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An oasis of fertility on a barren island: Earthworms at Papadil, Isle of Rum

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ABSTRACT

The Isle of Rum, Inner Hebrides, has an impoverished earthworm fauna as the soils are generally acidic and nutrient-poor. Species associated with human habitation are found around deserted crofting settlements subjected to “clearances” in the mid-19th century and at Kinloch, where a large volume of fertile soil was imported from the mainland around 1900. Earthworms, and the dew worm *Lumbricus terrestris* L. in particular, were investigated at Papadil, an abandoned settlement and one of the few locations on Rum where a naturally developed brown earth soil is present. The small (1.5 ha), fertile location is isolated, so was also suitable for field experimentation. Visits over six years allowed dew worm distribution to be assessed within low lying grassland and woodland and also within an adjacent sloping broadleaved woodland. The factors limiting dew worm distribution at the site were investigated with associated translocation to adjacent uninhabited areas. Small scale spatial dynamics were studied with density manipulation and containment experiments where Visual Implant Elastomer marking of individuals was utilised. Translocations from streamside woodland to adjacent grassland was successful over a short period (5 months), but the colonies did not persist over a longer term (5-6 years). Field trials with earthworm tagging were successful, but highest tag recovery rate was 25%. Where adults/sub-adults were removed, recruitment of juveniles was notable. Exceptionally large (>12 g live mass) individuals were found in soils of terraces on wooded slopes, suggesting that dew worms may be long lived at this location, where food is abundant and relatively few terrestrial predators are present.

INTRODUCTION

The earthworms of Scotland have been investigated for more than half a century (e.g. Guild 1951; Boyd 1957; Neilson & Boag 2003) but as with the rest of the British Isles, well defined distribution maps of native species are still lacking (Carpenter et al 2012). Nevertheless, in some Scottish island

locations, extensive studies have been undertaken, for example, across the Outer Hebrides by Boyd (1957) and more recently on the Isle of Rum in the Inner Hebrides (Butt & Lowe 2004; Callaham et al 2012; Gilbert & Butt 2012). Reasons for the interest in Rum are twofold. Firstly, Rum is a Natural Nature Reserve (NNR) and has been in the management of conservation organisations since 1957 (National Conservancy (Council) which became Scottish Natural Heritage (SNH)). As a result, considerable scientific research has been undertaken on many aspects of the island’s ecology, including soil surveys. Secondly, the history of Rum over recent centuries is reasonably well documented (e.g. Love 2001), so major aspects and impacts of soil management have been recorded. These include subsistence agriculture, the clearances in the 1860s and more recently, island management as a sporting estate. The latter involved tree planting and large scale importation of a quarter of a million tons of soil to improve the grounds of Kinloch Castle at the beginning of the twentieth century (Magnusson 1997).

Sixteen earthworm species have been recorded on Rum, 15 of these initially reported by Butt & Lowe (2004) with another, *Dendrobaena attemsi* (Michaelsen) subsequently identified and reported to SNH (Butt & Lowe 2008), see Table 1. Generally, Rum has an impoverished earthworm fauna as the soils are mainly infertile and acidic in nature. The octagonal-tailed worm *Dendrobaena octaedra* (Savigny), the gilt-tailed worm *Dendrodrilus rubidus* (Savigny) and the red worm *Lumbricus rubellus* (Hoffmeister), all epigeic (near-surface dwelling) acidophiles, are the most widely distributed species across the island but at very low population densities. Anthropochorous species (*sensu* Enckell & Rundgren, 1988), such as the rosy-tip worm *Aporrectodea rosea* (Savigny), the blue-grey worm *Octolasion cyaneum* (Savigny) and the dew worm *Lumbricus terrestris* (L.) are found only where human influence is apparent, e.g. around abandoned settlements, where ridge and furrow systems (“lazybeds”) can still be seen, or at Kinloch where

Table 1. Earthworms from the Isle of Rum, Inner Hebrides (adapted from Butt & Lowe 2004; 2008 and current work).

Location on Rum	Kin	Dib	Gur	Har	Kil	Pap	Mor
Earthworm species							
<i>Allolobophora chlorotica</i>	x	x	x	x		x	
<i>Aporrectodea caliginosa</i>	x	x	x	x		x	
<i>Aporrectodea longa</i>	x	x					
<i>Aporrectodea rosea</i>	x	x		x			
<i>Dendrobaena attemsi</i>	x						x
<i>Dendrobaena octaedra</i>	x	x	x	x	x	x	x
<i>Dendrodrilus rubidus</i>	x		x	x	x	x	x
<i>Eisenia fetida</i>	x						
<i>Eiseniella tetraedra</i>	x	x		x			
<i>Lumbricus castaneus</i>						x	
<i>Lumbricus eiseni</i>							x
<i>Lumbricus rubellus</i>	x	x	x	x	x	x	x
<i>Lumbricus terrestris</i>	x			x		x	
<i>Murchieona miniscula</i>			x				
<i>Octolasion cyaneum</i>	x	x	x	x	x	x	x
<i>Satchellius mammalis</i>	x					x	

(Kin – Kinloch, Dib – Dibidil, Gur – Guirdil, Har – Harris, Kil – Kilmory, Pap – Papadil, Mor – Open Moorland – see Figure 1 for locations on Rum.) Nomenclature from Sims & Gerard (1999).

fertile soils were imported from the mainland. Of the disused settlements around the island, some such as Kilmory and Harris are accessible from Kinloch by four-wheel-drive vehicle, whilst Dibidil and Papadil are only reached by a lengthy walk over pony-paths (Figure 1).

Rum is an island managed for conservation and has been described as an “outdoor laboratory” because of the intense study of its nature. However, even here there are locations that have been less well studied but possess specific attributes that are of unique interest to soil ecologists. One such place is Papadil (National Grid Reference NM365 922). This site, towards the very south of Rum, once supported a small crofting community and signs of ridge and furrow cultivation are still evident on nearby headlands. Papadil Loch and the sea beyond, act as one margin to the location which is then surrounded to the north and east by steep slopes of Ainshval (781 m) and to the west by boggy terrain and moorland. Within this, a small (approximately 1.5 ha) area of woodland (predominantly Ash *Fagus excelsior* and Sycamore *Acer pseudoplatanus*) and grassland (dominated by *Agrostis* spp. and *Festuca ovina* with *Luzula campestris*, *Primula vulgaris*, *Anthoxanthum odoratum* and *Viola* spp.) lie to the north-west of the Loch with a south-facing aspect (Figure 2).

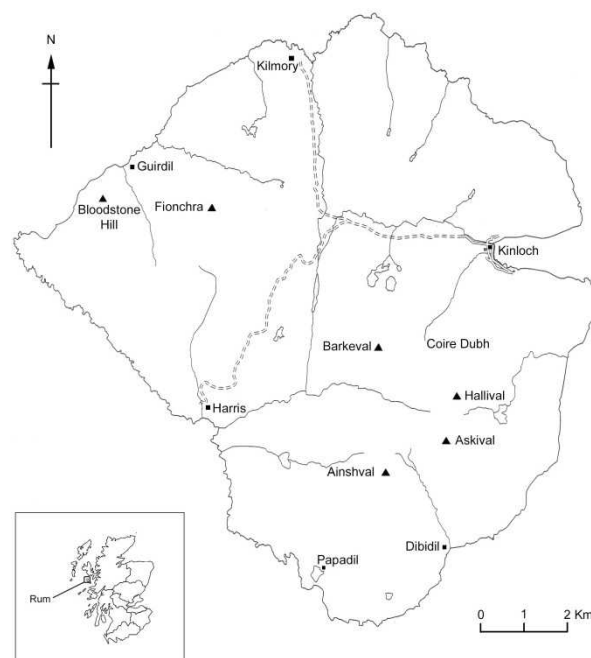


Fig. 1. Isle of Rum map with Papadil towards the south of the island. Insert shows the location of Rum in the Inner Hebrides, to the west of mainland Scotland (Adapted from Butt and Lowe 2004).



Fig. 2. Oblique aerial view of Loch Papadil, Rum, taken from the WSW. The woodland/grassland area investigated is clearly visible at the Loch margin (RCAHM, Scotland).

The trees were planted at Papadil and a hunting lodge built more than 100 years ago, when Rum was a shooting estate (Wormell 1968). The lodge is now in ruins but the wooded area including *Rhododendron ponticum* and gorse *Ulex europaeus* thicket remain. The soils at Papadil are exceptional for Rum, as they are naturally fertile brown forest soils. Ragg & Bogie (1958) and Ragg & Ball (1964) describe these soils in detail, but the main features are the freely-draining and crumbly structure in the A and B horizons, the friable consistency, together with a relatively uniform brown colour. Rooting depth and absence of large stones are favourable to plant growth and to deep burrowing earthworms. The relatively high levels of sunshine, combined with rainfall of only 1,780 mm per annum (compared with the highest records from some locations on Rum of 3,302 mm) are factors considered largely responsible for the presence of these soils in this location in Rum.

Worthy of note is that Papadil has a substantiated reputation for high numbers of blood-sucking parasites; “within a few minutes hundreds of ticks, eager for human blood, can find their way to all parts of the human body” (Clutton-Brock & Ball 1987). This may be another reason why this area is seldom visited for long, even by those hardy enough to walk across the island.

As part of an island-wide earthworm survey during 1995-2003, Papadil was visited twice with basic information on species presence determined (Butt & Lowe 2004). Among the seven earthworm species located here was the deep burrowing dew worm, a species which forms a midden (a collection of organic material) above a near vertical burrow (Butt & Nuutinen 2005). In places, this species was thought to be present at relatively high densities (23 middens m⁻²) compared with other locations on Rum where it is entirely absent. The nature of the soil at this site, the presence of the dew worm and the remote location of Papadil itself, meant that further investigations were warranted. To this end it was determined to record more detail of the distribution and abundance of this (and other) species at Papadil and undertake small scale population manipulations along with trialling of some novel ecological techniques associated with earthworms (Butt & Lowe 2007; Grigoropoulou & Butt 2010). Specific objectives were to: 1) determine the effects of dispersal on spatial distribution of dew worms at Papadil; 2) monitor recruitment rate within a populated area; and 3) test a novel mark-recapture technique in field trials.

METHODS

The work described here relates to 4 specific visits to Papadil over a five and a half year period which began in November 2005, when most experiments were set up (see Table 2).

Table 2. Earthworm research undertaken at Papadil, Isle of Rum.

Date of Visits	Activities undertaken
Apr 1999	General Earthworm Survey at Papadil.
May 2002	Initial Dew worm midden counts and further survey.
Nov 2005	Establishment of Dew worm Translocation Experiment.
Apr 2006	Establishment of Dew worm Distribution dynamics using tagging.
	Monitoring of Translocation Experiment.
	Monitoring and termination of Distribution dynamics using tagging.
	Survey of large Dew worm middens in woodland.
Apr 2007	Video recording of Dew worm surface behaviour.
	Further Monitoring of Translocation Experiment.
	Monitoring of large Dew worm middens in woodland.
	Hillside woodland transect.
May 2011	Final monitoring of the above and removal of materials.

Visits prior to 2005 were used to gather baseline information (Butt & Lowe, 2004). Visits of 2005-2011 required 27 field researcher days, achieved by camping at Papadil.

Translocation experiment

a) Earthworm survey work was undertaken on the short, red deer *Cervus elephas* and goat *Capra hircus*-grazed grassland to the west of Papadil Burn, a stream of approximately 4 - 5 m in width. Dew worm middens were searched for, by fingertip assessment and visual inspection of the soil surface as previously used in the Papadil woodland (Butt & Lowe 2004), adjacent to this site but separated by Papadil Burn. Standard vermifuge sampling to areas of 1 m² involved watering can application of 50 g mustard powder in 10 litres of water (Butt 2000). The suspension of mustard acts as a skin irritant and drives earthworms within burrows to the soil surface (Gunn 1992).

b) Further survey work took place in the low-lying, sparse woodland, where dew worms were known to exist. Here, 3 areas of 1 m² were permanently pegged and multiple applications of a mustard vermifuge were used to extract dew worms and other earthworm species. All earthworms emerging after vermifuge application were washed in water, blotted dry and had masses determined (using an Ohaus LS200 portable balance; 0.1 - 200 g). Adult and sub-adult dew worms were retained, but juveniles (<0.1 g) were returned to the point of extraction (as were other species) after irrigation of the soil with fresh water. This was to permit monitoring of subsequent population recovery. Repeat extractions from the same areas were conducted after periods of 5 and 19 months. In spring 2011, extraction could not be undertaken as the pegs were not present, thought eaten/displaced by goats or deer.

c) Dew worms extracted and retained from (b) were retained in pots of water, translocated to the dew worm-free surveyed grassland area (a) and released into 3 separate corresponding areas of 1 m². Two of these areas had been surrounded with fencing made from heavy duty polythene, dug into the ground to a depth of 20 cm with 25 cm above ground to form earthworm enclosures with ends overlapped and sealed together to prevent earthworm ingress/egress (Grigoropoulou & Butt 2010). The third release site was unfenced. These translocations were undertaken to establish if dew worms could persist at the grassland site. Release took place just prior to dusk to avoid potential avian predation. Numbers translocated were 19 and 11 into the two fenced areas and 12 into the unfenced area. Visual investigations and vermifuge extraction within all of these areas were made after 5 and 19 months and also after 5 years, at which point the fencing, still intact, was removed.

Short term, small scale distribution dynamics using tagging

Initially, in November 2005, all dew worm middens were counted and marked within 12 squares of 1 m²

of woodland (within area b above) and the squares subsequently photographed. The squares were established in three 4 m x 1 m strips, 10 m apart, which constituted the blocks for an experiment with three treatments and a control (randomly allocated in the blocks).

Removal Treatment (R) All midden-related dew worms were removed (or attempts were made at removal) with a mustard vermifuge (50 g in 10 l water) delivered directly into the burrow entrance below the midden with a 100 ml syringe (Butt & Grigoropoulou 2010). The mass of each earthworm extracted was determined and general condition noted after washing and drying. The burrow was then inundated with clean water. This treatment examined population recruitment/colonisation.

Tagging Treatment (T) All midden-related dew worms were removed as in (R) and tagged in the field with (yellow) Visual Implant Elastomer (VIE) - a fluorescent bio-polymer delivered by hypodermic needle (Butt & Lowe 2007) (Figure 3). This is a technique to permit specific earthworms to be recognised at a later date. These had masses determined and were returned to their individual home burrows, following inundation with fresh water. This treatment sought to monitor fidelity of burrow occupancy.

Tagging/Fencing Treatment (TF) Midden-related dew worms were treated as in (T) but then the square metre plot was isolated with fencing (as described above). This was to restrict movement away from the treatment square, if home burrows were compromised by the vermifuge extraction process.



Fig. 3. Large dew worm from Papadil with yellow Visual Implant Elastomer (VIE) tag immediately prior to release; scale bar of 10 cm.

Control (C) Here the middens were located, dew worms extracted, mass determined and condition noted and then returned to home burrows previously irrigated with water. (Control = extraction and return to burrow only).

Plot size (1 m^2) was thought appropriate (Grigoropoulou & Butt 2010), as it allowed for reach-access to all points within, but avoided a need to step inside the experimental area. In all instances the location of each burrow was recorded in cm with reference to x-y coordinates. After a period of 5 months (spring 2006) the plots were re-visited and sampled once again for dew worms. All middens, mapped from 2005 were relocated from their coordinates and targeted with a mustard vermifuge along with any additional middens located and subsequent application of a vermifuge across the plots. All dew worms extracted had masses and general condition recorded and were also checked for the presence of a VIE tag.

Hillside Woodland - midden observation and general survey

When descending from the Dibidil pony-path on a previous visit, dew worm middens had been observed on the wooded slopes which extend to 40 m in altitude above Papadil Loch. These middens were therefore investigated more closely (spring 2006, 2007 and 2011) as they appeared relatively large by comparison with observations in other UK woodlands (e.g. Grigoropoulou & Butt 2010) and those elsewhere at Papadil. Care was taken to investigate a very limited number as Rum is a NNR and the quantity of potentially large dew worms in this relatively sensitive area was unknown.

In spring 2007, additional investigations took place along transects across the wooded hillside slopes (to 35°), extending beyond the (now broken) deer-fence and tree-cover into scrub to both east and west. Here, sloping areas were compared directly with adjacent flatter areas (terraces) for dew worm burrow densities and visually for leaf litter presence.

Video recording of dew worms at the soil surface

In 2006, using low level light filming (Sony Handycam digital video camera with night-vision facilities - recording to 0 lux) records were made of any soil surface activities by targeted dew worms, as this is a species known to forage and mate above ground, whilst keeping its tail in its burrow (Butt et al 2003). The camera, supported on a tripod, was set up beside an obvious midden in the low lying woodland at dusk, and activated for remote filming, which was viewed the following morning ($n = 3$ nights).

Data Analysis

In most instances, the figures reported are as collected from the field. These relate directly to numbers of earthworms collected per area of soil sampled (density) or to live biomass (usually g m^{-2}) for the same. Where comparisons were made between treatments in the "Short term, small scale distribution dynamics using tagging" experiment a Kruskal-Wallis test was utilised as the assumptions

required for using a parametric method, such as ANOVA were not met.

RESULTS

Translocation experiment

a) No middens were found from hand-searching on the grazed grassland beside Papadil Burn. Additionally, application of a vermifuge failed to locate any dew worms. It was determined that this species was not present in this habitat and that a translocation experiment here was appropriate. The vermifuge did however reveal the green worm *Allolobophora chlorotica* (Savigny), the grey worm *Aporrectodea caliginosa* (Savigny), *L. rubellus* and *Satchellius mammalis* (Savigny) at community densities of 32 ind. m^{-2} .

b) Mean population density of adult and sub-adult dew worms in the streamside woodland was recorded at 14 m^{-2} with a mean biomass of 47.6 g m^{-2} from mustard extraction. Mean mass of clitellate (mature adult) individuals was 4.21 g ($n=17$). Removal of adult and sub-adults from experimental quadrats allowed subsequent population recovery estimations. After 5 months (over winter), mean results on extraction were 3 m^{-2} (4.5 g m^{-2}) and after 19 months were 6 m^{-2} (11.2 g m^{-2}). The mean number of dew-worm juveniles ($<0.1 \text{ g}$) after zero, 5 and 19 months was 9, 11 and 35 m^{-2} respectively.

c) At the translocation area after 5 months, a total of 11 dew worms were located from the two fenced squares ($11/30 = 37\%$ recovery). All were returned to the same fenced areas. At the non-fenced area, an additional six worms were located ($6/12 = 50\%$). Again, these were returned to the area after washing. This gave an overall recovery rate of 40%. After 19 months, vermifuge extraction in all three areas produced no dew worms and no signs of middens were located, although what proved to be two small (2 cm tall) ant hills were investigated. When the experiment was terminated in 2011, no dew worms or middens were found in all of the translocation areas.

Short term, small scale distribution dynamics using tagging

The mean density of adult and sub-adult dew-worms at the start of the experiment was $4.0\text{-}5.3$ individuals m^{-2} (Figure 4), thus generally much lower than at the translocation experimental source area. Five months later, the corresponding variation was $3.7\text{-}6.0 \text{ m}^{-2}$, where treatments did not differ statistically for density (Kruskal-Wallis test; $p=0.55$). The proportion of tagged individuals at the final sampling was 14% and 25% for T and TF treatments, respectively. From control and R treatment no tagged individuals were found.

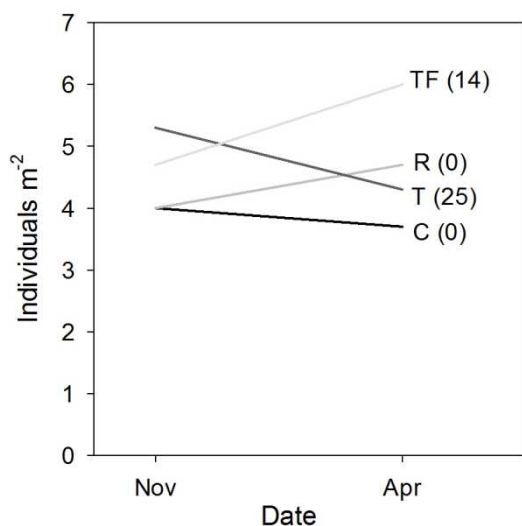


Fig. 4. Mean density of adult/sub-adult dew worms *Lumbricus terrestris* from a 5 month density manipulation and tagging experiment starting in November and ending in April (n=3). In "R" all individuals obtained in sampling were removed at the start of the experiment, in "C" they were returned to their burrows. In T and TF, sampled individuals were tagged and then returned to burrows, with plots fenced in TF. The values in parentheses give the % of tagged individuals from November sampling.

Hillside Woodland - midden observation and general survey

Preliminary investigations in parts of the woodland at Papadil in spring 2006 revealed very large dew worm burrows (10 mm in diameter) below large middens. Vermifuge application to four burrows extracted three exceptionally large individuals with masses of 10.0, 12.0 and 12.7 g. These were tagged (see Figure 3) and returned to home burrows previously irrigated with fresh water. A second investigation in spring 2007 failed to recover any of the tagged worms from these burrows, but an untagged individual of 10.1 g did emerge along with an immature of 2.9 g. No middens were found at this exact location in 2011 (pegged throughout these investigations).

The general survey across the woodland slopes in 2007 revealed dew worm middens on natural terraces, where leaf litter had collected but no signs of middens on slopes which were generally leaf litter-free. To the east and west of the fully wooded area, Gorse, Hawthorn *Cratageus monogyna* and Rhododendron were dominant. The soils here were wetter and more peat-like with no signs of any dew worms.

Video recording of dew worms at the soil surface

The moon-less nights and temperatures above 10 °C meant earthworm activity occurred and was recorded. Individual dew worms were observed to emerge from burrows and perform a "waving"

action in the air, prior to foraging for organic matter. This waving took the form of circular rotations of the anterior end, whilst in a vertical posture, as if "tasting" the air. This activity lasted for a period of less than 20 seconds after emergence.

DISCUSSION

It is almost certain that the dew worms found at Papadil originated from centuries of association with Man, either from times of subsistence agriculture and/or during the sport-related period of island ownership when the shooting lodge was constructed, perhaps brought to this location as fishing bait. The quality of the soils here permitted soil tillage and the planting of deciduous trees circa 1900 in fertile areas of brown earth soils beside Papadil Burn meant that an annual supply of organic matter was then available to these and other earthworm species.

Translocation experiment

As endogeic (shallow working) *A. chlorotica* and *S. mammalis* were not previously recorded at Papadil (Butt & Lowe 2004) their presence brought the total earthworm community composition to nine species, including examples from all ecological categories, at this location.

Mean dew worm density of 14 m⁻² midden-forming adults/sub-adults in the low lying woodland was considerably less than could have been expected based on the previous midden count estimate of 23 m⁻². However, the method used by Butt & Lowe (2004) estimated density based on feeling the soil surface for middens. The current work was based on vermifuge collection and therefore represented a more accurate technique. Also, closer investigations of what were thought to be middens on the grassland area nearby, were later shown to be diminutive ant hills.

The removal experiment of dew worms from the woodland showed a very slow recovery of adult animals to the manipulated area. Results suggested that over 5 months (November – April) no/little colonisation had occurred and that those collected were either hatchlings or smaller individuals not previously removed. Even after a period of 19 months, the majority of animals present were juvenile (less than 0.1 g) which showed a large increase with only a few adults present, which were likely to have colonised from nearby. This is unlike activity of this species in other woodland systems where movement over the soil surface has been shown to be frequent and burrow re-colonisation occurs when an adult is displaced or dies (Grigoropoulou & Butt 2012). Less dynamic changes suggest that disturbance to this site may be infrequent and may take considerable time to redress, although it is known, for example, that the nearby burn seasonally floods the woodland area, which could cause problems due to waterlogging of

burrows, but may also be positive and bring nutrients to this location.

The translocation work to the deer/goat-grazed, and slightly elevated grassland to the west of Papadil Burn proved to be unsuccessful but reasons for this are not clear. This could be a function of reduced organic inputs from the broadleaved trees, but dung from the grazing herbivores might compensate for this. The comparative elevation (1 to 2 m) of the more exposed grassland receptor site, but at a distance of less than 30 m from the woodland donor site could also be important, or the lack of trees might be less likely to dissuade the attention of potential avian predators (gulls and waders). If the burn itself had been a significant factor in preventing colonisation of the grassland, then the translocation would have overcome this. It is however, more likely that other physical factors such as soil depth, soil moisture content or an increased likelihood of predation are in operation.

Short term, small scale distribution dynamics using tagging

The tagging of dew worms produced a maximum recovery rate of 25% in one treatment of the controlled experiment. But even here, results from the fenced plot were lower (14%) which was unexpected, suggesting that fencing does not improve recovery (as also shown from the translocation work). This was the first field trial of the technique developed by Butt & Lowe (2007) but was beset mainly by problems associated with extraction method. The mustard vermifuge used may have made the burrow uninhabitable in the short term and either led to emigration or a higher likelihood of potential predation – through greater surface activity. More recent studies, e.g. by Grigoropoulou & Butt (2010) have shown that introduction of VIE tagged animals to woodland areas that have not been influenced by a vermifuge are successful when the animals have been obtained from an alternative location. However, even under such circumstances only 23-43% of tagged individuals were recovered after 12 months from woodland-based experimental treatments. To successfully collect, tag and return dew worms to their home burrow may well require the use of a non-invasive extraction technique, such as an electrical method (Thielemann 1986) that has no lasting effect on the integrity of the burrow and its mucus lining.

Hillside Woodland - midden observation and general survey

The dew worms from the hillside woodland, with a mean mass of 11.6 g, are significantly larger than those from other locations, which are normally less than half of this size, as shown from the lower lying woodland here (mean mass 4.21 g) and also from wider field collection (e.g. Nieminen et al 2011). As the Papadil animals were of an exceptionally large

size, consultations were undertaken with the Natural History Museum (NHM) in London and it was discovered that the NHM held no specimens of this size. It is suggested that the absence of many mammalian predators on Rum such as moles *Talpa europaea*, badgers *Meles meles*, hedgehogs *Erinaceus europaeus*, and foxes *Vulpes vulpes* (MacDonald 1983), a plentiful supply of organic matter and remoteness, hence undisturbed nature, of this site may permit individuals to live for long periods and attain above average masses. These findings suggest that Rum hosts the largest earthworms in Britain, as the largest on record (8.7 g) had previously (Butt, 2000) been obtained from soil at the base of a gryke in a limestone pavement at Malham, Yorkshire, where once again a protected environment was present.

Video recording of dew worms at the soil surface

The worm-waving recorded in the field confirmed observations previously recorded in a laboratory arena setting (Butt et al 2003) as a natural behaviour, undertaken as the animal senses its surroundings on emergence from its burrow. This warrants further investigation in line with recent novel behavioural observations associated with feeding of this species (Griffith et al 2013).

The work undertaken at Papadil revealed information on dew worm biology that was previously unknown. It also showed that a population of this species once established can persist in areas where soil conditions are conducive to its deep burrowing habit, provided that sufficient food supply, here deciduous tree leaves, are present. Attainment of large size may then be a function of a lack of predators and little disturbance at Papadil. The field trials, whilst thwarted in some areas, did provide useful data. More frequent visits over the study period would have given greater insights into dew worm population dynamics, but the remoteness of Papadil prevented this. Overall, this fertile area, on a barren island in the Inner Hebrides has provided a platform for further research into dew worm ecology.

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