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Dynamic study of the burrowing behaviour of *Aporrectodea nocturna* and *Allolobophora chlorotica*: interactions between earthworms and spatial avoidance of burrows

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Abstract The behaviour of earthworms belonging to two different species and ecological types (*Aporrectodea nocturna* and *Allolobophora chlorotica*) was studied using two-dimensional (2D) terraria. Two experiments were set up to gain insight into the nature of interactions between these earthworms. Firstly, the evolution of the burrow systems was analysed with the density of the earthworms varying from one to five individuals. Secondly, a burrow system was first established by using one earthworm which was then removed before the introduction of a second earthworm. This second earthworm therefore encountered a burrow system created either by a conspecific earthworm or by an earthworm of the other species. These experiments showed that: (1) intra- and interspecific interactions occur between earthworms, (2) these interactions are dependent on the physical presence of the earthworms, and (3) spatial avoidance can occur (*A. chlorotica* avoiding burrows created by *A. nocturna*). The results suggest that earthworm burrow systems are “individual structures”, rarely used by other earthworms when inhabited. When abandoned, the burrows may be recolonised depending on the ecological type of the earthworm under consideration.

Keywords Trajectory · Ecological type · Two-dimensional terrarium · Recolonisation

Introduction

Several studies have sought to describe earthworm burrow systems under natural conditions using either manual removal of soil layers (Kretzschmar 1982; Ligthart and Peek 1997) or computer-assisted tomography (Capowiez et al. 1998; 2000) and have shown that these systems vary both in space and time. This variability has

been assumed to be related to either: (1) variations in the specific composition of the earthworm communities (due to invasion or diapause), (2) interactions between earthworms (competition), or (3) the particular behaviour of some earthworms (backfilling with casts of burrows during summer). The variability has also been linked to high rates of burrow destruction (Ligthart 1997) due to physical (trampling, frost) and biological alteration. Biological alteration through burrow backfilling with cast is indeed thought to be the main factor governing burrow destruction, a phenomenon easily observed in two-dimensional (2D) terraria (Schrader 1993; Hirth et al. 1996). This kind of destruction is dependent on physical parameters such as soil compaction (Rushton 1986; Kretzschmar 1991) and on biological parameters such as the earthworm species under consideration, the structure of the earthworm community (Scullion and Ramshaw 1988) and the quantity and quality of the organic matter present in the soil (Abbott and Parker 1981). Computer-assisted tomography of earthworm burrow systems in artificial cores under laboratory conditions (Joshcko et al. 1991, 1993; Jégou et al. 1998; Langmaack et al. 1999) has revealed that the burrow systems made by different ecological types of earthworms vary in their structure (continuity, branching intensity, verticality). Burrow systems should be viewed as complex and dynamic systems rather than as constant and stable soil pores. As inferred from theoretical models (Monestiez and Kretzschmar 1992), the difference in the shape of the burrow systems and their development may in turn influence soil transfer properties associated with them (Bouma 1991; McCoy et al. 1994). Therefore, in order to be able to describe and take into account this variability in the structure of earthworm burrow systems, a better knowledge of the behaviour of these animals is required. Such studies could result in animal-based models of dynamic soil macroporosity. However, earthworm behaviour is poorly understood, mainly because these animals are concealed by the matrix in which they live. Even though they impose very artificial conditions on earthworms, observations using 2D terraria (Evans 1947) is the only approach

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that enables quantification of earthworm behaviour. In an earlier paper, Capowiez (2000) used this technique to study intra- and interspecific interactions between two earthworm species of two different ecological types (*Aporrectodea chlorotica* and *Allolobophora nocturna*). In particular, by computing the length burrowed and the surface explored by each earthworm, it was possible to show interspecific interactions with the presence of the anecic species influencing the behaviour of the endogeic species. Intraspecific interactions between anecic earthworms were also demonstrated.

Interactions between earthworms or between earthworm species present challenges for future studies in earthworm ecology. Earthworms are currently being introduced into soils to either help restore polluted sites (Butt et al. 1994) or to improve productivity of agricultural zones (Baker et al. 1999). It is important to obtain better understanding of interactions between species before such introductions take place in order to predict optimal associations of earthworm species (Butt 1998; Lowe and Butt 1999) and to ensure that introduced species will not interact adversely with native species (Dalby et al. 1998).

The objectives of the present study, were to study the nature of the interactions between *A. nocturna* and *A. chlorotica* in more detail. A set of experiments was conducted to try to answer the following questions:

1. Are species interactions sensitive to the density of earthworms present in the terraria?
2. Are these interactions dependent on the physical presence of earthworms?

Materials and methods

Terraria, earthworms and soil

The basic method was described by Capowiez (2000) and so only the general principles and modifications will be presented here. Twenty terraria (33×48 cm) made of two planar glass sheets separated by 3-mm-thick pieces of PVC around the edges were filled with 2 mm sieved soil (moisture=25%) so that the bulk density was ca. 1.24. Soil (30.2% clay, 48.7% silt, 21.1% sand and 5.1% organic matter) and earthworms were collected in an abandoned peach orchard in Montfavet near Avignon (SE France). Earthworms were weighed after washing off soil at the beginning and end of the experiment. Terraria were placed in a cool room (11±1°C). No food was added. Transparent sheets were attached to each side of the terrarium to trace burrow development.

Experimental design of the two experiments

Observations of the 2D terraria were made under red light 4 times a day (08:00, 13:00, 18:00 and 23:00 hours). The positions of each earthworm and the appearance of new burrows were recorded with coloured pencils.

In the first experiment, one, two, three, four or five earthworms of each species were observed in the terraria for a duration of 15 days. Two replicates were made. No attempt was made to reconstruct the trajectories of the observed earthworms because above a density of two earthworms per terraria, it was almost impossible to know precisely which earthworm had made which burrow.

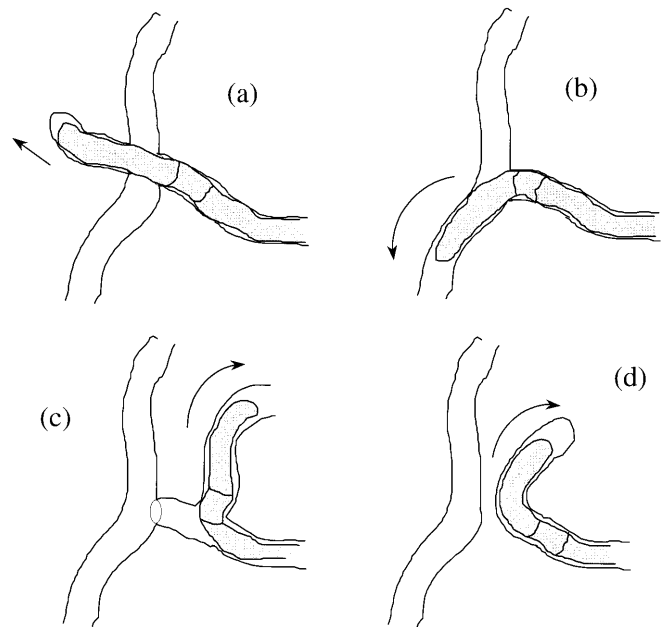


Fig. 1 The four possible patterns when approaching a burrow: the earthworm can **a** cross it, **b** reach it and use it, **c** reach it and veer away, or **d** avoid it. Arrows indicate the direction of the earthworm's movement

The second experiment involved two phases. In the first phase, an earthworm (either *A. nocturna* or *A. chlorotica*) was placed in each terrarium and observed for 5 days. The terraria were then gently opened and the earthworms carefully removed. The terraria were then closed again and sealed with adhesive tape. The presence of cracks in the soil due to the opening were recorded. In the second phase of the experiment, a second earthworm was introduced to each re-closed terrarium and the behaviour of the animals observed for 5 days. There were four possible treatments according to the species present in the first and second phase of the experiment: (1) *A. nocturna* then *A. nocturna*, (2) *A. nocturna* then *A. chlorotica*, (3) *A. chlorotica* then *A. nocturna* and (4) *A. chlorotica* then *A. chlorotica*. Observations were compared to those obtained by Capowiez (2000) where two (or one) earthworms were observed when introduced at the same time in the terraria. According to Capowiez (2000), T2 is the treatment when the earthworm is in the presence of a conspecific earthworm and T3 the treatment when in the presence of an earthworm of the other species. Therefore, in this work we have used T2+ for treatment (1) and (4) and T3+ for treatments (2) and (3). Observations made in the first phase of this experiment were called T1+ data, even if they were a true replicate of the treatment T1 (an earthworm alone in a terrarium) made by Capowiez (2000). The only difference between T1 and T1+ thus lay in the duration of the observations (8 days vs. 5 days). Therefore in the comparisons made here, observations from T1 were reduced to the values observed at day 5.

Data analysis

At the end of the first or the second experiment information gathered on each side of the terrarium was summarised on a single transparent sheet. The burrow traces were then digitised using a digitiser. Several characteristics [see Capowiez (2000) for methods] were computed in order to study the behaviour of the earthworms (total length burrowed, daily burrowed length and trajectories) and the topology of the resulting burrow networks (number of bifurcations and branches, connectivity m^{-1}).

In the second experiment, a new characteristic was also computed. Because trajectories were available it was possible to study

the behaviour of each animal as it approached an existing burrow. The trajectory was animated step by step on a computer screen and an observer noted the occurrence of the following four possibilities (Fig. 1): (1) the earthworm crossed the burrow, (2) reached contact with it and then used it, (3) reached it and then veered away, or (4) changed its direction and avoided contact with the burrow. This kind of classification is never unambiguous. For instance, the clear separation between case (2) and case (3) is dependent on the frequency of observation. Moreover case (4) can occur by chance alone. To offset such problems, only changes in direction that occurred less than 2 cm from the existing burrow were considered. This restriction enabled quantification of the “spatial avoidance” of a burrow by summing the frequencies of occurrence of cases (3) and (4). To ensure that the data were not dependent on the observer, two observers computed them independently. Because of the great variability (not all earthworms encountered the same number of burrows), the results of spatial avoidance were presented by summing all the earthworm data treatment by treatment. Data were analysed with a type I ANOVA followed by a Newman-Keuls’ a posteriori test, if normality occurred. Otherwise, for percentages, a Kruskal Wallis’ test was used followed by a least significant difference test (Sprent 1989).

Results

Experiment 1

The cumulative burrow lengths for each species in each terrarium are presented in Fig. 2. For each species the length of burrow generally increased with the number of earthworms in the terrarium. However, there was an obvious difference between species. Burrow lengths for *A. chlorotica* appeared to increase continuously with time, whereas burrow lengths for *A. nocturna* appeared to plateau after 100 h, especially when the number of earthworms was low (Fig. 2).

The connectivity of the network of burrows also appeared to increase with earthworm density in the case of *A. chlorotica*, but stabilised when there were three or more *A. nocturna* earthworms introduced into the terrarium (Fig. 3).

Experiment 2

No earthworm burrowing was observed to follow the cracks made by the opening of the terrarium. It was therefore assumed that this disturbance had no effect on the results. During the first phase of experiment 2, burrow lengths in treatment T1 and T1+ were not significantly different for either species (Fig. 4). This suggests that the protocol was acceptable and that the behaviour of the earthworms was similar in this study to that of Capowiez (2000). In the following, for the sake of simplicity, we represent “is not significantly different from” by “=” and “is significantly different from” by “<” or “>”. *A. nocturna* burrowed less in the treatment T2+ than in all other treatments. In particular, we noted that *A. nocturna* burrowed less when introduced where another *A. nocturna* had been present compared to when introduced with another *A. nocturna* at the same time (T2+ <T2) or when introduced after *A. chlorotica*

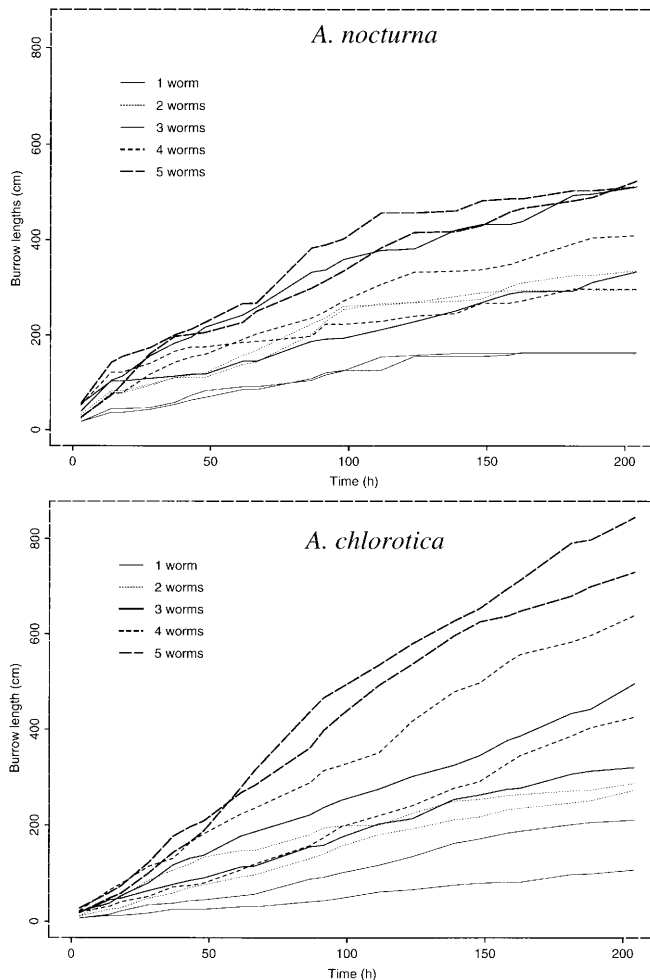


Fig. 2 Cumulative lengths of burrow systems in time as a function of the number of earthworms in terraria. There are two replicates for each treatment

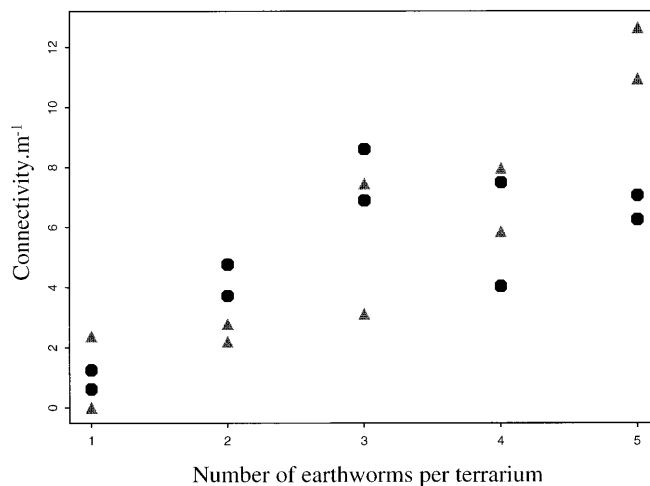
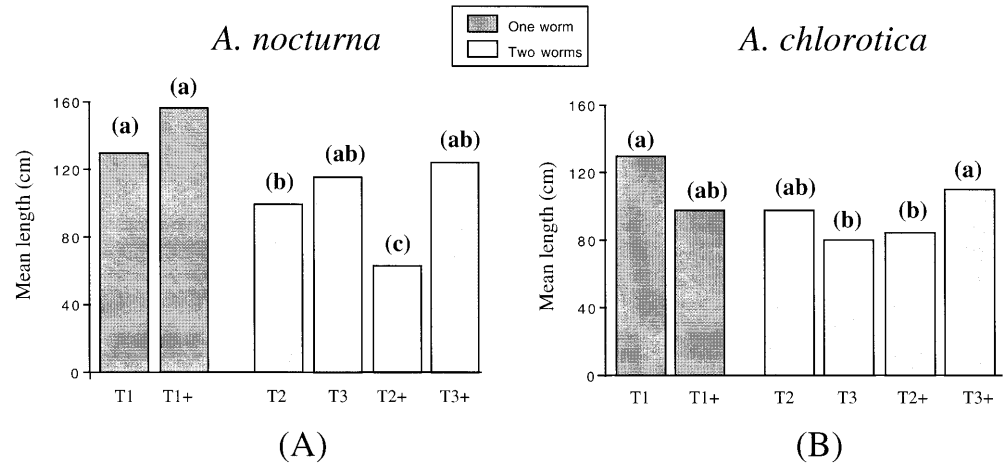


Fig. 3 Connectivity of the burrow systems relative to the number of earthworms inside the terraria (black circles, *Aporrectodea nocturna*; grey triangles, *Allolobophora chlorotica*). There are two replicates for each treatment

Fig. 4 Mean burrow lengths for *A. nocturna* (A) and *A. chlorotica* (B). Bars with different letters indicate statistically significant differences at $P=0.05$. Treatments are the following: alone in a terrarium (T1), with a conspecific earthworm (T2) or with an earthworm of the other species (T3). + Indicates one after another (except for T1+ which is a true replicate of T1)



($T2+ < T3+$; Fig. 4A). *A. chlorotica* burrowed more when introduced after *A. nocturna* compared to when introduced with *A. nocturna* at the same time ($T3+ > T3$). However this earthworm burrowed as much in this case as when alone in the terrarium ($T3+ = T1$; Fig. 4B).

For the analysis of the trajectories, only the results of the second phase are presented here because results for the first phase (T1+) were not significantly different from those obtained by Capowiez (2000), both for the total distance covered and the rate of burrow reuse. *A. nocturna* covered almost the same distance whatever its biotic environment (Fig. 5A) whereas *A. chlorotica* covered a larger distance when introduced after *A. nocturna* ($T3+$; Fig. 5A). *A. nocturna* reused less of its own burrows when introduced after another *A. nocturna* ($T2+$; Fig. 5B). *A. chlorotica* reused more of its own burrows when it followed *A. nocturna* ($T2+ > T2$). In addition, *A. nocturna* reused far more of its own burrows in general than *A. chlorotica* did (except for $T2+$; Fig. 5B). The most striking results were obtained for the distance covered in burrows created by other earthworms. Both *A. nocturna* and *A. chlorotica* covered greater distances in burrows made by other earthworms if the latter had been removed ($T2+ > T2$ and $T3+ > T3$; Fig. 5C). However, it is important to note that the distances for *A. chlorotica* were small (15%) compared with those for *A. nocturna*. When *A. nocturna* was introduced into a terrarium after another *A. nocturna*, up to 50% of the total distance was covered in burrows made by the other earthworm.

When an earthworm approached a burrow its behaviour was affected by: (1) the species of the earthworm that was approaching, (2) the species of the earthworm that made the encountered burrow, and (3) the presence or absence of the earthworm that made the burrows (Table 1). When the two earthworms were present at the same time in the terrarium, *A. chlorotica* frequently avoided the burrows made by *A. nocturna* but rarely behaved the same way when the burrows were made by a conspecific. *A. nocturna* often avoided burrows made by a conspecific earthworm but, in this case, avoidance had the same probability of occurrence as using the encoun-

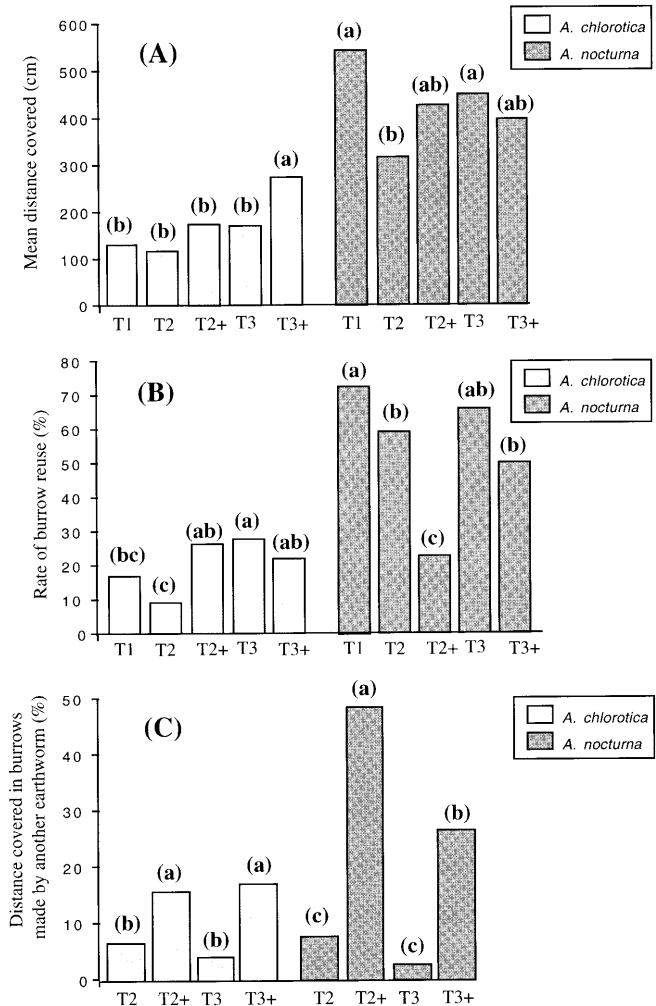


Fig. 5 Mean distance covered (A), mean rate of burrow reuse (B) and mean percentage of the distance that was covered in burrows made by another earthworm (C) for the two earthworm species. Bars with different letters indicate statistically significant differences at $P=0.05$. For abbreviations, see Fig. 4

Table 1 Numbers (and frequencies) of occurrence of three behavioural patterns when an earthworm approached a burrow: in the presence (T2 and T3) or in the absence of the worm that built the burrow (T2+ and T3+). For each row, the trajectory of ten earthworms was analysed. For description of the three patterns, see Fig. 1

Species approaching	Species that built the burrow	Pattern when an earthworm approached a burrow		
		Avoidance	Use	Crossing
In the presence of the worm that built the burrow				
<i>Allolobophora chlorotica</i>	<i>A. chlorotica</i>	10 (18%)	27 (49%)	18 (33%)
	<i>A. nocturna</i>	66 (77%)	11 (13%)	9 (10%)
<i>Aporrectodea nocturna</i>	<i>A. chlorotica</i>	5 (10%)	23 (47%)	21 (43%)
	<i>A. nocturna</i>	26 (43%)	30 (50%)	4 (7%)
In the absence of the worm that built the burrow				
<i>A. chlorotica</i>	<i>A. chlorotica</i>	7 (16%)	30 (70%)	6 (14%)
	<i>A. nocturna</i>	41 (44%)	44 (47%)	8 (8%)
<i>A. nocturna</i>	<i>A. chlorotica</i>	5 (9%)	22 (42%)	26 (49%)
	<i>A. nocturna</i>	3 (5%)	22 (39%)	31 (55%)

tered burrow. In the two other cases of interspecific interactions, avoidance was a rare pattern (10% and 18%). These results changed greatly when the earthworms faced an uninhabited burrow system. Avoidance was less frequently observed: only 44% when *A. chlorotica* encountered a burrow made by *A. nocturna* and only 5% when *A. nocturna* approached a burrow made by a conspecific earthworm. When *A. chlorotica* approached an uninhabited burrow created by *A. nocturna*, it either avoided it or used it with equal probability.

Discussion

2D terraria impose very artificial conditions on earthworms, firstly because of spatial limitation (only two dimensions and a depth limited to 40 cm) and secondly because of the absence of the natural physical gradients for temperature, water and organic matter that influence the behaviour of earthworms (Kretzschmar 1984). In spite of these limitations, this technique has enabled us to make interesting and consistent observations. This illustrates the important plasticity of the behaviour of these animals (Lavelle 1988) and shows that burrowing activity can be considered as a response of earthworms to the constraints of their environment (Kretzschmar 1984).

Differences between *A. chlorotica* and *A. nocturna*

In experiment 1, total burrow length increased as a function of earthworm density. This increase was constant and continuous in the case of *A. chlorotica*, but in the case of *A. nocturna* a plateau was reached which suggested that earthworms of this species decreased their rate of digging of new burrows. Experiment 2 revealed that *A. nocturna* indeed reused previously dug burrows. This observation is in agreement with the postulated burrowing behaviour of each ecological type of earthworm (Lee and Foster 1991; Capowiez 2000).

Interactions between earthworms

The development of the burrow network when earthworm density increased (experiment 1) was different between the two species. There was a constant and continuous increase in connectivity in the case of *A. chlorotica* whereas for *A. nocturna*, there was no further increase in connectivity when density was greater than three earthworms per terrarium. Connectivity of the network describes the complexity and increases as the number of bifurcation points in the network increases. As contacts between earthworms result in higher numbers of triple or quadruple points in the network, we can assume that the number of bifurcation points is related to interactions between earthworms. One may therefore assume that the intensity of contacts decreases for *A. nocturna* when the earthworm density is higher than three per terrarium. This indirect sign of intraspecific interaction for *A. nocturna* is confirmed by our previous study (Capowiez 2000).

Results of experiment 2 revealed that this intraspecific interaction, and the interspecific one between *A. chlorotica* and *A. nocturna*, are dependent on the physical presence of earthworms. Indeed, when earthworms encountered an uninhabited burrow system, they clearly used it more than if the burrow system was inhabited. However, there was an important difference between the two studied species. Even though *A. chlorotica* reused more burrows when they were abandoned, the rate of burrow reuse remained low and the length of burrow made by the earthworm was in contrast high. For *A. nocturna*, the rate of burrow reuse was high (especially when the burrow system was created by another *A. nocturna*) and the rate of burrow creation was low. This suggests that anecic species tend to recolonise an abandoned burrow system whereas endogeic species do not. We assumed that this different behaviour is linked to the ecological significance of burrows for these two ecological types of earthworm. Indeed, it may be advantageous for an anecic species to recolonise an abandoned burrow system since it represents a saving of energy and necessary features (being both a shelter and a way to

reach the surface). This assumption is in agreement with current opinions on the role and trade-offs of burrow systems for subterranean species (Hansell 1993; Eisenberg and Kinlaw 1999; Kinlaw 1999). In contrast, the recolonisation of a burrow system may be less advantageous for an endogeic species. Indeed, the main ecological role of burrows for this ecological type is to provide a pathway towards food patches in the soil. One can imagine that, in this case, using an abandoned burrow system may only guide the earthworm to patches that have been already foraged. Moreover these results suggest also that burrows may be rather "individual structures", made and used by only one earthworm. But the reason for this may not be the same for the two species, it may depend on interactions and possible spatial competition between *A. nocturna* earthworms whereas burrows of *A. chlorotica* are not reused because they may not be advantageous for other *A. chlorotica* earthworms.

A precise analysis of trajectories enabled us to study in more detail the nature of interactions between earthworms. By observing the behaviour of earthworms when they approached a burrow, we noted that *A. chlorotica* avoided burrows made by *A. nocturna*. Results were not so clear concerning the intraspecific interactions for *A. nocturna*, but it was clear that avoidance was reduced when the encountered burrow was uninhabited. It is possible that spatial avoidance of burrows for *A. nocturna* depends on the presence of the earthworm in the vicinity of the crossing point. This assumption could explain why the probability of using an encountered burrow is as high as avoiding it in the *A. nocturna/A. nocturna* interaction.

The question of how do earthworms perceive: (1) the vicinity of a burrow, and (2) the possible presence of an earthworm remains unanswered. Besides, it is important to note that some avoidance patterns were observed before physical contact with the burrow (Fig. 1d). The nature of the signal leading to an avoidance pattern could be linked to: (1) a chemical product (for instance an "all-omone" present in the mucus), (2) the noise made by the earthworm occupying the burrow, or (3) a decrease in the soil density near the burrow wall. The third assumption is not supported by the results of experiment 2. Moreover if the signal is linked to a chemical molecule, its half-life must be short because interactions were not observed in the second phase of our experiment.

In conclusion, 2D terraria are useful tools with which to study earthworm ecology. The consistency of some of our observations suggests that the behaviour of the earthworms was not altered in a drastic way. It remains true, however, that it would be necessary to confirm the observed results in more natural conditions. But for technical reasons, such confirmation would have to be based on indirect observations and therefore would be difficult to achieve. Our results and those of previous work (Capowiez 2000) confirm the postulated burrowing behaviour of the two ecological types of earthworm which is linked to the ecological significance that burrows have for these two ecological types. Anecic species build a true burrow that is often reused and enables them to

reach the surface whereas endogeic species build a network of macropores that represents pathways, used only temporarily, towards food patches. Differences in the shape of the burrow systems cannot be studied by the technique used, as it is obvious that the orientation, the sinuosity and the vertical extension of the burrows are very constrained by the spatial limitations.

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