

## Is earthworms' dispersal facilitated by the ecosystem engineering activities of conspecifics?

Gael Caro, Anick Abourachid, Thibaud Decaens, Lorenza Buono, Jérôme Mathieu

► **To cite this version:**

Gael Caro, Anick Abourachid, Thibaud Decaens, Lorenza Buono, Jérôme Mathieu. Is earthworms' dispersal facilitated by the ecosystem engineering activities of conspecifics?. *Biology and Fertility of Soils*, Springer Verlag, 2012, pp.Online. <10.1007/s00374-012-0694-1>. <bioemco-00712684>

**HAL Id: bioemco-00712684**

**<https://hal-bioemco.ccsd.cnrs.fr/bioemco-00712684>**

Submitted on 27 Jun 2012

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Is earthworms' dispersal facilitated by the ecosystem engineering activities of conspecifics?

2

3 Gaël Caro<sup>1\*</sup>, Anick Abourachid<sup>2</sup>, Thibaud Decaëns<sup>3</sup>, Lorenza Buono<sup>1</sup>, Jérôme Mathieu<sup>1</sup>

4

5 1:UPMC Univ. Paris 06 - Bioemco, 46 rue d'Ulm, 75005, Paris, France

6 2: FRE2696, CNRS, MNHN, Univ. Paris 06, Collège de France, Département Ecologie et

7 Gestion de la Biodiversité, Pavillon d'Anatomie Comparée, CP 55, 57 rue Cuvier, 75231

8 Paris cedex 05, France

9 3: Laboratoire d'Ecologie, EA 1293 ECODIV, FED SCALE, UFR Sciences et Techniques,

10 Université de Rouen, 76821 Mont Saint Aignan cedex, France

11

12 \*Corresponding author:

13 Gaël Caro

14 UMR Bioemco – ENS

15 46 rue d'Ulm

16 75005 Paris

17 France

18

19 E-mail: [gael.c.car@gmail.com](mailto:gael.c.car@gmail.com)

20 Tel : +33 637 97 28 68

21

22

23 Summary

24

25 In this work we documented the influence of earthworm's galleries on their speed of  
26 movements during dispersal events in the soil. We quantified, by using X-rays, the dispersal  
27 behaviour of earthworms in the soil. The observations were conducted in mesocosms in  
28 controlled conditions during 12 hours. Our experiments revealed that during a dispersal  
29 sequence of a batch of individuals of the species *Aporrectodea terrestris* (Savigny 1826): i)  
30 individuals used preferentially existing conspecifics galleries, ii) individual velocity increased  
31 after each dispersal event, and iii) the lag time before each dispersal event did not seem to be  
32 influenced by previous dispersers. Therefore, dispersal seems to be facilitated by  
33 conspecifics' activity, which strongly supports the hypothesis of a feedback between  
34 ecosystem engineers' activity and their dispersal speed.

35

36

37

38 **Keywords:** Cineradiography; X-ray Imagery; Conspecific facilitation; Dispersal behaviour;  
39 Earthworms activity; Ecosystem engineering.

40

## 41 Introduction

42 Earthworms have a profound influence on soil physical and chemical properties (Zhang and  
43 Schrader 1993; Blanchart et al. 1999). Consequently, they play a central role in soil  
44 functioning and in plant growth (Lee 1985; Edwards and Bohlen 1996; Scheu 2003). Their  
45 impacts on soil functioning and soil biota through the engineering of their physical  
46 environment have been the subject of a large number of studies. In contrast, there is little  
47 information available on the consequences of the potential feedback of these activities on  
48 their own life condition, although this is expected to play an important role in earthworm  
49 ecology and activity (Odling-Smee 1995; Mathieu et al. 2010). We now need to grasp these  
50 feedbacks in order to understand the driving factors of earthworm activity and spatial  
51 distribution. Here, we propose to explore the potential feedback between the construction of  
52 galleries and the dispersal speed of earthworms in the soil.

53

54 Dispersal is a central ecological process that allows both the colonization of new  
55 habitats and the exploitation of spatially and temporally variable resources (Ronce 2007).  
56 Active dispersal of animals (opposed to passive dispersal, where individuals are transported  
57 by an external agent) involves three successive behavioural stages: departure from a breeding  
58 site, crossing to a new place, and settlement (Clobert et al. 2001; 2009). A recurrent finding of  
59 evolutionary models is that dispersal rate depends on the balance between the costs and  
60 benefits of dispersal (Bowler and Benton 2005), which are strongly determined by  
61 environmental factors (e.g. habitat quality, habitat fragmentation, patch size, density,  
62 predation) and individual life traits (e.g. age, hormonal levels, (Bonte et al. 2006; Schtickzelle  
63 et al. 2006)). In consequence, strategies that reduce these costs, such as the capacity to use  
64 cues based on conspecifics and/or environmental conditions were selected over evolutionary  
65 times in many groups (Clobert et al. 2009). Such use of cues is not known in earthworms, but

66 previous studies suggest it might exist (Mathieu et al. 2010; Zirbes et al. 2010; 2012). It was  
67 noticed that the products of engineering activities, such as burrows, might be used as cues by  
68 earthworms to evaluate the state of the environment.

69

70         Based on these results, the existence of a feedback between earthworm activities and  
71 their dispersal behaviour was questioned. For instance, Mathieu et al (2010) showed that  
72 earthworm dispersal rate, during the departure stage, could be reduced when individuals were  
73 inoculated in a soil that was pre-used by conspecific individuals - which were no longer  
74 present - showing that earthworms can detect the former activity of conspecifics. Other  
75 studies showed that anecic earthworms use the galleries of conspecific individuals or of other  
76 species, but not specifically for dispersal (Capowiez 2000; Bastardie et al. 2003). These  
77 observations raise the question of the influence of earthworm activities on the speed of their  
78 movement during the second stage of dispersal (crossing stage).

79

80         In this work we specifically investigated the potential feedback between earthworms'  
81 activities and their dispersal rate by addressing three questions: i) do individuals use  
82 preferentially pre-existing conspecific galleries to disperse? ii) does dispersal velocity  
83 increase in a soil where conspecific already dispersed? and iii) is dispersal triggered by the  
84 departure of previous dispersers (like in a collective movement)? To answer these questions  
85 we developed a new technique based on X-rays imagery that allows to take pictures of  
86 earthworms in the soil, and to quantify their behaviour.

87

88 Materials and methods

89

90 We used the species *Aporrectodea terrestris* (Savigny 1826), more commonly called  
91 *Aporrectodea giardi* (Ribaucourt 1901), an anecic species (size: 130-170mm; mean weight:  
92  $3.3 \pm 0.9$  g), which lives in the soil and feeds on surface litter (Bouché 1972, 1977). Adult  
93 earthworms were collected in North of France (49°27'N, 1°4'E) and were kept in suitable soil  
94 (see below) at low density (1.5 individuals per litre of soil), at 15°C during the day and 10°C  
95 at night. All earthworms were used once and were adult during the experiments. To overcome  
96 the problem of transparency of worms to X-rays and to have an accurate tracking point, we  
97 tagged individuals subcutaneously with a rod of lead of 2mm. Tags do not affect the growth  
98 of earthworms (Butt and Lowe 2007). Preliminary tests comparing dispersal behaviour  
99 between tagged and control individuals (not tagged) showed no effect on dispersal response  
100 (unpublished data).

101

102 Two types of soil were used for the experiments: an unsuitable and a suitable soil. The  
103 unsuitable soil consisted in a very sandy soil with low pH (Table 1) collected in an area  
104 deprived of earthworms in the forest of Fontainebleau, France (48°24'N, 2°44'E). The  
105 suitable soil (Table 1) contained more organic matter and clay than the unsuitable soil and  
106 was sampled in a grassland of the IRD research centre of Bondy, France (48°54'E, 2°29'N).  
107 Both soils were air dried, sieved at 2mm and rewetted manually to 25% of humidity (on a  
108 massic basis). The preference of earthworms for the suitable compared to the unsuitable soil  
109 was tested in a previous experiment (Mathieu et al. 2010).

110

111 The experiments were conducted in mesocosms following the procedure developed in  
112 Mathieu et al. (2010). Mesocosms consisted of dispersal corridor of 100 cm long, 20 cm wide  
113 and 20 cm height. They were composed of three equal parts (Figure 1): (1) the inoculation  
114 section, which was filled with unsuitable soil; (2) the intermediate “crossing section”,

115 composed of unsuitable soil, (3) the arrival section composed of suitable soil. All soils were  
116 disposed at density of  $1\pm 0.1 \text{ g.cm}^{-3}$ . This setup triggered dispersal as individuals tend to  
117 disperse from habitats of low quality (Mathieu et al. 2010). It allows reproducing the three  
118 stages of dispersal: departure, crossing and settlement in a suitable site (Clobert et al. 2009).  
119 Earthworms were filmed in the crossing section, which was thinned by 40% to allow  
120 earthworms detection by X-rays. Each experimental unit was closed over by a tarp, to keep  
121 humidity and to prevent worms to escape. The experiment was replicated 5 times with  
122 different experimental units and different individuals each day.

123

124 In each replicate, 10 individuals were inoculated at the same time in the inoculation  
125 section (Figure 1). In order to prevent any contact between individuals during the inoculation,  
126 we ensured that each individual was inoculated at a sufficient distance from the others (10  
127 different locations distant from at least 5cm from each others), and we checked that all  
128 individuals entered in the ground (on average, five minutes).

129

130 The X-ray filming device was composed of a video fluoroscopy machine (Philips  
131 Diagnostic C generator with a Basler A 504 K with digital video camera recorder), which  
132 could not moved. The X-rays were generated at 1.6 mA and 54.0 kV, which allowed seeing  
133 the worms in the soil within a 20 cm radius. After inoculation of the 10 earthworms,  
134 snapshots of the first 20 cm (in length) of the crossing section were taken (Figure 1) every  
135 minute during 12 hours. Dispersal events occurred without any artificial stimulation, which  
136 could have disturbed the dispersal behaviour of earthworms. In consequence we observed at  
137 most 3 passages in each replicate.

138

139

140

141           The X-rays filming device allowed us to take pictures of earthworms and their  
142 galleries in the soil, and to measure their dispersal velocity as well as the lag time between  
143 subsequent passages of individuals within replicates. For each individual, we determined the  
144 entrance and exit time in the observed section (approximately 315 cm<sup>2</sup>), which was centered  
145 on the crossing section. The velocity (V) was determined by the ratio between the travelled  
146 distance and the time required to travel over the corresponding distance. The difference of  
147 time between the moment where a worm left the observed section and the moment the next  
148 conspecific entered was used to calculate the lag time between two crossing events. The ratio  
149  $V_{n+1}/V_n$  between the velocity during the passage n+1 and during the passage n was used to  
150 quantify the relative change in the dispersal velocity. We evaluated the link between the  
151 different components of dispersal behaviour (movement speed and lag time between dispersal  
152 events) and the order of passage or to the presence/absence of gallery with a linear regression  
153 model. All analyses and graphs were performed with the software R (Ihaka and Gentleman  
154 1996).

155

## 156 Results and discussion

157 Despite the low number of dispersal events, we can clearly see that after the first crossing  
158 event, a majority (84% in the second dispersal event and 100% in the third) of the new  
159 dispersers used a gallery already built, rather than burrowing a new one. One individual  
160 started a new gallery but ended up in an existing gallery.

161

162           Our results showed a striking increase of dispersal velocity due to previous  
163 earthworm's activities. We observed a significant increase of dispersal velocity along the  
164 sequence of dispersal events (linear regression  $r^2=0.58$ , p-value=0.002, Figure 2): during the



165 gallery construction phase (see the attached accelerated video file about gallery construction),  
166 the average velocity was  $0.6 \pm 0.3 \text{ cm} \cdot \text{min}^{-1}$ , which was the lowest speed observed. This result  
167 can be related to the low colonization rate of non-inhabited or previously tilled plots usually  
168 observed in the field (Butt et al. 1995; Nuutinen et al. 1997; 2006; Grigoropoulou and Butt  
169 2010; Eijsackers 2011). Our observations of dispersal velocity are well above observations  
170 made in earthworm-free soils (Eijsackers 2011), reporting colonization rate of  $5\text{-}8 \text{ m} \cdot \text{year}^{-1}$  for  
171 *Aporrectodea longa* and  $1.5\text{-}4 \text{ m} \cdot \text{year}^{-1}$  for *Lumbricus terrestris*. however comparison  
172 between our results in experimental device to these field observations must be done with  
173 caution due to the differences in environmental conditions (spatial and temporal  
174 heterogeneity, weather, interspecific interactions), in scale (1 m versus a few km) and in the  
175 length of observation (12 hours versus years). However, our results provide new insights in  
176 the understanding of dispersal mechanisms of earthworms. Indeed, our observations supply  
177 evidences of the capabilities of earthworms to move faster than expected from field  
178 observations.

179

180         Average velocity of second dispersal events was three times faster ( $1.8 \pm 0.7 \text{ cm} \cdot \text{min}^{-1}$ )  
181 than during the first one. This result can be explained by the fact that moving in existing  
182 galleries requires much less efforts than moving in a pristine soil, as no burrowing work is  
183 required (Ehlers 1975; Edwards and Lofty 1980; Hirth et al. 1997). During the third passage,  
184 earthworms exclusively used existing galleries, and the average velocity was then even higher  
185 ( $4.5 \pm 2.8 \text{ cm} \cdot \text{min}^{-1}$ ), than during the first and second dispersal events. This can hardly be  
186 explained by a decrease of burrowing costs, because they are low during the second and third  
187 dispersal events. This suggests that the observed increase in dispersal velocity along dispersal  
188 sequence should be triggered by another mechanism. Non-selective detection of conspecific  
189 activity, like detection of empty spaces in the soil, would result only in the preferred use of

190 conspecifics' galleries. It cannot explain the increase in speed between the second and third  
191 dispersal events. The most parsimonious explanation for this increase in speed is the  
192 retrieving of cues related to conspecifics' activity or presence, such as chemical cue (Schmidt  
193 Jr 1955; Ressler et al. 1968; Jiang et al. 1990). These cues could be non specific by-products  
194 of earthworms' transit in the galleries (like urea, faeces or the results of the interaction  
195 between mucus, microflora and soil on the walls of the galleries (Pan et al. 2010) or less  
196 likely, could be specific molecules like pheromones, like in ants (Dorigo et al. 1996).

197

198         The lag time between two consecutive passages was apparently not influenced by the  
199 presence of galleries or the number of previous departures (p-value = 0.5, Linear Model).

200 Therefore it seems that dispersal was not induced by the existence of galleries or by social  
201 interactions during the departure of conspecifics, in contrast to previous observations  
202 (Zirbes et al. 2010).

203

## 204 Conclusion

205 Our results show that earthworm dispersal movements are much faster in areas previously  
206 engineered (i.e. burrowed) by conspecifics. Individuals selectively follow existing galleries  
207 rather than building new galleries, raising the question of the mechanisms involved in the  
208 localization of the galleries. This shows that earthworms' dispersal in soil is facilitated by  
209 their own activity, highlighting the existence of a feedback between engineering activities and  
210 dispersal velocity. It would be interesting to determine if this feedback is accidental (not  
211 specific, like autogenic engineers (Jones et al. 1994; Jouquet et al. 2006) or intended. Finally,  
212 our findings ask the question about the potential role of dispersal facilitation in community  
213 dynamic of earthworms, and the influences of this facilitation between different earthworm

214 species or ecological categories, especially regarding colonization pattern of new habitats  
215 (Uvarov 2009; Eijsackers 2011).

216

## 217 5. Acknowledgement

218 This work was funded by the French National Research Agency (ANR) as a part of the  
219 project EDISP no. ANR-08-JCJC-0023. We would like to thank the Centre IRD Ile de France  
220 and specifically Corinne Rouland-Lefèvre for access to the climatic room and to the park. A  
221 great thank to Sébastien Barot, Manuel Blouin, Lise Dupont and Hélène Dudeck for their  
222 help. Gaël Caro was supported by a French grant Ph.D. from the Ministère de la Recherche.

223

224

225

226

227

228

229

230 Bibliography

231

232 Bastardie F, Capowiez Y, de Dreuzy JR, Cluzeau D (2003) X-ray tomographic and hydraulic  
233 characterization of burrowing by three earthworm species in repacked soil cores. Appl  
234 Soil Ecol 24:3-16.

235 Blanchart E, Albrecht A, Alegre J, Duboisset A, Gilot C, Pashanasi B, Lavelle P, Brussaard L  
236 (1999) Effects of earthworms on soil structure and physical properties. Earthworm  
237 manag in trop agro. Wallingford.

238 Bonte D, Borre JV, Lens L, Jean-Pierre M (2006) Geographical variation in wolf spider  
239 dispersal behaviour is related to landscape structure. Anim Behav 72:655-662.

240 Bouché MB (1972) Lombriciens de France, écologie et systématiques. INRA, Paris.

241 Bouché MB (1977) Strategies lombriciennes. Ecol Bull:122-132.

242 Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies:  
243 relating individual behaviour to spatial dynamics. Biol Rev 80:205-225.

244 Butt KR, Frederickson J, Morris RM (1995) An earthworm cultivation and soil inoculation  
245 technique for land restoration. Ecol Eng 4:1-9.

246 Butt KR, Lowe CN (2007) A viable technique for tagging earthworms using visible implant  
247 elastomer. Appl Soil Ecol 35:454-457.

248 Capowiez Y (2000) Differences in burrowing behaviour and spatial interaction between the  
249 two earthworm species *Aporrectodea nocturna* and *Allolobophora chlorotica*. Biol  
250 Fertil Soils 30:341-346.

- 251 Clobert J, Danchin E, Dhondt AA, J.D. N (2001) Dispersal. Oxford University press.
- 252 Clobert J, Le Galliard JF, Cote J, Meylan S, Massot M (2009) Informed dispersal,  
253 heterogeneity in animal dispersal syndromes and the dynamics of spatially structured  
254 populations. *Ecol Lett* 12:197-209.
- 255 Dorigo M, Maniezzo V, Colorni A (1996) Ant system: Optimization by a colony of  
256 cooperating agents. *IEEE Trans on Sys Man and Cyber Part B-Cyber* 26:29-41.
- 257 Edwards CA, Bohlen PJ (1996) *Biology and Ecology of earthworms*. Chapman and Hall,  
258 London.
- 259 Edwards CA, Lofty JR (1980) Effects of earthworm inoculation upon the root growth of  
260 direct drilled cereals. *J Appl Ecol* 17:533-543.
- 261 Ehlers W (1975) Observations on earthworm channels and infiltration on tilled and untilled  
262 loess soil. *Soil Science* 119:242-249.
- 263 Eijsackers H (2011) Earthworms as colonizers of natural and cultivated soil environments.  
264 *Appl Soil Ecol* 50:1-13.
- 265 Grigoropoulou N, Butt KR (2010) Field investigations of *Lumbricus terrestris* spatial  
266 distribution and dispersal through monitoring of manipulated, enclosed plots. *Soil Biol*  
267 *Biochem* 42:40-47.
- 268 Hirth JR, McKenzie BM, Tisdall JM (1997) Do the roots of perennial ryegrass elongate to  
269 biopores filled with the casts of endogeic earthworms? *Soil Biol Biochem* 29:529-531.
- 270 Ihaka R, Gentleman R (1996) R: A language for data analysis and graphics. *J Comput Graph*  
271 *Stat* 5:299-314.

- 272 Jiang XC, Inouchi J, Wang D, Halpern M (1990) Purification and characterization of a  
273 chemoattractant from electric shock-induced earthworm secretion, its receptor  
274 binding, and signal transduction through the vomeronasal system of garter snakes. J  
275 Biol Chem 265:8736-8744.
- 276 Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373-  
277 386.
- 278 Jouquet P, Dauber J, Lagerlöf J, Lavelle P, Lepage M (2006) Soil invertebrates as ecosystem  
279 engineers: Intended and accidental effects on soil and feedback loops. Appl Soil Ecol  
280 32:153-164.
- 281 Lee KE (1985) Earthworms: Their ecology and relationship with soil and land use. Academic  
282 Press, Sydney.
- 283 Mathieu J, Barot S, Blouin M, Caro G, Decaëns T, Dubs F, Dupont L, Jouquet P, Nai P  
284 (2010) Habitat quality, conspecific density, and habitat pre-use affect the dispersal  
285 behaviour of two earthworm species, *Aporrectodea icterica* and *Dendrobaena veneta*,  
286 in a mesocosm experiment. Soil Biol Biochem 42:203-209.
- 287 Nuutinen V, Nieminen M, Butt KR (2006) Introducing deep burrowing earthworms  
288 (*Lumbricus terrestris* L.) into arable heavy clay under boreal conditions. Eur J Soil  
289 Biol 42:S269-S274.
- 290 Nuutinen V, Pitkänen J, Kuusela E, Widbom T, Lohilahti H (1997) Spatial variation of an  
291 earthworm community related to soil properties and yield in a grass-clover field. Appl  
292 Soil Ecol 8:85-94.

- 293 Odling-Smee FJ (1995) Niche construction, genetic evolution and cultural change. Behav  
294 Proc 35:195-205.
- 295 Pan X, Song W, Zhang D (2010) Earthworms (*Eisenia foetida*, Savigny) mucus as  
296 complexing ligand for imidacloprid. Biol Fertil Soils 46:845-850.
- 297 Ressler RH, Cialdini RB, Ghoca ML, Kleist SM (1968) Alarm pheromone in the earthworm  
298 *Lumbricus terrestris*. Science 161:597-599.
- 299 Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal  
300 evolution. Annu Rev Ecol, Evol Syst 38:231-253.
- 301 Scheu S (2003) Effects of earthworms on plant growth: patterns and perspectives: The 7th  
302 international symposium on earthworm ecology · Cardiff · Wales · 2002.  
303 Pedobiologia 47:846-856.
- 304 Schmidt Jr H (1955) Behavior of two species of worms in the same maze. Science 121:341-  
305 342.
- 306 Schtickzelle N, Mennechez G, Baguette M (2006) Dispersal depression with habitat  
307 fragmentation in the bog fritillary butterfly. Ecology 87:1057-1065.
- 308 Uvarov AV (2009) Inter- and intraspecific interactions in lumbricid earthworms: Their role  
309 for earthworm performance and ecosystem functioning. Pedobiologia 53:1-27.
- 310 Zhang H, Schrader S (1993) Earthworms effects on selected physical and chemical-properties  
311 of soil aggregates. Biol Fertil Soils 15:229-234.

312 Zirbes L, Brostaux Y, Mescher M, Jason M, Haubruge E, Deneubourg J-L (2012) Self-  
313 Assemblage and Quorum in the Earthworm *Eisenia fetida* (Oligochaete,  
314 Lumbricidae). PLoS One 7:e32564.

315 Zirbes L, Deneubourg JL, Brostaux Y, Haubruge E (2010) A new case of consensual  
316 decision: collective movement in earthworms. Ethology 116:546-553.

317

318

319

320

321

322



323 Table

324

325 Table 1: Selected properties of the used soils in the experiments.

326

Soil Properties (Unit)	Unsuitable	
	Soil	Suitable Soil
Clay (%)	4.7	15.7
Silt (%)	18.5	13.4
Sand (%)	76.8	70.9
Organic C (g kg <sup>-1</sup> )	8.5	28.1
Total N (g kg <sup>-1</sup> )	0.33	2.61
C:N	25.8	10.8
Organic Matter (g kg <sup>-1</sup> )	14.6	48.6
pH	3.8	7.5
CEC (Metson) (cmol kg <sup>-1</sup> )	2.9	11.7

327

328

329

330

331

332

333

334

335

336

337 Figure captions

338

339 Figure 1: Experimental design of the study (100 cm long; 20 cm wide; 20 cm height, 8cm  
340 height for the thinned section); Grey area = unsuitable soil; White area = suitable soil. The  
341 clearest circle represents the observed area. Each triangle represents an inoculation point,  
342 where a single earthworm was introduced. Arrows represent the section observed by X-rays,  
343 which have been captured by a camera. A dashed arrow symbolizes the direction of  
344 movement.

345

346 Figure 2: Individuals' dispersal velocity ( $\text{cm}\cdot\text{min}^{-1}$ ) according to their rank of passage during  
347 the dispersal sequence. A line links earthworms belonging to the same mesocosm. The dashed  
348 line represents the linear regression.

349

350

351

352

353

354

355

356

357

358

359

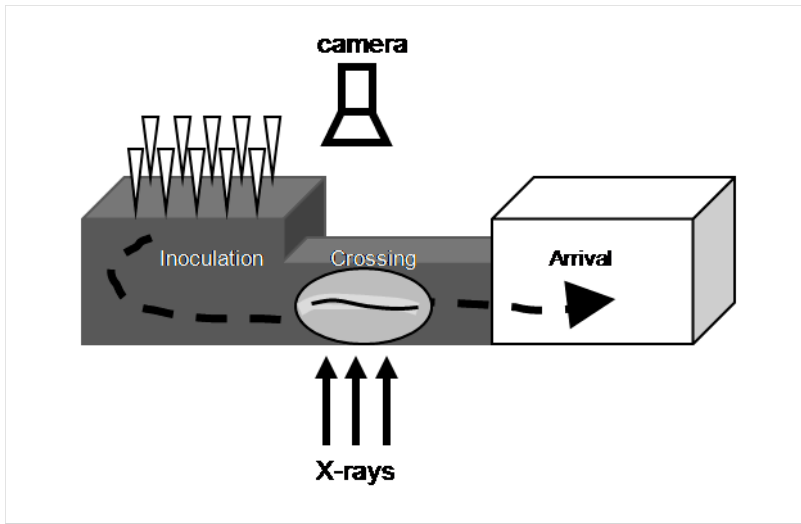
360

361

362 Figures

363

364 Figure 1



365

366

367

368

369

370

371

372

373

374

375

376

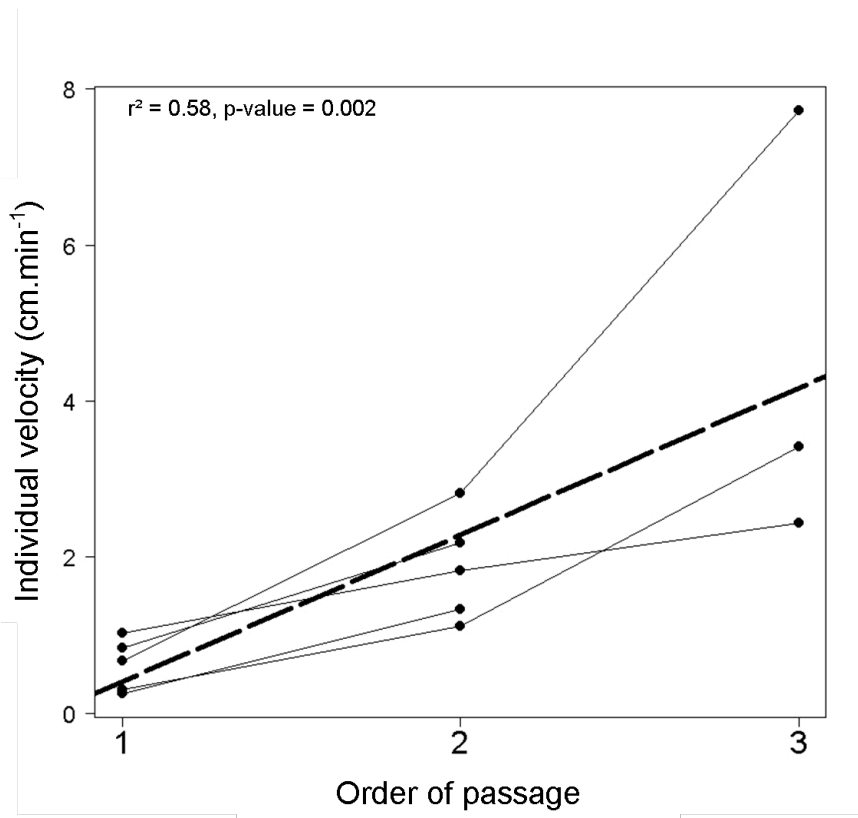
377

378

379

380

381 Figure 2



382

383

384

385

386

387

388

389

390