

Population dynamics and adaptive strategies of Martiodrilus carimaguensis (Oligochaeta, Glossoscolecidae), a native species from the well-drained savannas of Colombia.

Juan J. Jiménez^{†*}, A.G. Moreno[†], P. Lavelle[‡] & T. Decaëns[¶]

[†] Departamento Biología Animal I (Zoología). Facultad de Biología. Universidad Complutense de Madrid. 28040. Madrid. SPAIN.

[‡] Laboratoire d'Ecologie et Biologie des Sols Tropicaux. ORSTOM. 72, route d'Aulnay. 93143. Bondy Cx. FRANCE.

[¶] CIAT-Carimagua. AA 6713. Cali. COLOMBIA.

* Corresponding author

Complete correspondence address:

Juan J. Jiménez

Departamento de Biología Animal I (Zoología). Facultad de Biología. Universidad Complutense. 28040. Madrid. ESPAÑA.

Phone Number: (34) 1 394 49 55

Fax Number: (34) 1 394 49 47

E-mail: jjimenez@eucmax.sim.ucm.es

1 **Abstract**

2
3 Martiodrilus carimaguensis (Oligochaeta, Glossoscolecidae) is a large, dorsally
4 dark-grey anecic native earthworm species that was found in natural and disturbed
5 savannas in the Oxisols of the Colombian Llanos. The population dynamics of this
6 species were studied in a native savanna and in a 17-yr old grazed grass-legume pasture
7 from April 1994 to September 1995 (except June 1994). High values of density and
8 biomass were obtained in the latter system compared to the former. The difference in
9 population was reflected in the number of fresh casts deposited on the soil surface.
10 Monthly deposition in the improved pasture system was 38.4×10^3 fresh casts. ha⁻¹,
11 eleven times greater than that in the native savanna. A strong relationship was found
12 between numbers of M. carimaguensis and numbers of fresh surface casts. Different
13 patterns of adaptation to the dry season were observed for adults and juveniles. Adults
14 are active for 8 months whereas juveniles enter diapause 3-4 months earlier. Vertical
15 distribution of earthworm populations also shows marked seasonal changes.

16
17 Key words: Population dynamics, Adaptive strategies, Martiodrilus carimaguensis,
18 Oligochaeta, Glossoscolecidae, Savannas.

19 20 21 **1. Introduction**

22
23 There is a lack of information concerning the biology of tropical earthworms
24 (Dash and Patra, 1977; Lavelle, 1978). Of the few species which have been fully studied
25 in both temperate tropical ecosystems, most have been introduced by man, e. g.,
26 Pontoscolex corethrurus Müller, 1856 and Dichogaster bolaui (Michaelson, 1891). In
27 most disturbed areas local earthworm communities disappear, being displaced by
28 introduced species (Lavelle and Pashanasi, 1989; Lavelle et al., 1987; Bohlen et al.,
29 1995).

30 However, less attention has been paid to the role of those native earthworm
31 species that are well-adapted to perturbation of natural ecosystems. In Carimagua, man-
32 made pastures derived from natural savannas retained the in-original earthworm
33 biodiversity and their biomass increased from 4.8 g fresh weight m⁻² in the native

34 savanna up to 51.1 g fresh weight m⁻² (Decaëns et al, 1994). One species, Martiodrilus
35 carimaguensis (Jiménez and Moreno, in press) has been greatly favoured by this land
36 practice, increasing significantly in abundance and biomass (P<0.001).

37 M. carimaguensis. is a large anecic earthworm species belonging to the family
38 Glossoscolecidae, with an average adult size of 9.3 mm in diameter and 194.3 mm in
39 length and a fresh weight of 11.2 g (in 4% formaldehyde) (n = 29). Its body colour is
40 dark-grey on the dorsal side and light-grey on its ventral side (Jiménez y Moreno, in
41 press).

42

43

44 **2. Material and methods**

45

46 *2.1. Study site*

47

48 The study area is located at the CIAT-CORPOICA (Centro Internacional de
49 Agricultura Tropical and Corporación Colombiana de Investigación Agropecuaria
50 agreement) Carimagua Research Station, in the well-drained isohyperthermic savannas
51 of the Eastern Plains of Colombia (4° 37' N and 71° 19' W and 175 meters altitude).
52 Average annual rainfall and temperature are about 2280 mm and 26°C respectively, with
53 a dry season from December to March. Soils are of two types: predominant low-fertility
54 Oxisols in the upland (“altos”) and Ultisols in the low-lying (“bajos”) savannas. The
55 former are characterized by their acidity (pH (H₂O) 4.5), a high Al saturation (> 90%)
56 and low values of exchangeable Ca, Mg and K. Chemical factors that contribute to acid-
57 soil infertility and subsequent effects on plant growth are complex and include Al
58 toxicity, low content of available P and low rates of N mineralization (Rao et al., 1993).

59 Two different and contrasting systems were evaluated: A native savanna (NS)
60 without management, in which the predominant plant species are Andropogon bicornis,
61 Gymnopogon sp., Panicum spp., Trachypogon spp. and Imperata sp., and a 17-yr old
62 grazed improved pasture (IP) comprising an exotic african grass, Brachiaria decumbens
63 cv. Basilisk, and a tropical forage herbaceous legume species, Pueraria phaseoloides
64 CIAT 9900 (“kudzu”).

65

66 *2.2. Earthworm sampling*

67

68 One 90x90 m plot was selected in each system and divided into 10x10 m regular
69 quadrats. Earthworms were hand-sorted monthly from five 1x1x0.5 m soil monoliths
70 (after Lavelle, 1978) extracted at random within five randomly-chosen quadrats in each
71 plot. The sampling depth was varied seasonally to take into account the vertical
72 migration of this species. The sample was split into 10 cm layers and earthworms
73 collected from each layer washed in water and fixed in 4% formalin. They were
74 separated in the laboratory into adults (with clitellum and associated glands) and
75 juveniles (lacking clitellum and glands), counted and weighed. The cocoons obtained
76 were also counted and weighed.

77

78 2.3. *Surface cast deposition*

79

80 Part of the soil ingested by earthworms is ejected on the soil surface. As an
81 anecic species M. carimaguensis has the ability to deposit large tower-like casts, up to
82 15 cm in height, on the soil surface. In both systems these surface casts, which are easily
83 recognised, from other depositions were counted in two monthly randomly-chosen 1m²
84 samples and classified into two broad categories, fresh and dry. Casts were oven-dried at
85 60 °C for 72 hours and weighed.

86

87

88 3. Results

89

90 3.1. *Density and biomass*

91

92 Monthly fluctuations in the abundance and biomass of M. carimaguensis are
93 shown in Figure 1. Average population of 17.9 m⁻² and 0.2 m⁻² were observed in the
94 improved pasture and native savanna, respectively (Table 1).

95

96 In the natural savanna values of density ranged from 0 in November 94 to 0.6 m⁻²
97 in September 95. Under the improved pasture density ranged from 11 m⁻² (September
98 94) to 23.2 m⁻² (May 95). The highest values of density were recorded at the beginning
99 of the rainy season and the increase in numbers in October 94 was due to the hatching of
new juveniles.

100 Earthworm biomass ranged from 0.24 g m⁻² (March 94) to 8.76 g m⁻² (September
101 95) in the native savanna. In the improved pasture values of biomass ranged from 26.5 g
102 m⁻² (January 95) to 94.8 g m⁻² (May 94). A significant correlation was found between
103 monthly values of biomass and precipitation in the improved pasture ($r = 0.821$; $P <$
104 0.01), but not in the native savanna. The highest values of biomass appeared at the onset
105 of the wet season when all the population was active. In July-August there was a
106 reduction in biomass due to the inactivation of juveniles. At the end of the rainy season
107 values of biomass declined 50% as adults went deeper into the soil to become inactive
108 after emptying their guts.

109 In the native savanna, M. carimaguensis comprised up the 15.1% of the total
110 earthworm biomass whereas in the improved pasture this value rose to 85.1%. The 84.9
111 % of earthworm biomass in native savanna and the 14.9% in improved pasture was
112 apported by other native species found along with M. carimaguensis, four endogeics and
113 one epigeic.

114 No relationship was found between average monthly numbers of individuals and
115 soil moisture, but significant correlations were observed between soil moisture and biomass
116 ($r = 0.651$; $P < 0.01$) and the percentage activity of the overall population ($r = 0.673$; $P <$
117 0.01).

118

119 3.2. *Surface cast production*

120

121 On average, fresh cast production in the improved pasture was eleven times
122 greater than in the native savanna (Table 2). The total dry weight of earthworm casts
123 collected during one year in the native savanna was 31.3 Mg ha⁻¹, whereas in the
124 improved pasture it was 37.7 Mg ha⁻¹.

125 Both average monthly fresh cast and total cast production were significantly
126 higher ($P < 0.01$, t-test) in improved pasture than in native savanna, reflecting the
127 differences in abundance of M. carimaguensis (Figure 2). Fresh cast production declined
128 during July 94 and July 95 when all the juveniles had already descended some tens of
129 centimetres to enter diapause and only adults remained active. A positive correlation
130 between numbers of fresh casts and the density of individuals in the first 10 cm was
131 observed in the improved pasture ($r = 0.907$; $P < 0.01$).

132

133 3.3. *Vertical distribution*

134

135 Data on the vertical distribution of M. carimaguensis are only available for the
136 improved pasture, since abundance in the native savanna was too low to establish
137 patterns of vertical distribution throughout the soil profile. M. carimaguensis occurred at
138 an average depth of 30.1 cm, with a minimum in May (13.5 cm) and a maximum during
139 the summer (47.6 cm). More than 50% of the total population was located in the top 30
140 cm and in the wet season more than 80% of individuals were close to the surface where
141 the organic matter content is higher. Cocoons were layed at a depth of 20 to 50 cm. In
142 Figure 3 the vertical distribution of the overall population in some periods is shown.

143

144 3.4. *Adaptation to the dry season*

145

146 M. carimaguensis showed interesting behaviour, with a true diapause, although
147 different patterns were found between adults and juveniles. The latter were only active for
148 four months, from April to July, so they entered diapause much earlier than adults which
149 remained active until December (for 8 months). Inactivation occurred after the individuals
150 went down to 60-110 cm depth. Each individual built an aestivating chamber at the end of
151 its semi-permanent burrow in which it coiled itself up, after emptying its gut, and ceased
152 activity until the onset of the wet season. The end of the burrow was usually sealed with
153 several septae to avoid loss of tegumental moisture, which is vital to support a minimal rate
154 of respiration. The degree of activity during the whole study period is shown in Figure 4. In
155 the second year of study there seemed to be a delay in resumption of activity as the rainfall
156 in April 95 (155.7 mm) was very similar to that in March 94 and approximately 60% of the
157 population was active. By May 95 the entire population was active again.

158

159 3.5. *Reproductive strategy*

160

161 In August, after juveniles became inactive, adults started the reproductive period
162 and one month later the first cocoons were deposited at 20-50 cm depth. Cocoons collected
163 in the field, nearly always from pasture sites and incubated under laboratory conditions
164 were found to have a maximum incubation period of 48 days. The incubation time was

165 long compared to other tropical earthworms since they are exposed to minimal
166 environmental fluctuations at that depth.

167 The cocoons were yellowish, becoming slightly brown just before hatching, oval in
168 shape (25x15 mm) and weighing on average 1804 mg. Two individuals (1.91 ± 0.3 ; $n = 46$),
169 with an average weight of 760 mg, hatched out from each cocoon and rapidly burrowed
170 down to enter diapause.

171 The fecundity (number of cocoons per adult per year) was somewhat low (c.
172 0.49) though the cocoon weight: adult weight ratio was 0.19, the highest ever recorded
173 in temperate or tropical ecosystems . A single cocoon peak was observed in August 94
174 just after juveniles descended into the deeper soil layers and adults started the
175 reproductive period (Figure 5).

176

177

178 **4. Discussion**

179

180 To date no studies have considered the population dynamics of anecic species in
181 tropical soils and their response to changes in natural environments. Most references
182 deal with exotic species that have been introduced by man, e.g. P. corethrurus (Lavelle
183 et al., 1987) or D. bolau (Senapati, 1980; Sahu et al., 1988).

184 M. carimaguensis is an endemic species in the well-drained savannas of
185 Carimagua. It may be considered as an anecic species, as defined by Bouché (1972) and
186 Lavelle (1981), being of large size, dorsally pigmented, and litter feeding and surface-
187 casting through opened semi-permanent burrows. After heavy rains they are normally
188 observed on the soil surface.

189 There is little information on the population dynamics of anecic species in other
190 comparable sites. Data from Lavelle (1978) in the savannas of Lamto, Ivory Coast, show
191 that the anecic species Millsonia lamtoiana (Omodeo et Vaillaud, 1967) ranged in
192 density from 0.02 ind. m^{-2} to 1.43 ind. m^{-2} and from 0.01 g. fresh weight. m^{-2} to 8.43 g.
193 fresh weight. m^{-2} in biomass, very similar values to those obtained in the present study.

194 Soil moisture is the most important of all environmental variables for
195 earthworms in tropical soils (Lavelle, 1983). Garnsey (1994) also reported a correlation
196 between earthworm biomass and soil moisture in the Midlands of Tasmania. A
197 relationship between soil moisture content at different depths and numbers of

198 individuals must be sought since no relationship was obtained between average monthly
199 abundances and soil moisture.

200 M. carimaguensis has a patchy distribution pattern with high density spots
201 alternating with low density areas (Jiménez, unpubl.). There is strong evidence for
202 vertical migration of this species during unfavourable conditions, with the population as
203 a whole reaching 80 cm depth before the onset of the summer. Both juveniles and adults
204 obtain the enough energy for their metabolic processes; the former to enter a facultative
205 diapause mainly in August and the latter to initiate the reproductive period followed by
206 cocoon deposition. The ability to aestivate before the onset of summer and to construct
207 deep semi-permanent burrows explain why the population is less affected by drought
208 and is able to maintain its density during the dry season.

209 Earthworm aestivation has been observed throughout in temperate regions
210 (Evans and Guild, 1948; Nordstrom, 1975; Anderson, 1980), in Africa (Madge, 1969)
211 and in Australia (Garnsey, 1994), but this is the first time it has been studied in
212 SouthAmerican glossoscolecid earthworms.

213 Soil surface casting activities have been reported by Madge (1969) and Lavelle
214 (1978), although there are few reports dealing with cast production by earthworms in
215 agroecosystems (Bhadoria and Ramakrishnan, 1989). Watanabe and Ruaysoongnern
216 (1984) reported 24.5 Mg ha⁻¹. year⁻¹ of cast material, less than obtained here in both
217 systems, and 15.7 to 40 Mg ha⁻¹. year⁻¹ in 5 and 15-year old fallows, respectively
218 (Bhadoria and Ramakrishnan, 1989).

219 Despite no data on carbon and nutrient dynamics are presented here, the anecic
220 effect of this earthworm must be taken into account since it is of the utmost importance
221 in regard to cycling of carbon and nutrients. Grass-legume pastures need the nitrogen
222 input provided by the legume. When the N content is high the C/N ratio is reduced and
223 in soils with low C/N earthworm densities decline (Kale and Krishnamoorthy, 1981).
224 But pastures at Carimagua are also introducing C into the soil (Fisher et al., 1994) so the
225 C/N ratio becomes higher and this may, subsequently, be related to an earthworm
226 increase. The C/N ratio in the savannas is 25, three times greater than in temperate soils,
227 and the C/N ratios for tropical pastures with and without legumes are 30 and 35
228 respectively (Fisher, pers. comm.). Further studies must be focused on the role of
229 earthworm activities in carbon and nutrient cycling.

230 It has been also observed that grass and legume roots colonize the casts that are
231 in the burrows, and that a small Ocnerodrilidae oligohumic earthworm feeds upon these
232 casts (Jiménez et al., 1994). To date no data are available on the interrelations among
233 earthworms, casts in burrows and roots located very close to these casts in the soil
234 profile. We consider this task of great relevance if M. carimaguensis is proved to be, in
235 part, responsible on the growth of these roots, and so contributing to incorporate Carbon
236 into the soil.

237 Grasslands are known to support high earthworm populations and biomass (Lee,
238 1985; Syers and Springett, 1983). Litter composition is the first factor determining these
239 high values (Cuendet, 1984; Mishra and Ramakrishnan, 1988). Differences in the litter
240 quality and a great amount of cow dung, which is rapidly incorporated into the soil by
241 this species and dung beetles, may also be factors responsible for the enhancement of M.
242 carimaguensis activity in improved pastures.

243 Despite the low density of this species and the low number of fresh casts in the
244 native savanna, the weight of total casts collected during one year does not differ much
245 from that in improved pasture. Perhaps in the latter system the high activity of
246 earthworms leads to a reingestion of their own casts, after a microbial incubation has
247 occurred (Swift et al., 1979).

248 Finally, improved pastures have greatly enhanced soil micro- and
249 macrobiological activity which in turn improves chemical and physical properties, i.e.,
250 soil quality parameters. Recent studies at Carimagua are considering the possibilities of
251 management in agricultural plots where zones of great earthworm activity, i. e.
252 improved pastures, are placed adjacent to annual crops in order to facilitate the spread of
253 populations and colonization of those systems. Since Lavelle et al. (1994) have provided
254 a better understanding of local soil faunal activities and the potential use of native
255 species in tropical agroecosystems, we suggest that further studies should take into
256 account the influence of such activities on both physical and chemical soil properties.

257

258

259 **5. Acknowledgements**

260

261 This work is included in a research grant from the Macrofauna project (STD3 EC
262 Program) to which we are greatly indebted.

263 We also wish to thank CIAT (International Center for Tropical Agriculture),
264 especially the Tropical Lowlands Program for human and technical support, and for
265 scientific discussions on this study. Our deepest gratitude is expressed to all the people at
266 Carimagua station, and especially to field workers, for their invaluable help.

267

268

269 **6. References**

270

271 Anderson, C. 1980. The influence of climatic conditions on activity and vertical
272 distribution of earthworms in a Danish arable soil. *Kongelige Veterinaer -og*
273 *Landbohojskole. Arsskrift*, 57-68.

274 Bhadauria, T. and Ramakrishnan, P. S. 1989. Earthworm population dynamics and
275 contribution to nutrient cycling during cropping and fallow phases of shifting
276 agriculture (Jhum) in North-east India. *J. Appl. Ecol.*, 26: 505-520.

277 Bohlen, P. J., Edwards, W. M. and Edwards, C. A. 1995. Earthworm community
278 structure and diversity in experimental agricultural watersheds in Northeastern
279 Ohio. *Plant and Soil*, 170: 233-239.

280 Bouché, M. 1972. *Lombriciens de France. Ecologie et Systematique*. I.N.R.A. Paris. 671
281 p.

282 Cuendet, G. 1984. A comparative study of the earthworm population of four different
283 woodland types in Wytham woods, Oxford. *Pedobiologia*, 26: 421-439.

284 Dash, M. C. and Patra, U. C. 1977. Density, biomass and energy budget of a tropical
285 earthworm population from a grassland site in Orissa, India. *Rev Ecol. Biol. Sol.*,
286 14: 461-471.

287 Decaëns, T., Lavelle, P., Jiménez Jaén, J. J., Escobar, G. & Rippstein, G. 1994. Impact
288 of land management on soil macrofauna in the Oriental Llanos of Colombia. *Eur.*
289 *J. Soil Biol.*, 30 (4): 157-168.

290 Evans, A. C. and Guild, W. J. 1948. Studies on the relationships between earthworms
291 and soil fertility. IV. On the life cycles of some british Lumbricidae. *Ann. Appl.*
292 *Bio.*, 35 (4): 473-493.

293 Fisher, M.J., Rao, I.M., Ayarza, M.A., Lascano, C.E., Sanz, J.I., Thomas, R.J. and Vera,
294 R.R.. 1994. Carbon storage by introduced deep-rooted grasses in the South
295 American savannas. *Nature*, 371: 236-28.

- 296 Garnsey, R. B. 1994. Seasonal activity and aestivation of Lumbricid earthworms in the
297 Midlands of Tasmania. *Aust. J. Soil Res.*, 32: 1355-1367.
- 298 Jiménez, J. J., Decaëns, T., Moreno, A. G., Rossi, J-P. and Lavelle, P. 1994. Dynamics
299 and short-term effects of earthworms in natural and managed savannas of the
300 Eastern Plains of Colombia. In: P. Lavelle (Editor). *Conservation of soil fertility*
301 *in low-input agricultural systems of the humid tropics by manipulating*
302 *earthworm communities (Macrofauna Project, STD2 EC)*. pp. 52-61.
- 303 Jiménez, J. J. y Moreno, A. G. Martiodrilus carimaguensis sp. nov. (Oligochaeta,
304 Glossoscolecidae), una nueva especie de lombriz de tierra para Colombia.
305 *Megadrilogica*, (in press).
- 306 Kale, R. D. and Krishnamoorthy, R. V. 1981. What affects the abundance and diversity
307 of earthworms in soils?. *Proc. Indian Acad. Sci.*, 90 (1): 117-121.
- 308 Lavelle, P. 1978. Les vers de terre de la savane de Lamto (Côte d'Ivoire): peuplements,
309 populations et fonctions dans l'écosystème. Thèse de Doctorat, Paris VI. Publ.
310 *Lab. Zool. E.N.S.*, 12, 301 p.
- 311 Lavelle, P. 1981. Stratégies de reproduction chez les vers de terre. *Acta Oecol.*, 2 (2):
312 117-133.
- 313 Lavelle, P. 1983. The soil fauna of tropical savannas. II. The earthworms. In: F
314 Bourlière (Ed.), *Tropical Savannas*. Elsevier Scientific Publishing Company, The
315 Netherlands. pp. 485-504.
- 316 Lavelle, P., Barois, I., Cruz, I., Fragoso, C., Hernández, A., Pineda, A. and Rangel, P.
317 1987. Adaptive strategies of P. corethrurus (Glossoscolecidae, Oligochaeta), a
318 peregrine geophagous earthworm of the humid tropics. *Biol. Fertil. Soils*, 5: 188-
319 194.
- 320 Lavelle, P., Dangerfield, M., Fragoso, C., Eschenbrenner, V., López-Hernández, D.,
321 Pashanasi, B. and Brussard, L. 1994. The relationship between soil macrofauna
322 and tropical soil fertility. In: P. L. Woomer and M. J. Swift (Editors). *The*
323 *Biological Management of Tropical Soil Fertility*. John Wiley & Sons, U. K. pp
324 137-169.
- 325 Lavelle, P. and Pashanasi, B. 1989. Soil macrofauna and land management in Peruvian
326 Amazonia (Yurimaguas, Loreto). *Pedobiologia*, 33: 283-291.
- 327 Lee, K. 1985. *Earthworms: Their Ecology and Relationships with Soils and Land Use*.
328 Academic, New York. 411 p.

- 329 Madge, D. S. 1969. Field and laboratory studies on the activities of two species of
330 tropical earthworms. *Pedobiologia*, 9: 188-214.
- 331 Mishra, K. C. and Ramakrishnan, P. S. 1988. Earthworm population dynamics in
332 different jhum fallows developed after slash and burn agriculture in north-eastern
333 India. *Proc. Indian Acad. Sci.*, 97 (4): 309-318.
- 334 Nordström, S. 1975. Seasonal activity of lumbricids in Southern Sweden. *Oikos*, 26:
335 307-315.
- 336 Rao, I. M., Zeigler, R. S., Vera, R. and Sakarung, S. 1993. Selection and breeding for
337 acid-soil tolerance in crops. Upland rice and tropical forages as case studies.
338 *Bioscience*, 43: 454-465.
- 339 Sahu, S. K., Mishra, S. K. and Senapati, B. K. 1988. Population biology and
340 reproductive strategie of Dichogaster bolau (Oligochaeta: Octochaetidae) in two
341 tropical agroecosystems. *Proc. Indian Acad. Sci.*, 97 (3): 239-250.
- 342 Senapati, B.K. 1980. Aspects of ecophysiological studies on tropical earthworms
343 (Distribution, population dynamics, production, energetics and their role in the
344 decomposition process). Ph. D., Sambalpur University, India. 154 p.
- 345 Swift, M. J., Heal, O. W. and Anderson, J. M. 1979. Decomposition in Terrestrial
346 Ecosystems: Studies in Ecology, Vol. 5. Blackwell, Oxford. 372 p.
- 347 Syers, J. K. and Springett, J. A. 1983. Earthworm ecology in grassland soils. In: J. E.
348 Satchell (Editor), *Earthworm Ecology*. Chapman and Hall, London. pp. 67-84.
- 349 Watanabe, H. and Ruaysoongnern, S. 1984. Cast production by the megascolecid
350 earthworm Pheretima sp. in North-eastern Thailand. *Pedobiologia*, 26: 37-44.

Table captions

Table 1. Average values of density and biomass of *M. carimaguensis* in g m^{-2} in the two systems studied.

Table 2. Monthly average production of casts by *M. carimaguensis* per m^2 (numbers \pm Std. dev.) in the two systems.

Figure captions

Figure 1. Abundance and biomass of M. carimaguensis in the native savanna and improved pasture.

Figure 2. Monthly average number of fresh casts per m² of M. carimaguensis.

Figure 3. Vertical distribution of M. carimaguensis in improved pasture in May 1994 (a), July 1994 (b), November 1994 (c) and January 1995 (d).

Figure 4. Activity of the total population of M. carimaguensis in improved pasture (Arrows indicate months with subestimated values).

Figure 5. Monthly total number of cocoons obtained in improved pasture during the whole study period.

Table 1

Average values of density and biomass of M. carimaguensis in g m⁻² in the two systems studied.

	Native savanna	Improved pasture
Density	0.22 ± 0.3	17.89 ± 4.3
Biomass	0.64 ± 1.0	52.56 ± 20.33

Table 2

Monthly average production of casts by *M. carimaguensis* per m² (numbers ± std. dev.) in the two systems.

Condition	Native savanna		Improved pasture	
	Wet season	Study period	Wet season	Study period
Dry casts	7.15 ± 3.5	6.38 ± 3.4	20.38 ± 7.9	17.35 ± 8.9
Recent fresh casts	0.31 ± 0.5	0.23 ± 0.5	3.25 ± 3.8	2.48 ± 3.6
Non recent fresh casts ¹	0.12 ± 0.2	0.09 ± 0.21	1.77 ± 2.1	1.39 ± 2.0
Total	7.58 ± 3.6	6.72 ± 3.6	25.43 ± 10.3	21.21 ± 11.9

¹ Fresh cast with a dry basis.

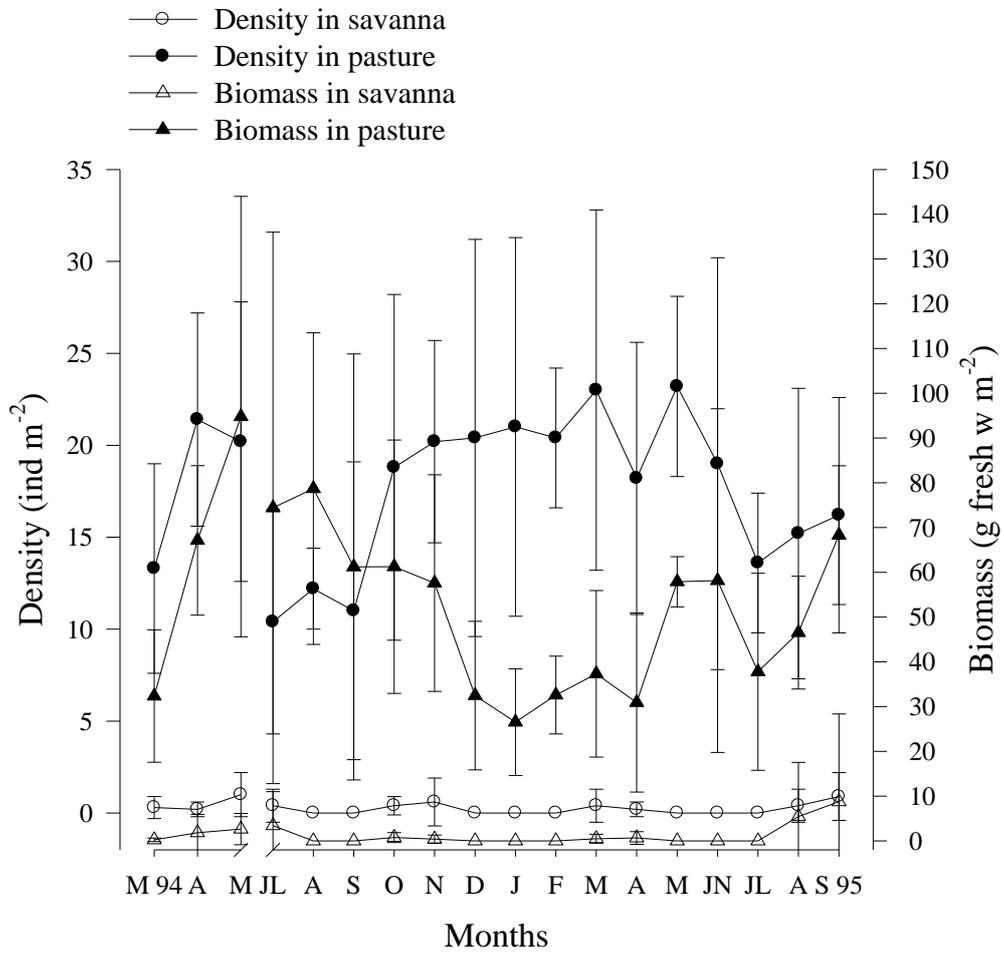


Figure 1

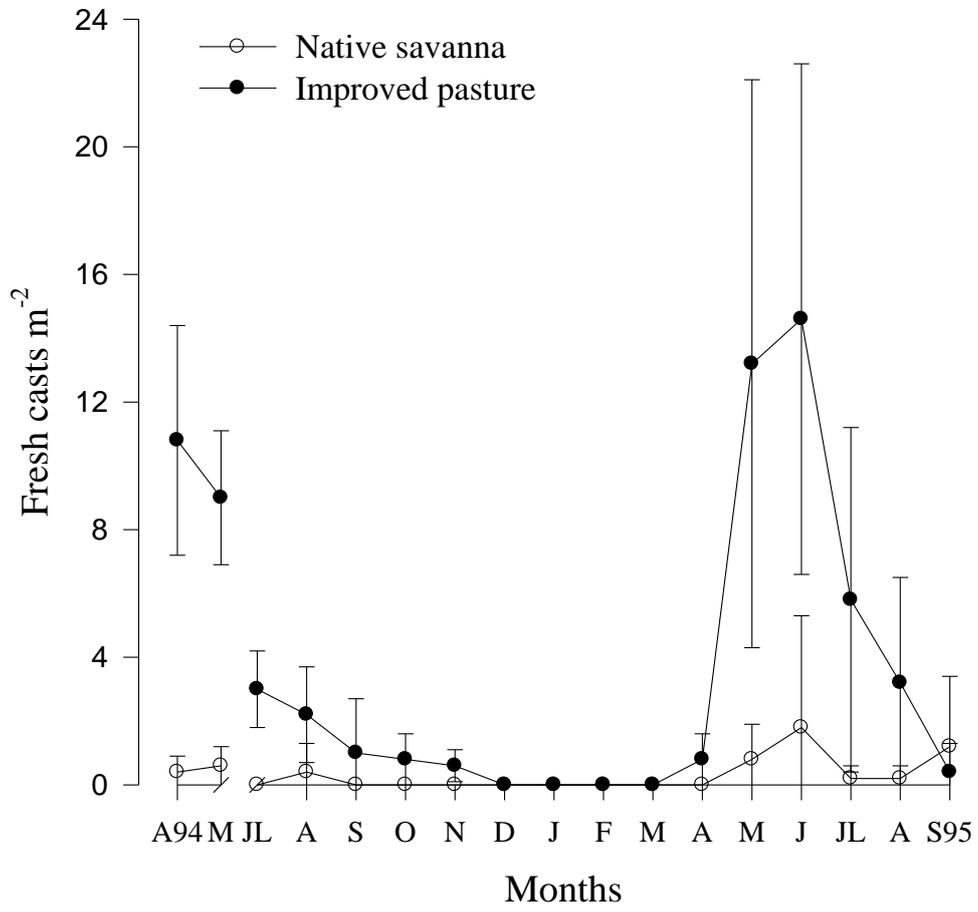


Figure 2

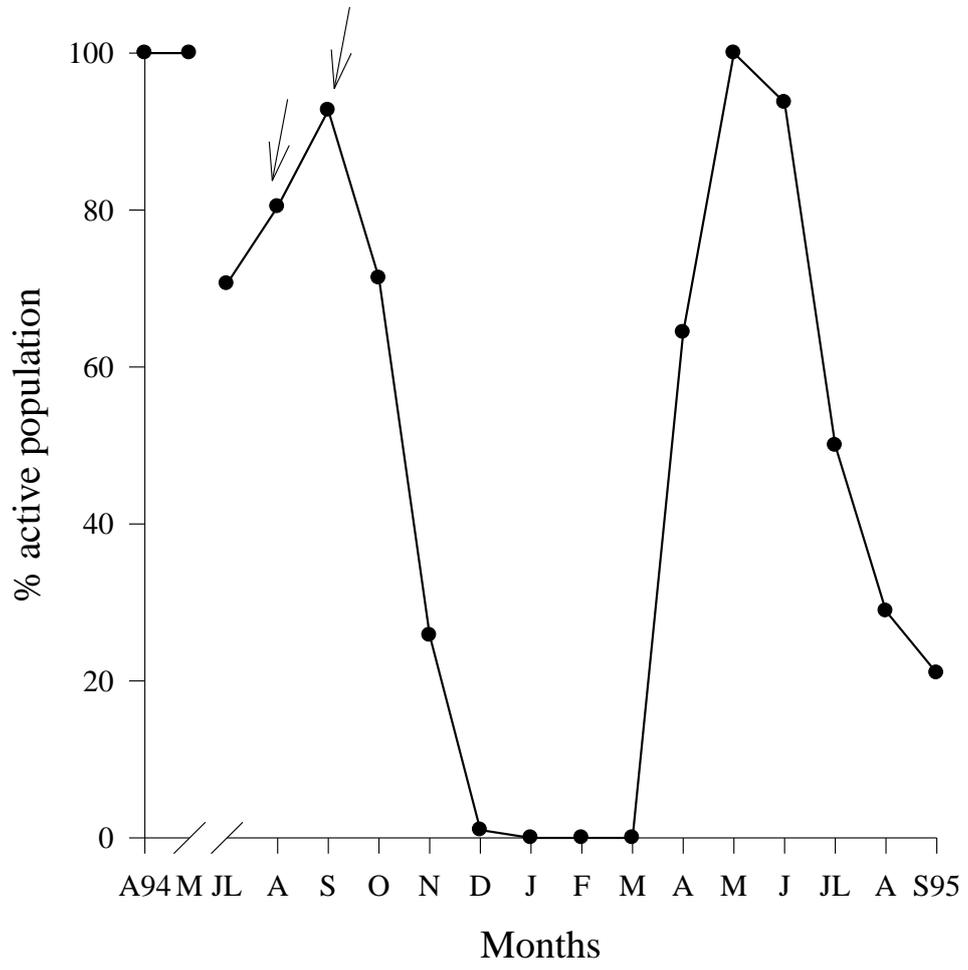


Figure 3

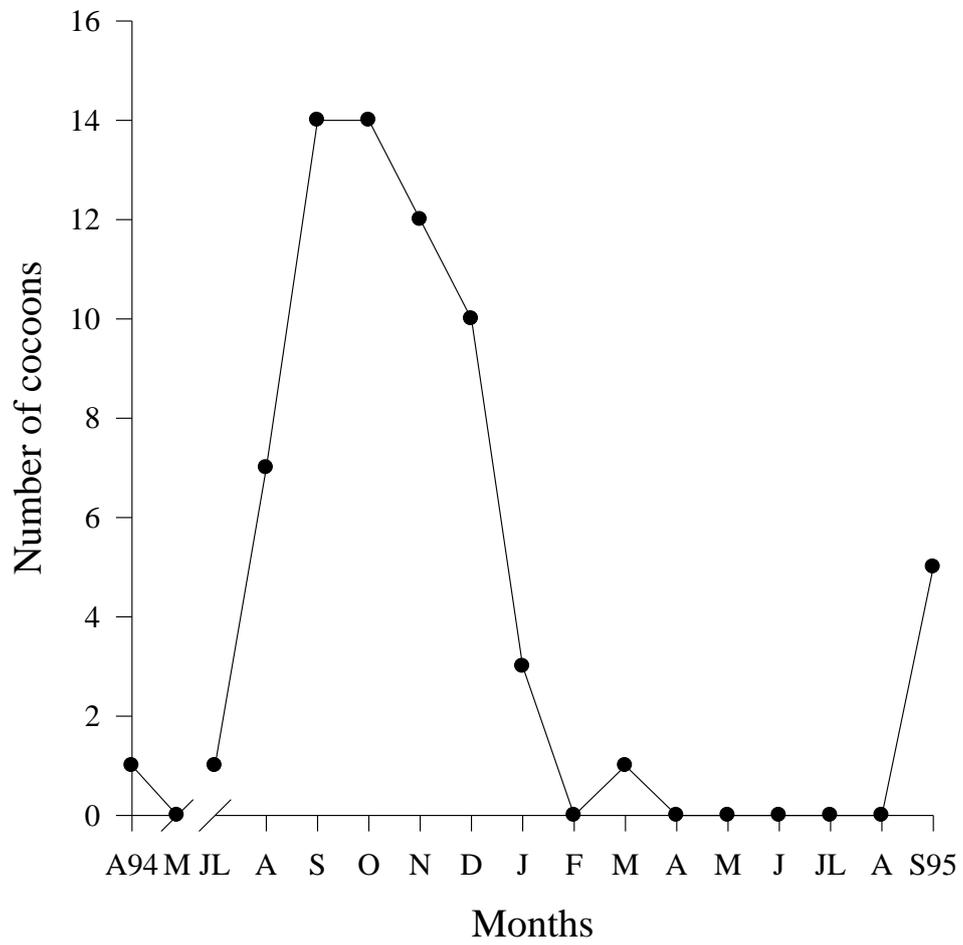
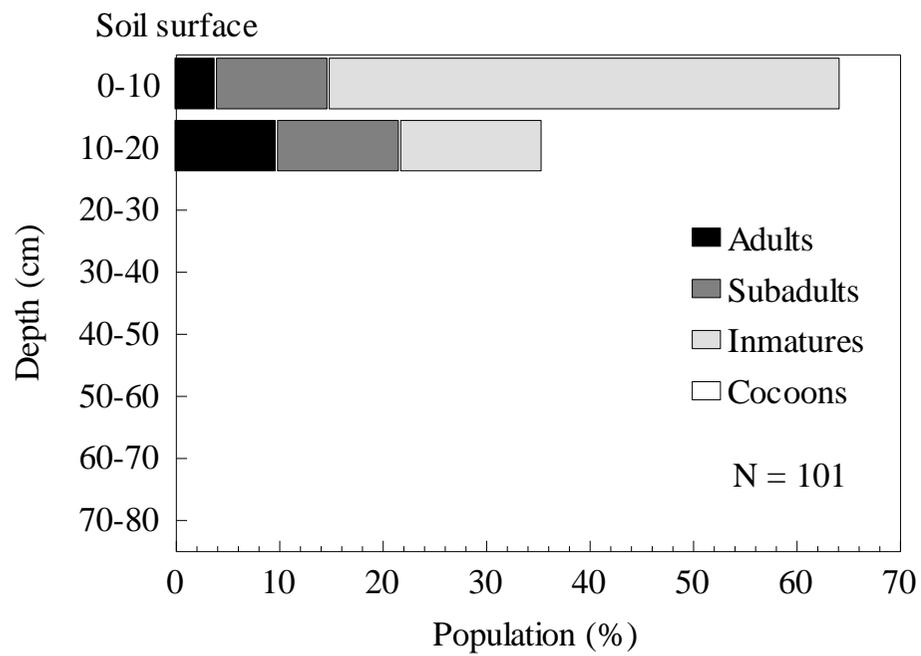
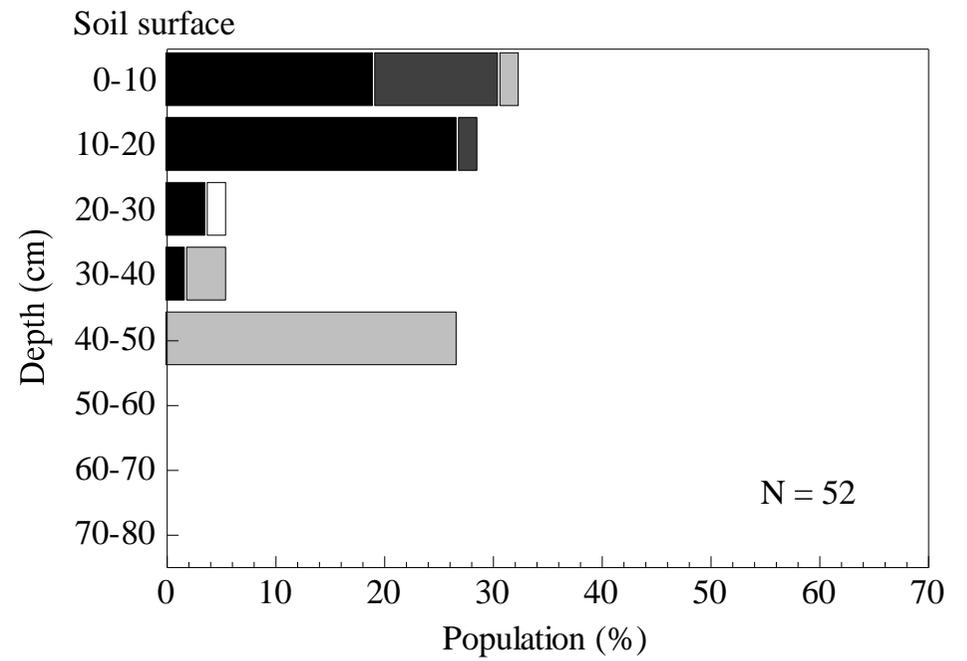


Figure 4

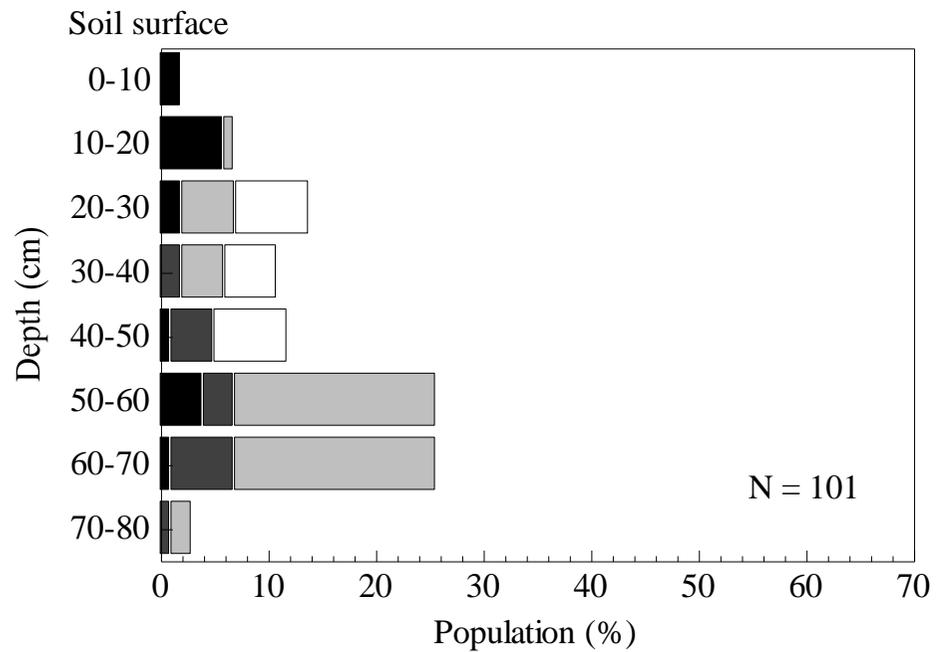


a)

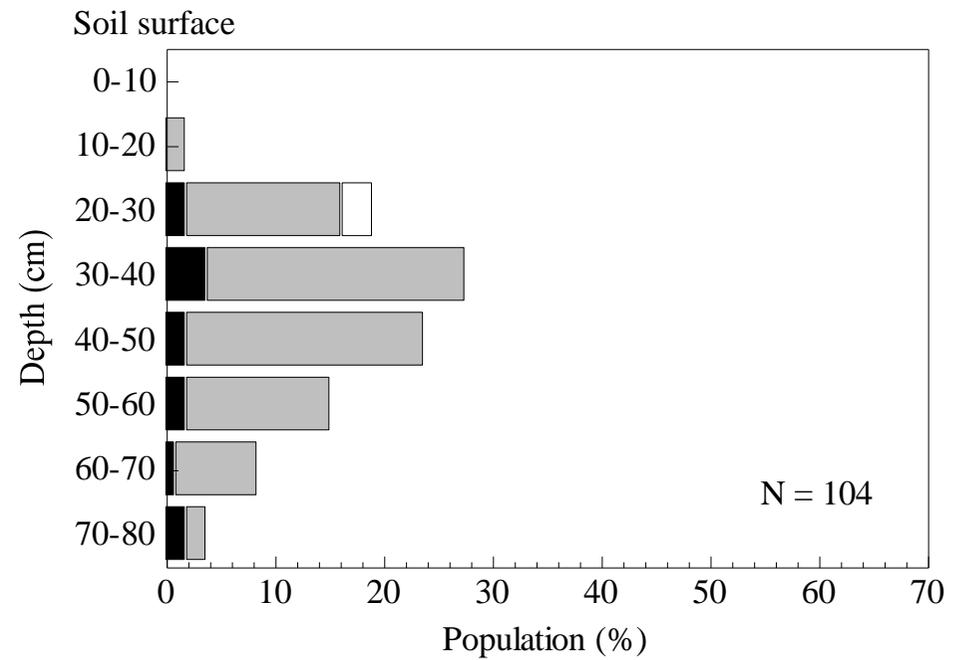


b)

Figure 5



c)



d)

Figure 5