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NIKI GRIGOROPOULOU, KEVIN R. BUTT

University of Central Lancashire, School of Built and Natural Environment
Preston PR1 2HE, UK

ASSESSMENT OF BURROW RE-USE BY LUMBRICUS TERRESTRIS L. THROUGH FIELD EXPERIMENTATION

An 11 month field experiment was set out to investigate evidence of burrow re-use by Lumbricus terrestris. This was established in a temperate, broadleaved woodland and involved removal of adult L. terrestris from 12, 1 m^2 *plots, with subsequent monitoring of re-colonisation. The spatial distribution and duration of L. terrestris middens was examined statistically. These observations suggest that L. terrestris burrows could be recycled or inherited. Such behaviour could be a means of minimising energy expenditure for burrow construction or due to a preference for a more favourable microenvironment in the drilosphere. Although evidence of burrow re-use is presented, the limitations of the experimental work are noted.*

Keywords: earthworms, burrow re-use, middens, spatial pattern

I. INTRODUCTION

Lumbricus terrestris L., although studied in some detail, is in many ways, a relatively unique species of anecic earthworm. For example, it copulates on the soil surface and also creates middens – structures at the entrance of its vertical burrow - which are thought to have a number of functions (e.g. could offer protection from predators, by concealing earthworms foraging on the soil surface; protect earthworms and cocoons from environmental fluctuations, by moderating moisture and temperature levels in the burrow; serve as a food store for adults and hatchlings) [6,9]. The spatial distribution of *L. terrestris* middens has been recorded from a field site over a period of 10 years and was found to be permanent. This, over a time period thought considerably longer than the lifetime of an individual *L. terrestris* [6]. In laboratory studies, *L. terrestris* adults and juveniles have been observed to make use of existing vacated burrows without altering burrow shape [12]. The authors' unpublished observations have also found smaller sub-adult individuals emerging from adult-sized burrows during burrow-targeted field-collection of this species. Such laboratory and field results suggest re-use of *L. terrestris* burrows by either offspring of the burrow resident or other conspecifics. Recently, other researchers have observed a similar behaviour in other earthworm species. Mathieu et al. [17], found reduction in

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* *Pracę recenzowała:* dr hab. prof. UR Joanna Kostecka, Uniwersytet Rzeszowski

dispersal of other earthworm species in areas where soil was pre-used by conspecifics that were no longer present and Caro et al. [8] observed dispersing individuals of the species of *Apporectodea terrestris* to preferencially use existing conspecific's galleries.

In this study, a simplified, relatively short term approach was used to detect evidence of burrow re-use (recycling) by *L. terrestris*, i.e. inheritance of *L. terrestris* burrows by offspring of the burrow resident or their re-use by others of the same species in a field situation. Moreover, to examine whether there is a difference in the colonisation rate of an area formerly inhabited or not by conspecifics An experiment was established in September 2006 in a broadleaved woodland, which involved removal of *L. terrestris* individuals and manipulation of the soil within 1 m^2 plots and the subsequent monitoring of re-colonisation in these areas.

II. MATERIALS AND METHODS

Experimental Design

Twelve 1 m^2 plots were established in managed woodland (53°40′33″N, 02°48′54″W), 11 km to the south west of Preston. The experimental site supports species of *Acer, Betula*, *Fagus*, *Quercus* and *Tilia*. Soil at the site is a silty clay loam with a pH of 6.3 [11]. Manipulation of *L. terrestris* density in 1 m^2 plots resulted in 2 x 2 treatments, each of which were either enclosed or open. Enclosed plots were fenced by digging a trench 0.3 m deep and inserting plastic "damp proof material" (Wickes, UK) extending 0.3 m above the soil surface. These treatments were associated with removal of large *L. terrestris* (through mustard application as used by Butt [3] and soil sterilisation with the use of microwave radiation [25]. Thus:

1. Removal of *L. terrestris* individuals while preserving *L. terrestris* burrows (Rem) from (a) 1 m^2 open plots (RemO) to examine re-use and inheritance of vacated burrows by adult conspecifics and offspring of removed adults. (b) 1 m^2 enclosed plots (RemE) to examine inheritance of vacated burrows by offspring only.
2. Removal of *L. terrestris* individuals and cocoons through soil sterilisation and the destruction of *L. terrestris* burrow systems (Ster) from, (a) 1 m^2 open plots (SterO) to examine colonisation of unoccupied space. (b) 1 m^2 enclosed plots (SterE) used as a control for the sterilisation method.

Each of the treatments was replicated 3 times to give a total of 12 x 1 m^2 plots. Detailed information on the method of fence installation is described by Grigoropoulou and Butt [11].

L. terrestris middens were removed to expose burrow openings that were targeted with a mustard suspension (5 g l^{-1}). A further 4 l of mustard suspension were applied over the soil surface of plots to expel any remaining *L. terrestris*. The coordinates of burrows from which earthworms emerged were recorded. The efficiency in earthworm extraction was calculated by taking into consideration the number of observed middens prior to manipulation and the number of captured *L. terrestris* after mustard application. Mustard suspension has similar extraction efficiency with other commonly used expellants such as AITC and formalin and a near-optimum extraction of earthworm numbers at a high concentration of 4.5 g l^{-1} [23]. Captured *L. terrestris* in the Rem treatment had masses determined on-site and those which were smaller than 1.5 g (considered to be juveniles with no clittelum and no permanent burrow) were carefully washed and re-introduced on the soil surface, into their corresponding 1 m^2 plots. A distinction between adult and juvenile stage for results assessment, was made by the presence of clittelum.

Excavated soil from the Ster plots was defaunated on-site, using two 700 Watt (2450 MHz) microwave ovens (Matsui MS-106WH; Currys, UK). Microwavable containers were filled with soil (0.2 - 0.3 kg) moistened to 15-20 % and were placed in the microwave (with lids on) for three minutes at full power. Whilst more traditional soil sterilisation was possible through steaming [2] or freezing [14] and might have been preferable, the nature of this work required a more immediate technique which minimised soil removal from plots and none taken off site. Microwave radiation (at 2450 MHz for 180 sec) was chosen to eliminate soil fauna mainly due to its time efficiency and convenience of application on site, but also due to its advantage of not leaving toxic residues in the soil and having a minimal impact on soil properties [25]. The use of a conventional sterilisation oven (dry heat) was not feasible as this would have required the transport of (6 x 0.3 m^3) 1.8 m^3 of soil to the laboratory and a 60 minute sterilisation period for every 0.025 m^3 of soil. Therefore the large amount of excavated soil in this experiment required an alternative method of sterilisation. Before soil replacement in excavated plots, 4 l of mustard suspension (5g l^{-1}) were added m^{-2} to expel earthworms inhabiting the soil profile below 0.3 m. Replacement of the sterilised soil in Ster treatment plots and *L. terrestris* removal from Rem treatments marked the start of the experiment, in September 2006.

Monitoring

The initial and subsequent number and distribution of active *L. terrestris* middens was measured in each plot, every month over a period of 11 months. Detailed information on the methodology of midden recording using digital photography is provided by Grigoropoulou and Butt [11]. Re-use of burrows was determined using the same algorithm throughout the analysis. Re-used burrows were considered to be the burrows whose midden areas encircled vacated burrows at a time during the experiment. Ripley's L function was used to analyse the spatial distribution of *L. terrestris* middens and the bivariate Ripley's L function [21] to compare the spatial pattern of middens prior to and after experimental manipulation and between successive months. One of the most popular means of analyzing point patterns is the use of second-order statistics. Ripley's K function [21] is a measure of the average number of points found within a set distance t, from each point, divided by the mean intensity of the pattern (λ). If the points are randomly distributed throughout the plot, the expected number of points in a circle of radius t is $\pi t^2 \lambda$. Therefore, the theoretical expectation for K(t) is πt^2. Commonly K(t) is presented as the linearised L function. The expected value of L(t) is zero when points are randomly distributed; values less than zero indicate regular spacing while values greater than zero indicate aggregation. The significance of any observed patterns is usually assessed by comparing the observed distribution function with that expected under Complete Spatial Randomness (CSR). The 95% confidence envelope for CSR is obtained by Monte Carlo permutations. Furthermore, each point in a spatial point pattern can carry additional information called a "mark". In this case the Bivariate Ripley's K function is used, derived by counting for each point of type i the number of type j points lying closer than t units away [1]. Point patterns were analysed using Spatstat package in R. Repeated measures ANOVA was performed on data to examine differences in *L. terrestris* midden number throughout the experiment for Rem and Ster treatments with enclosure effect as a fixed factor. Significant differences are reported at a 0.05 probability level. The experiment was terminated by application of a mustard suspension (5g l^{-1}) to expel resident *L. terrestris* from all 12 plots, at which time (11 months) their positions on expulsion from burrows were recorded. Individuals captured from each plot were collected, washed and kept in separate containers of water until transfer to the laboratory, where they had masses determined and general condition recorded. Analysis of variance (ANOVA) was used to examine differences in *L. terrestris* number captured at the end of the experiment, in enclosed and open plots of the two treatments. All analyses were computed using Statistica v.10 [22].

III. RESULTS

At the start of the experiment a mean (±S.E.) of 20.83 ± 3.03 *L. terrestris* were extracted from 28.33 ± 1.98 middens m^{-2} in Rem treatment. More specifically in RemO plots the initial mean (±SE) midden number prior the manipulation was 29.67 ± 2.33 middens m^{-2}, from which a mean (±SE) of 15.33 ± 2.73 *L. terrestris* were extracted at the start of the experiment, whereas the initial mean (±SE) midden number in RemE plots was 27.00 ± 3.5 middens m^{-2} from which 26.33 ± 2.85 *L. terrestris* were extracted (Table 1).

Table 1

Summary data of individual plots for *L. terrestris* midden number, numbers extracted and extraction efficiency at the start of the experiment, density at destructive sampling, cumulative percentage of re-used burrows, comparison of burrow patterns before and one month after experimental manipulation and aggregation distances of patterns in earthworm removal treatments (RemO: earthworm removal in open plots, RemE: earthworm removal in enclosed plots)

Treatment type	*L. terrestris* midden number m^{-2} prior to manipulation	Number of extracted *L. terrestris* m^{-2}	Extraction efficiency (%)	*L. terrestris* number m^{-2} found at final sampling	Cumulative percentage of re-used burrows (%)	Aggregation of burrow patterns prior to and one month after manipulation	Aggregation distances (m)
RemO	32	10	31.25	28	50	L function above upper envelope	0.025-0.06
RemO	32	19	59.38	34	52.63		0.01-0.07
RemO	25	17	68	34	35.29	L function inside envelopes	
RemE	23	24	104.35	50	54.17	L function inside envelopes	
RemE	34	32	94.12	35	34.38	L function above upper envelope	0.03-0.04
RemE	24	23	95.83	45	56.52		0.018-0.044

The cumulative percentage of re-used burrows did not differ ($F_{1,4}$=0.07, P=0.80) between RemO and RemE plots with means (±SE) of 45.98 ±5.39 and 48.36 ± 7.02 % of burrows m^{-2} respectively (Fig. 1). Throughout the monitoring period, from October to August, the mean (±SE) midden number in RemO plots was 29.70 ± 1.65 middens m^{-2} and did not significantly differ ($F_{1,27}$=2.11, P= 0.158) from 27.67 ± 1.72 middens m^{-2} of RemE plots. A greater number of *L. terrestris* middens was observed in SterE plots, with a mean (±S.E.) of 29.38 ± 2.32 m^{-2}, compared with SterO treatment with a mean (±S.E.) of 24.61 ± 1.32 middens m^{-2}, over the entire duration of the experiment (Fig. 2). This difference was significant during October 2006 ($F_{1,4}$=48.4, P<0.01), January 2007 ($F_{1,4}$=196, P<0.01) and April 2007 ($F_{1,4}$=13.14, P=0.02).

The distribution of *L. terrestris* middens in all twelve plots and sampling dates was examined using Ripley's L function giving a total of 104 midden patterns, of which 14.42 % (n=15) could not be examined as the number of middens was too low to compute Ripley's L function. *L. terrestris* middens in 43.27% (n=45) of point patterns, were regularly distributed at distances ranging from 0.084 ± 0.029 m to 0.130 ± 0.063 m. On a further 14.42% (n=15) occasions, *L. terrestris* middens tended to be regularly distributed, although the linear form of Ripley's K function, remained inside the lower confidence envelope. Finally, in 27.89% (n=29) of point patterns, *L. terrestris* middens were found to be randomly distributed within the 1 m^2. Patterns of *L. terrestris* middens prior to and 1 month after earthworm removal were found to be aggregated at mean (±S.E.) distances ranging from 0.021 ± 0.004 to 0.05 ± 0.007 m in 4 out of 6 Rem plots. (Table 1, Fig. 3). Comparisons of midden distribution between successive months, from October 2006 to August 2007, revealed that patterns were aggregated at mean (±S.E.) distances from 0.019 ± 0.001 to 0.06 ± 0.002 m in 40 out of 42 instances.

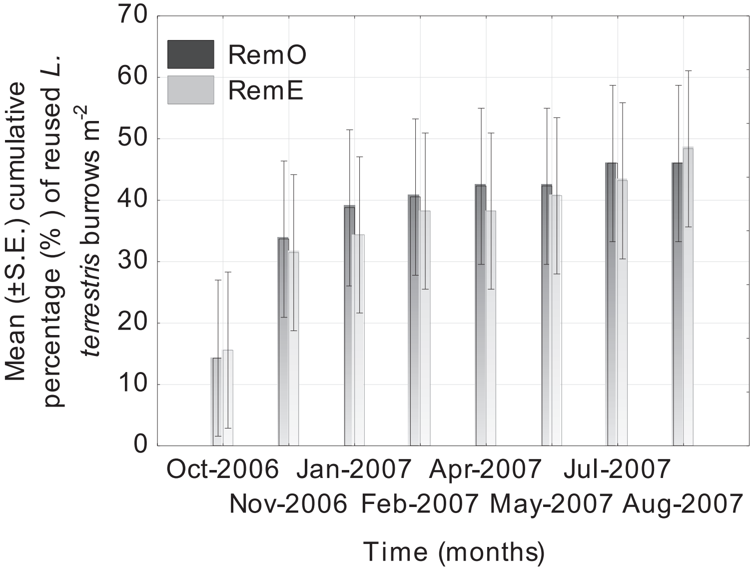
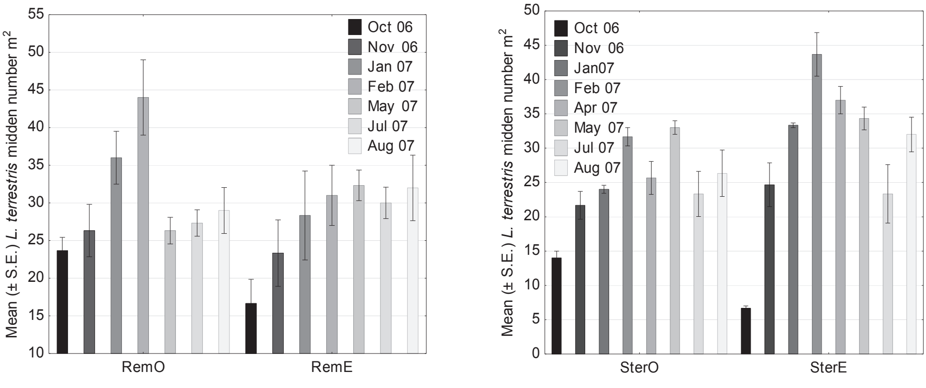
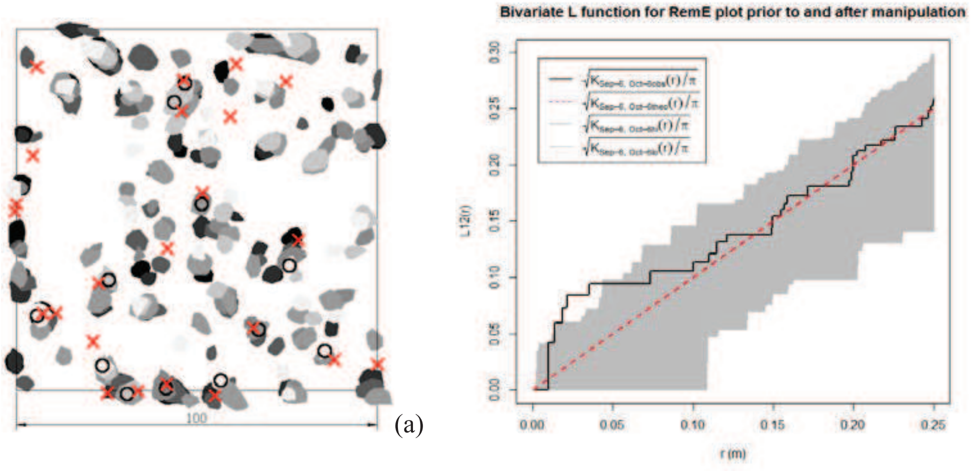


Figure 1. Mean (±S.E.) cumulative percentage of vacated *L. terrestris* burrows re-used over time in open and enclosed 1 m^2 plots (RemO: *L. terrestris* removal from open plots, RemE: *L. terrestris* removal from enclosed plots), in a field experiment to examine *L. terrestris* burrow recycling



(a) (b)

Figure 2. Mean (±S.E.) *L. terrestris* midden number m^{-2} observed in (a) removal plots (RemO: earthworm removal in open plots, RemE: earthworm removal in enclosed plots) and (b) sterilised plots (SterO: soil sterilisation in open plots, SterE: soil sterilisation in enclosed plots), from October 2006 to August 2007, in a field experiment to examine *L. terrestris* burrow recycling



(a)

(b)

Figure 3. Example of (a) midden distribution in a 1 m^2 enclosed plot of the removal treatment (RemE). Crosses (x) indicate position of vacated burrows at the start of the experiment and circles (o), position of re-used burrows. Midden areas are represented by shades of grey (darkest: October '06 to lightest: August '07). (b) The associated bivariate Ripley's L (the linear form of Ripley's K) function compares the spatial pattern of burrows prior to and one month after earthworm removal. The observed L (solid black line) lies above the calculated envelopes (grey area) from 99 simulations of Complete Spatial Randomness (dashed red line) at distances from 0.018 to 0.044 m indicates aggregation of the burrow patterns at those distances

At destructive sampling in August 2007, the mean (±S.E.) *L. terrestris* number in RemO plots was 32.00 ± 2.00 individuals and marginally different ($F_{1,4}$=5.48, P=0.08) from RemE plots with mean (±S.E.) number 43.33 ± 4.41 *L. terrestris*. In sterilised treatment however, enclosure of experimental plots had a significant effect ($F_{1,4}$=19.55, P=0.01) on *L. terrestris* number captured with a mean (±S.E.) of 27.67 ± 0.88 individuals in SterO plots and 48.67 ± 4.67 individuals in SterE plots. A significantly greater number of immature animals were extracted from plots of both Rem ($F_{1,8}$=102.01, P<0.01) and Ster ($F_{1,8}$=83.78, P<0.01) treatments with means (± S.E.) of 33.33 ± 3.05 and 33.83 ± 6.64 *L. terrestris* respectively, compared to adult numbers that were 4.67 ± 1.20 and 1.83 ± 0.60 in those plots. The mean (± S.E.) mass of immature *L. terrestris* was 1.29 ± 0.07 g and of mature individuals was 4.6 ± 0.14 g.

IV. DISCUSSION

A high proportion of vacated *L. terrestris* burrows (nearly half) were found to be re-used in both open and enclosed plots of the Rem treatment by the end of the experiment. Furthermore, the spatial pattern of *L. terrestris* middens prior to and one month after manipulation were found to be aggregated in 4 plots, whereas comparison of midden distribution between successive months showed that the patterns remained stable from October 2006 to August 2007 in all plots. Interestingly, midden patterns remained stable through time in plots where a large number of earthworms was extracted, i.e. 94 and 96% extraction efficiency. The test statistic used poses problems in the analysis of midden permanence, in plots where extraction efficiency was low, as the initial midden arrangement was compared with subsequent patterns. Still, it can be seen that midden distribution in those plots remained constant following habitat disturbance, i.e. targeting burrows with mustard suspension. In a small scale (1 m^2 arena) laboratory experiment, Butt et al. [7] found *L. terrestris* individuals to settle within existing burrows, even when initially occupied by conspecific adults. Moreover, the permanence of *L. terrestris* middens has been recorded for more than a decade at a forest site in Finland [18]. In laboratory experiments [13] immature *L. terrestris* were observed to make use of existing adult burrows. Specifically, in the absence of an adult, the proportion of immature earthworms observed to occupy existing adult burrows (75.39%) was significantly greater than that resting within their own created burrows (24.62%). Similar behaviour has been observed for other species of earthworms by Mathieu et al. (2010). These authors observed a reduced dispersal rate of *Apporectodea icterica* and *Dendrobaena veneta* in pre-used soil by conspecifics that were no longer present. Equally, Caro et al. [8] observed dispersing individuals of *Apporectodea terrestris* to preferentially use existing conspecific's galleries. Furthermore, disproportionately smaller *L. terrestris* have been sampled from within burrows with adult dimensions [18]. These observations suggest that *L. terrestris* burrows could be recycled or inherited. Such behaviour could be a means of minimising energy use for burrow construction [6]. For example soil compaction has been found to affect the burrowing behaviour of *L. terrestris* [16]. The authors suggested that the burrowing activity of earthworms could change to minimise energy expenditure in compacted soil. It is also possible, that the soil modification in the drilosphere (i.e. the soil volume under earthworm influence) can create a favourable microenvironment for conspecifics and offspring compared with adjacent areas. Butt and Lowe [4] found the soil within and below *L. terrestris* middens to sustain a greater number of earthworms compared with nearby non-midden, control samples. However, in other studies such behaviour was not observed. More particularly, in a laboratory study by Valckx et al. [24], *L. terrestris* that dispersed away from burrows due to waterlogging and habitat disturbance were not observed to colonise empty burrows.

The regularity observed in midden distribution at a small scale (1 m^2) can be attributed to the distinctive behaviour of *L. terrestris*, i.e. with respect to feeding and mating. Intraspecific competition for food and space may impose a minimum distance between individuals, whereas the need to settle in close proximity to conspecifics in order to secure mating opportunities may impose a maximum distance between individuals [6,19].

The midden number observed in Rem and Ster plots could not be compared directly in this experiment to examine differences in colonisation rate of *L. terrestris*, as initially, removal of *L. terrestris* individuals from Rem plots was not efficient. The low extraction efficiency was most likely a result of very dry conditions at the site during September 2006. Earthworms may become inactive when soil moisture is low and can retreat deep into their burrows to avoid unfavourable environmental conditions [20]. Enclosing plots facilitated earthworm capture because horizontal dispersion of individuals after mustard application was hindered by the enclosure walls.

Over the course of the experiment, a significantly greater number of *L. terrestris* middens was observed in plots of SterE compared with SterO treatment. This was unexpected, as no earthworms were anticipated in plots of the SterE treatment. Furthermore, destructive sampling of sterilised plots revealed that *L. terrestris* number was significantly greater in enclosed plots compared with open plots. This suggests that the sterilisation method used was inefficient in eliminating earthworms and cocoons. Moreover, the combination of plot sterilisation and the enclosing method could have had a different effect, as enclosures may have prevented earthworms from dispersing away from these high population density plots (48.67 ± 4.67 *L. terrestris* m^{-2} at destructive sampling).

Despite the limitations in the experimental design (inefficiency in earthworm extraction and soil sterilisation), results from the current experiment are useful as they provide evidence of burrow re-use by conspecifics and further support the views of other researchers [6,18] of possible burrow inheritance in *L. terrestris*. Recycling of burrow systems could have an effect on the temporal stability of *L. terrestris* distribution, which is very important as this species is considered an ecosystem engineer [15]. Such an engineering capability, could not only influence other organisms, but determine the selection pressures to which both ecosystem engineers and their descendants are exposed [10]. Further field research is required to examine the persistence of distribution in *L. terrestris* at different scales in time and space. This would usefully avoid undue experimental manipulation and intervention (such as creation of large numbers of adjacent vacant burrows) but perhaps tag resident animals using an appropriate method [5] and periodically record status of residents.

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OCENA PONOWNEGO WYKORZYSTYWANIA KORYTARZY PRZEZ LUMBRICUS TERRESTRIS L. W EKSPERYMENTACH POLOWYCH

Streszczenie

Badano dowody na ponowne wykorzystywanie korytarzy wykonanych przez Lumbricus terrestris. Badania prowadzono przez 11 miesięcy w klimacie umiarkowanym, w lesie liściastym. Polegały na usuwaniu dorosłych osobników tego gatunku z dwunastu powierzchni (1 m^2*), przy monitorowaniu ponownej kolonizacji tego obszaru.*

Cechy stwierdzonego rozkładu przestrzennego koprolitów i detrytusu wciąganego do korytarzy przez L. terrestris przebadano statystycznie.

Obserwacje sugerują, że korytarze L. terrestris mogą być dziedziczone lub ponownie wykorzystywane. Takie zachowanie dżdżownic może być sposobem na zminimalizowanie wydatków na energię do budowy nory lub wskazywać na preferencję bardziej korzystnego mikrośrodowiska w glebie. Choć praca sugeruje dowody na powyższą strategię, autorzy zdają sobie sprawę ze złożoności zagadnienia i ograniczeń przeprowadzonego eksperymentu.

Słowa kluczowe: dżdżownice, ponowne wykorzystanie korytarzy, koprolity, wzorzec przestrzenny