full story remains shrouded in the mists of time, but that mist is slowly lifting; ongoing scientific advances and discoveries in field and laboratory will provide further revealing insights.

Quammen (1997) provides a sparkling but salutary account of island wildlife under threat around the world, and its relevance to the biodiversity of the ever more isolated pockets of natural habitat on the world's continental land masses. The Orkney Vole, however, reminds us that the global test-beds of island biogeography are not restricted merely to the likes of the Galapagos Islands.

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An Orkney Vole peeps out. Tim Martin

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