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A radio-labelled study of earthworm behaviour in artificial soil cores in term of ecological types

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Abstract A new apparatus developed by Capowiez et al. (Eur J Soil Sci 52:365–375, 2001), called "gamma column", enables the continuous movements of radio-labelled earthworms to be tracked in artificial soil cores (3D space). Each individual was radio-labelled by injecting a small source of ^{60}Co (13 μCi) into its coelomic cavity, then individuals were released into artificial soil cores for 12 to 23 days. An analysis of tracks divided the continuous movements of earthworms into three kinds of movements ("burrowing", "displacement", and "inactivity"). Trajectories of several earthworm species presumed to be anecic, such as *Nicodrilus giardi* (NG), *Lumbricus terrestris* (LT) and *Nicodrilus nocturnus* (NN), or presumed to be endogeic, such as *Aporrectodea icterica* (AI) and *Octalasium lacteum* (OL), were studied. Analysis of these trajectories revealed ecological differences between species, in particular in terms of morphologies of the burrow systems (burrows created by LT were the simplest and those by NG and NN more complex), the ratio between the time spent to burrow and the time spent to reuse, called time allocation (TA) ratio ($LT_{TA}<1$; $NN_{TA}=NG_{TA}=1$; $OL_{TA}=4$; $AI_{TA}=6$), and the time spent in inactivity (LT>NN=NG=OL>AI). For *L. terrestris* and *A. icterica* the match between the observed characteristics of behaviour and their theoretical characteristics based on usual ecological types was demonstrated. These species could be considered as archetypes of anecic and endogeic ecological types, respectively. By contrast, the behaviour of *N. giardi* and *N. nocturnus* was unexpected, particularly regarding their anecic description, because not only did they reuse existing burrows intensively but they also created numerous and long burrows. The reuse of burrows was also strongly heterogeneous for these two species, with a partition of the burrow system in permanent and temporary burrows. Similarly, *O. lacteum* could not be considered as a purely endogeic species since it reused its burrows. Assessment of the ecological types of earthworm species will be improved by analysing earthworm behaviour using this tracking method. This will lead to better prediction of the effects of the various behaviours on burrow structures and their contribution to soil functioning.

Keywords Earthworm · *Lumbricus terrestris* · *Nicodrilus giardi* · *Nicodrilus nocturnus* · *Aporrectodea icterica* · *Octalasium lacteum* · Burrowing behaviour · Radio-labelled · Burrow system · Ecological types

Introduction

By their excavation activities, earthworms can regulate some of the physical, chemical and biological soil environmental conditions. Thus, earthworms have been termed "ecosystem engineers" (Jones et al. 1994) since they can modify soils in a favourable way for their needs and for those of organisms inhabiting the soil. Earthworms could influence the soil hydraulic regime via their burrows, which act as preferential pathways or volume storage for water (Beven and Germann 1982; Bouma 1991). Earthworms could influence the carbon or the nitrogen cycle by the relocation of surface litter or organic matter through the soil profile (Görres et al. 2001) and the microbial activity of soils (Tinuov and Scheu 1999; Scheu et al. 2002).

However, agricultural management such as tillage or pesticide use could result in a decrease in earthworm diversity and consequently cause an alteration in soil functioning (Lavelle and Spain 2001). For soil rehabilitation

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or conservation, identifying earthworm species playing a major role ("key species") in the soil is necessary (Butt et al. 1997). Thus, a classification of earthworm diversity is valuable depending on their complementary activities or their redundancies regarding burrow structures and effects on soil functions. By creating a functional classification of earthworms, it should be possible to quantify, at the ecosystem scale, the diversity of functions influenced by the earthworm community. The sampling of such a key species on the field could act as an indirect "indicator" of the soil functioning or the soil health (defined by Doube and Schmidt 1997 as long-term plant productivity).

Beyond the taxonomy, a classification into ecological types between species level and community level was made independently by Lee (1959) and Bouché (1977) to delimit complementarities and redundancies inside earthworm communities. Three ecological types termed anecic, endogeic and epigeic were linked with three strategies selected during species evolution. Lee and Foster (1991) underlined that the specificity of needs (localisation of food, biophysical conditions, etc.) between the ecological types could lead to different earthworm behaviours. Lee and Foster (1991) made a direct link between earthworm behaviour, ecological type and morphology of earthworm burrows from which they infer a functional typology of burrows. They assumed that earthworm species with the same characteristics, gathered into ecological types, have similar functions in the soil ecosystem. Although Bouché's classification is used by all the researchers on earthworms, it is based on few experimental studies due to the difficulty in observing earthworm activity in soil. Experimental validations of divergences in behaviour and burrow morphology between these ecological types are needed.

Several authors (Kobel-Lamparski and Lamparski 1987; Kretzschmar and Aries 1990; Ligthart et al. 1993; McKenzie and Dexter 1993) reconstituted burrow systems in the field after visually mapping all earthworm pores depending on depth soil layer by soil layer. A new method, X-ray tomography, first applied by Joschko et al. (1991) to study earthworm burrows, enabled direct and rapid 3D visualisation of burrows without disturbing the soil sample (Capowiez et al. 1998; Langmaack et al. 1999; Bastardie et al. 2005). However, X-ray tomography only provides "snapshots" of burrow systems. The dynamics of the creation, use and destruction can only be studied with successive (and costly) scanning of cores (Francis and Fraser 1998).

Direct study of earthworm behaviour requires tracking burrow formation and the position of earthworms. Joschko et al. (1993), using successive X-ray tomography on a repacked soil core, attempted to analyse the dynamics of creation of burrows by *Octalasium lacteum*. However, successive images of burrow systems were far from enabling a precise behavioural description. On the other hand, Capowiez and Belzunces (2001) used a 2D terrarium to reconstitute the hypothetical trajectory of several individuals of the endogeic species *Allolobophora chlorotica* and the anecic species *Nicodrilus nocturnus*. Although new behavioural observations were made, 2D terraria are confining spaces and could alter the movements of earthworms. Joyner and Harmon (1961) were able to track the activity of a radio-labelled *L. terrestris*; recently, a new apparatus, called "gamma column", was designed to track radio-labelled earthworm movements (Capowiez et al. 2001a). With this technology, we aimed to:

- Reconstruct the trajectories of earthworms in the soil and the shape of the burrow systems
- Quantify the dynamics of the creation and use of burrow systems
- Test the postulated relationships between ecological types and behaviour for three anecic and two endogeic earthworm species

Materials and methods

Gamma column apparatus and earthworm localisation

The full description of the design and the functioning of the gamma column apparatus is provided in Capowiez et al. (2001a). Earthworms are radio-labelled by injecting a small source of ^{60}Co (length, 0.5 mm; diameter, 0.25 mm; average activity, 13.5 μCi) into their coelomic cavity with a modified syringe posterior to the clitellum in order to avoid damage to organ. To close the wound, the earthworms were kept in plastic dishes with sterile filter paper at 12°C for 24 h before the beginning of behavioural experiments.

The emission of gamma rays from the source was recorded by the gamma column apparatus, which is composed of a set of three scintillation detectors placed at 120° from each other and carried on a disc that oscillates vertically around the soil core with the earthworm on the surface. A control computer was connected to (1) a spectrometer, which computed the number of gamma rays received during a span counted by the three detectors, and (2) a position detector, which gave the vertical position. In contrast to the previous method, data were collected both downwards and upwards. Then, at the end of each descent or ascent phase (approximately 1 min), gamma ray profiles as a function of the disc's vertical position were obtained for each detector.

To estimate the spatial position (X, Y and Z) of the earthworm in the soil core a mechanistic model was developed (Capowiez et al. 2001a), which assessed the absorption of the gamma rays by the different media (soil, air and lead) based on the arbitrary position of the ^{60}C source. After data collection, by inverting the model and using non-linear fitting procedures, we estimated the position of the ^{60}Co source in the earthworm using the profile given by each detector.

Analysis of earthworm burrows

To identify and quantify the movement patterns of earthworms in soil cores, a reconstruction of their paths was computed from the successive positions of the ^{60}C source (a point X, Y and Z every minute).

An algorithm was written to split the continuous movement of an earthworm into three kinds of movements (“burrowing” a new tunnel, “displacement” in an existing burrow, or an “inactivity” phase) by detecting the break points that separated them. Break points were classified as either the starting of a new digging event or the first point in an existing burrow. Break points were determined according to the following procedure: The whole trajectory was scanned point by point in chronological order. Two assumptions were made to detect the break points. First, the digging of burrows by earthworms must be slower than the displacement inside their burrow systems. Each point whose distance is longer than the arbitrary length of 2 cm from the previous point was classified as a USE point. Other points were presumed as DIG points (characterised by points very close to each other). Second, the earthworm cannot burrow twice in the same part of the space. Each point classified as a DIG point according to the first assumption but which overlapped the previous DIG point was classified as an INACTIVITY point (the overlapping was defined as a threshold of three DIG points or more in an arbitrary sphere 1.2 cm in diameter around the tested point). All of the DIG, USE or INACTIVITY points that were consecutive were gathered and constituted homogeneous DIG, USE or INACTIVITY portions, respectively.

From the DIG portions, the “skeleton of earthworm burrowing”, i.e. the burrow systems, can be traced. First, each DIG portion was fitted separately in 3D to obtain a better assessment of the length of the movement. Second, the start point of each DIG portion was linked with the nearest point belonging to the nearest DIG portion among the previous ones. This computation enabled lateral branching of burrows to be identified. A skeleton of burrows is thereafter visualized using the Rotater software (available at http://www.casr.adelaide.edu.au/rotater/).

Using both the skeleton structure of burrowing and successive positions of the radio-labelled earthworms, we could compute quantifications characterizing the dynamic of burrow formation and burrow use such as (1) the length, (2) the duration and the speed of each movement (burrowing, displacement and inactivity), (3) the age of each point, (4) the number of burrow reuses and (5) the residence time at each point. Thus, all the USE points were projected in an orthogonal way on the skeleton of burrowing to improve the assessment of length. Then, all the intermediate DIG points between each pair of consecutive USE points were identified and inserted between the concerned USE points as supplementary points for displacement. The displacements matched exactly with the structure of the skeleton, so the length of displacement could be accurately assessed. The number of reuses of each point of the skeleton (i.e., DIG points) was given as the number of times that a point was reused as an intermediate point between the USE points. In the same way, the residence time at each point of the skeleton was given as a cumulative time spent at this point during the displacement by its intermediary.

Earthworms, soil cores and conditions of incubation

The movements of at least two individuals belonging to three presumed anecic species [*Lumbricus terrestris* (Linnaeus 1758), *Nicodrilus giardi* (Bouché 1977) and *N. nocturnus* (Bouché 1977)] and to two presumed endogeic species [*Octalasion lacteum* (Örley 1881) and *Aporrectodea icterica* (Savigny 1826)] were tracked and reconstituted between November and March 2000, 2001 and 2003.

Each earthworm was kept in an artificial core of soil. Earthworms and soil (the 30 cm of top soil, a sandy loam with 22.4% clay, 22.9% silt, 57.7% sand and 2.67% organic matter) were from experimental grassland in Theix (central France) and were kept at 12±1°C for 2 months before experiments. Artificial soil cores were constructed with a hydraulic press as follows: 20 layers of soil were compacted successively in a PVC cylinder (40 cm in height, 20 cm in diameter) with a hydraulic press (0.95 kg of soil per layer, 3 min of compaction) to obtain homogeneous cores with a soil density of 1.1 g cm^{-3}.

Before each experiment, an artificial soil core was watered to field capacity and placed in the centre of the gamma column apparatus with the bottom standing in water (height, 2 cm) to reproduce an artificial gradient of humidity (about 35% of gravimetric water content at the top against 46% at the bottom) and prevent oxygen input from the bottom of the core. Incubation was in a cold chamber at 12±1°C but an artificial temperature gradient was created by a light (100 W) placed 25 cm above the soil with a photoperiod of 12 h (up to 16°C in the first centimetre of the soil after 12 h light). At the beginning of the experiment, 5 g of fresh litter (ryegrass) was spread on the surface of the soil core and an

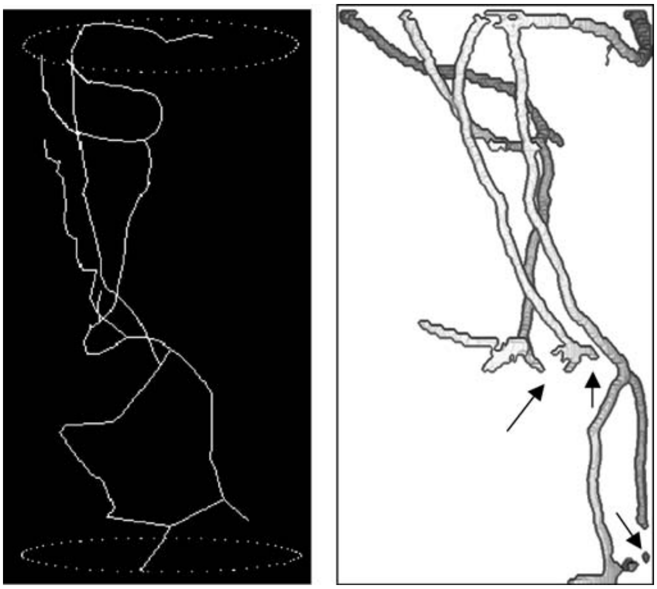


Fig. 1 Match between a 3D reconstitution of a burrow system from X-ray tomography (see Bastardie et al. 2003 for the methods) and the skeleton of burrowing after analysis of tracks of a burrow system created by a radio-labelled *N. giardi*. The *arrows* indicate the refilling burrows

earthworm was placed on the centre (during a dark phase). Because the computer connected to the gamma column sometimes failed for unknown reasons, earthworm movements could only be tracked over a period of less than 23 days.

Results

Burrowing skeletons

The determination of burrows based on the successive positions of the earthworms enabled burrowing skeletons to be constructed. If these skeletons constituted the pathways of earthworms into the repacked soil cores, they were not the direct equivalent of the structure of the burrow systems since some discontinuities may have been created with the refilling of the burrows by below-ground casts (Fig. 1). Except for the refilling, the skeletons and the corresponding reconstitutions from X-ray tomography recorded a good similarity, as illustrated by Fig. 1.

The burrow systems (i.e., skeletons) created by *L. terrestris* differed most in comparison with the systems burrowed by the other earthworms (Fig. 2a to e). All *L. terrestris* created simple burrow systems, usually one vertical burrow having sometimes one ramification. Other earthworms (*N. giardi* and *N. nocturnus*) constructed complex interconnected burrow systems with at least two inter-

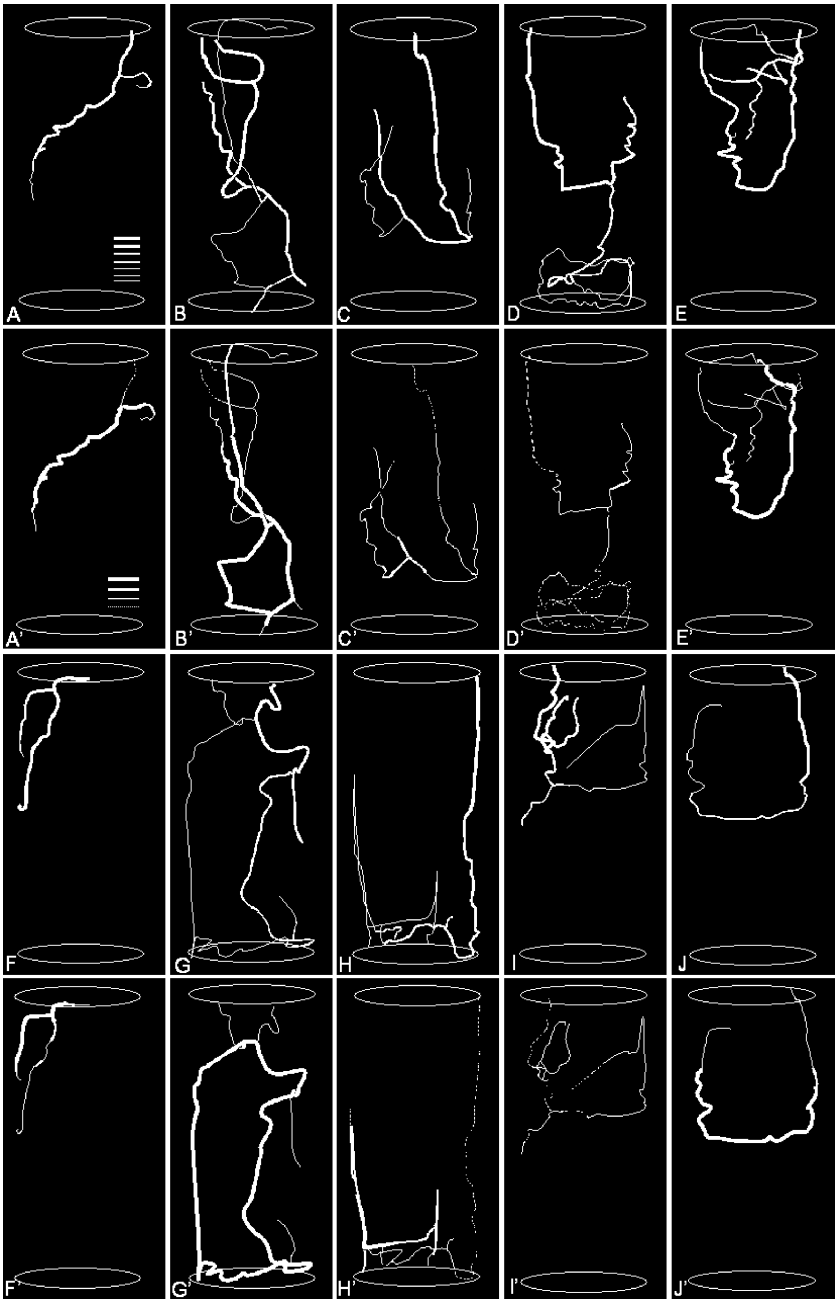
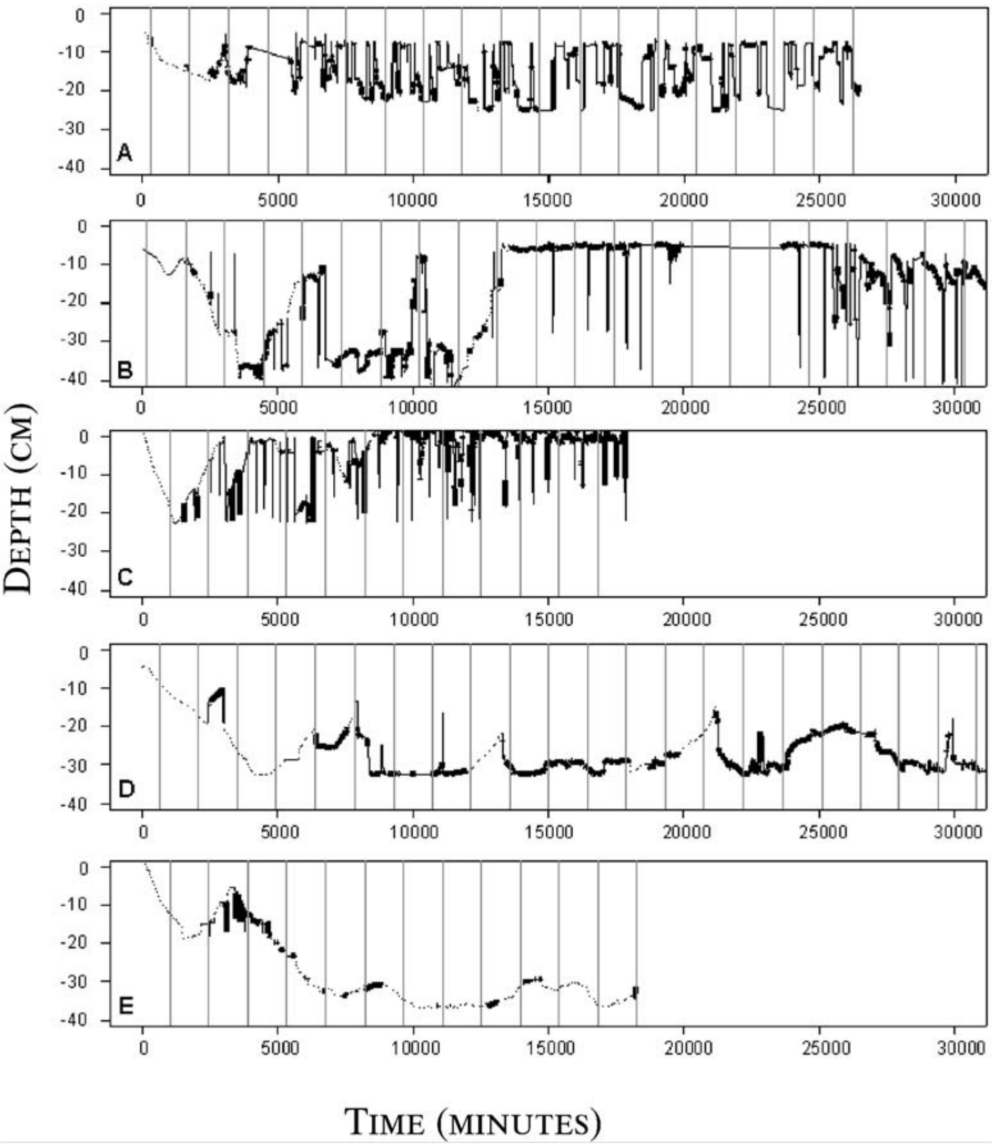


Fig. 2 3D reconstitution of burrow systems created by the radio-labelled earthworms in repacked soil cores (**a**, **f**: *L. terrestris*; **b**, **g**: *N. giardi*; **c**, **h** *N. nocturnus*; **d**, **i** *O. lacteum*; **e**, **j** *A. icterica*). The increasing line thickness gives either the decreasing age of the burrows (**a** to **j**) or the number of reuse of the specific burrow (**a′** to **j′**)

Fig. 3 Depth (centimeters) occupied by the radio-labelled individuals (**a** *L. terrestris*; **b** *N. giardi*; **c** *N. nocturnus*; **d** *O. lacteum*; **e** *A. icterica*) during incubation with the indication of the type of activity (*dotted line*, burrowing; *solid line*, displacement; *thick line*, inactivity). The *vertical lines* indicate the beginning of nights during the incubation. These graphics were computed from the burrow systems **a** to **e** according to Fig. 2



connected burrows open to the soil surface. All earthworms created vertical burrows, running from the top to the bottom of the core (*N. giardi* and *A. icterica*); burrows with various subhorizontal orientations and U-shaped burrows occurred near the soil surface.

Earthworm movements and time allocation

Earthworm burrowing, displacement and inactivity phases can be distinguished for each species trajectories except for *L. terrestris*, which had very short burrowing phases

Fig. 4 Percentage of the total incubation time spent on burrowing, displacement and inactivity for the five species studied (LT, *L. terrestris*, *n*=4; NG, *N. giardi*, *n*=6; NN, *N. nocturnus*, *n*=2; OL, *O. lacteum*, *n*=2; AC, *A. icterica*, *n*=2)

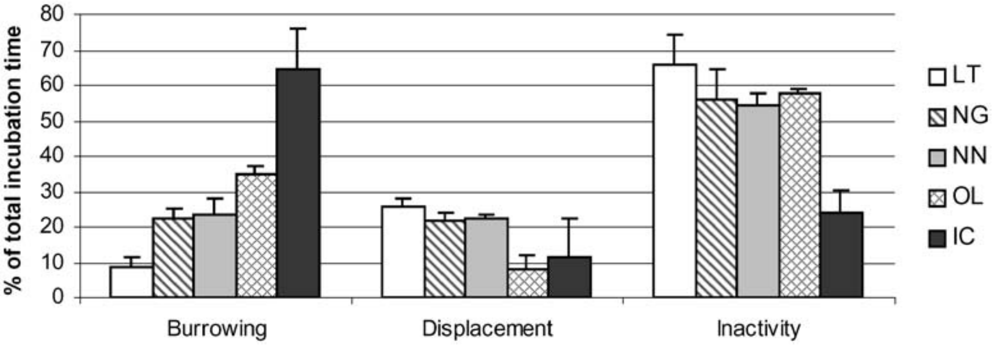


Table 1 Burrowing and displacement lengths and burrowing and displace speeds computed from analysis of earthworm tracks for the five species studied

	Burrowing length (m day^{-1})	Displacement length (m day^{-1})	Burrowing speed (cm h^{-1})	Displacement speed (cm h^{-1})
L. terrestris (*n*=4)	0.02±0.01	2.90±0.78	1.9±0.4	38.9±3.4
N. giardi (*n*=6)	0.13±0.02	1.95±0.13	9.9±2.5	56.1±6.4
N. nocturnus (*n*=2)	0.10±0.02	2.54±0.09	2.3±0.3	38.6±6.2
O. lacteum (*n*=2)	0.06±0.01	0.54±0.07	4.1±3	47.8±16.7
A. icterica (*n*=2)	0.11±0.01	0.17±0.07	3.2±0.2	34.6±9.0

The burrowing and displacement lengths are the ratios between the cumulated lengths and the total duration of the incubation. The burrowing and displacement speeds are the ratios between the length and the duration of each movement. The standard errors are also given

(Fig. 3). Burrowing phases were longer for species *A. icterica* and *O. lacteum*. The displacement into pre-existent burrows were distinct, in particular for *N. giardi*, *N. nocturnus* and *L. terrestris*; these earthworms displayed sharp oscillatory movements between preferential positions at the top and bottom of the cores. The phases of inactivity were very frequent in all burrows and represented up to 65% of the total positions taken up by *L. terrestris* (Fig. 4).

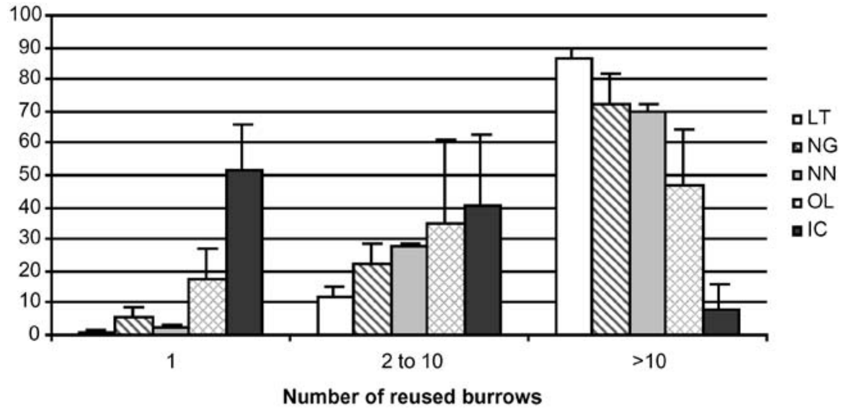
All species had different time allocations in each category of movement (Fig. 4). The ratio between burrowing and displacement was biased towards displacement for all the *L. terrestris* (time for burrowing / time for displacement=0.36), but this balance equilibrated for *N. giardi* and *N. nocturnus* (1.04 and 1.06, respectively). By contrast, the time allocated for burrowing was greater than displacement for *O. lacteum* and *A. icterica* (5.57 and 4.38, respectively). Inactivity was greater for *L. terrestris*. The times allocated for inactivity was similar between *N. giardi* and *N. nocturnus* (55.9 and 54.3%, respectively). The inactivity periods were more important for *O. lacteum* than for *A. icterica* (57.5 and 23.8% of time, respectively).

The rate of burrow formation by the earthworms during the total period of the incubation varied between species (Table 1), partly because of differences in speed of movement. *L. terrestris* burrowed the least total distance (0.02 m day^{-1}) and *N. giardi* the most (0.13 m day^{-1}). Although *N. nocturnus* and *N. giardi* burrowed globally the same distance, *N. giardi* burrowed faster than *N. nocturnus* (9.9 against 2.3 cm h^{-1}). Regarding the rates of displacement *L. terrestris*, *N. nocturnus* and *N. giardi* (2.9, 2.54 and 1.9 m day^{-1}, respectively) had higher values than the *O. lacteum* (0.54 m day^{-1}). *A. icterica* showed the lowest total length of displacement (0.17 m day^{-1}) and can be distinguished from *O. lacteum*. For all the earthworms, the speeds of displacement were 6–20 times greater than those of burrowing. *N. giardi* moved the fastest into the pre-existing burrows (displacement speed=56.1 cm h^{-1}).

Rate of burrow reuse and residence time

Most of the burrows created by *O. lacteum* and *A. icterica* were not reused (Fig. 5; 18 and 52% of the total length, respectively). This part represented less than 5% of the burrows created by the other species. By contrast, *L. terrestris*, *N. giardi* and *N. nocturnus* reused pre-existing burrows intensively. Up to 72% in mean total length of burrow was reused more than ten times by *L. terrestris*. Equally, 47% was reused by *O. lacteum* more than ten times. If burrow use by *L. terrestris* was distributed uniformly (Fig. 2b), the burrow reuse was heterogeneous for *N. giardi* and *N. nocturnus* since parts of the total burrow length were not reused. The similarities between Fig. 2a and b illustrated that no simple relationship could be demonstrated between the age of the burrows and their degree of reuse. Concerning the burrow systems created by *O. lacteum* and *A. icterica*, the most reused burrows seemed to correspond to the parts of the burrows where lateral branching was created. The part of burrow system for which the earthworms remained more than 250 min was greater for the burrow systems created by the *L. terrestris* (47% in mean) and, in decreasing order, was 22% for *O. lacteum*, 18% for *A. icterica*, 14% for the *N. giardi* and 9% for the *N. nocturnus*.

Fig. 5 Number of burrow reuse by the five species studied (LT, *L. terrestris*, *n*=4; NG, *N. giardi*, *n*=6; NN, *N. nocturnus*, *n*=2; OL, *O. lacteum*, *n*=2; AC, *A. icterica*, *n*=2)



Discussion

Implications of the earthworm behaviour

This is the first report of earthworm burrowing behaviour automatically tracked. The gamma column apparatus seems to be a promising technique in studies of earthworm ecology. The tracking paths of the earthworms inside soil cores enabled us to reconstruct the structure of burrow systems as a "burrowing skeleton". Concerning the three species *L. terrestris*, *N. giardi* and *O. lacteum*, the geometry of the burrows are in agreement with those developed from previous studies working on 3D reconstitutions of monospecific and individual burrow systems using X-ray tomography on repacked soil cores (Bastardie et al. 2003). To date, no 3D reconstitution of the individual burrow systems created by *N. nocturnus* or *A. icterica* is available (Capowiez et al. 2001b). Interpretation of burrow tracks and quantification of the length and duration of earthworm movements showed that earthworms not only excavate burrows but also reuse them. It also demonstrated that earthworms do not move or burrow continuously but remain inactive most of the time. The various degrees of burrow reuse could affect the continuity of burrows or the structural properties of the burrow walls and create a structural heterogeneity. If the expelling of the radio-labelled earthworm could be made in a non-destructive manner, quantification of burrow reuse and residence time should be linked with structural or biological measurement on burrow walls. Because burrow continuity determines the volume of burrows linked to the soil surface for water drainage and storage, information concerning the intensity of burrow reuse and burrow continuity is necessary.

The match between theoretical and observed behaviours

It is often assumed that main theoretical differences between anecic species and endogeic species (Lee and Foster 1991) result from differences in the ecological interpretation of burrows. Anecic species are thought to create burrows to be used as "shelters" and are maintained by constant reuse. By contrast, endogeic species create a great number of burrows to explore and to ingest soil. Behavioural tracks under experimental conditions confirmed that the burrow system can be reused intensively. Therefore, burrows could constitute relatively permanent structures, often reused. On the contrary, some tracks showed that burrows are little or maybe little used and could constitute temporary structures; some burrows are deserted because they may become useless for the earthworms that created them.

Thus, our results confirm that the species *L. terrestris* and *A. icterica* display the expected ecological behaviours, depending on the time allocation (TA) ratio burrowing/displacement. By contrast, it appears that the observed behaviours for *N. giardi*, *N. nocturnus* and *O. lacteum* did not correspond strictly to the theoretical behaviour patterns. These species seem to occupy an intermediate position between anecic and endogeic. An intermediate position (between endogeic and anecic) has already been suggested by Jégou et al. (1999) for *N. giardi*, using the burrow visualization given by X-ray tomography. Other studies on a 2D terrarium with *N. nocturnus* (Capowiez and Belzunces 2001; Capowiez et al. 2001b) showed that this species was able to create well-developed and well-branched burrow systems, showing numerous discontinuities under experimental conditions; these characteristics are usually expected for the endogeic species. Burrow systems of *Apporectodea longa* were studied by Kretzschmar (1989) and were similar to the burrow characteristics described here for *N. giardi* and *N. nocturnus*. As far as behaviour and burrow systems are concerned, it appears that *N. giardi*, *N. nocturnus* or *A. longa* are not isolated cases but are rather representative cases of a real ecological type, and these species could be called "endoanecic" species. Their behaviour could be placed between the expected behaviour of anecic (with *L. terrestris* as an archetype) and endogeic species (with *A. icterica* as an archetype). Thus, although it is too early to generalize on the observed earthworm behaviours as specific due to the low number of repetitions, it seems that burrows created by a species classified in a given ecological type would have other ecological functions (mixed strategy between litter ingestion or soil organic matter ingestion, etc.). The ecological needs of the intermediate species *N. giardi*, *N. nocturnus* and maybe *O. lacteum* should be explored to better describe their functions. In the same way, Schmidt et al. (1997), Briones et al. (1999), and Neilson et al. (2000) compared the ^{13}C and ^{15}N isotope enrichments in the stomach of epigeic, endogeic and anecic earthworm species as an increase in ecological functions. Contrary to previous studies, Neilson et al. (2000) did not verify that epigeic species would be strictly "humus feeders" and endogeic species strictly "humus formers" (Perel 1977), with anecic species occupying an intermediate position between these two behaviour patterns.

Conclusion

We have shown that the morphology of earthworm burrow systems is related to the species rather than to ecological types. We also demonstrated that the different burrow systems result from specific behaviour patterns. However, because these results were obtained under particular experimental conditions (homogeneous soil, litter on soil surface, artificial gradients of humidity and temperature, earthworms starting from the soil surface) no information on the commonness of these behaviour patterns can be given. Indeed, some authors have stated that earthworms, such as *L. terrestris*, could exhibit plasticity in their behaviour (Lavelle 1988). The variability in behaviour patterns and burrow systems among earthworm species belonging to the same type may be explained by the variability of ecological needs, which remains to be assessed. However, if the creation of a new ecological type intermediate between anecic and endogeic, called endoanecic, could be artificial, there should be a more careful use of the existing categories.

Our results underline that the assessment of the earthworm contributions to soil functions may not be relevant, using the ecological types as they are currently defined.

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