Adaptive strategies of *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta), a peregrine geophagous earthworm of the humid tropics

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Summary. *Pontoscolex corethrurus* is a medium-sized geophagous earthworm species which has invaded most cultivated land in the humid tropics. It is generally found in gardens, cropland and fallowland, where it has been introduced accidentally by man. The species has quite narrow microclimatic requirements. Reproduction only occurs at 23°−27°C, and the worms are fully active only where soil moisture is well above field capacity (pF 2.5). This limitation is balanced by the ability to live in a great variety of soils differing in pH, organic matter content and texture. The demographic profile is typically of the *r* type, which gives populations a colonization capacity greater than that of comparable native species. This can be explained by the limited size of individuals and the great efficiency of their mutualist digestion system, in association with the free soil microflora. As a result, growth is fast and a great amount of energy may be invested in reproduction, which is made even more efficient by parthenogenesis.

Key words: Tropical-earthworms − Adaptive-strategies − Demography − Peregrine-species − *Pontoscolex corethrurus* − Parthenogenesis

In tropical areas, most earthworm species have rather limited geographical distributions. Species with a pantropical distribution are often small, and are used to living in rich organic environments (Lee 1985). *Pontoscolex corethrurus* is one of the few that have a geophagous regime. It is an unpigmented worm, 7−10 cm long and 3−4 mm in diameter. Adults may weigh up to 600−3500 mg fresh mass, and the cocoons' mean weight is about 40 mg (fresh weight).

This species has been transported by man all over the humid tropics from its original centre of dispersion, which was most probably located in forests of the Guayanese plateau in South America (Righi 1984).

The most likely reasons for the extraordinarily wide distribution of this species are investigated here. There are four major factors:

− a wide range of tolerance to soil physico-chemical characteristics;
− a wide range of tolerance to moisture and temperature conditions;
− a very efficient assimilation of low-quality soil organic matter;
− an outstanding ability to colonize due to its demographic profile.

An understanding of these factors is of great relevance to the design of new, low-input agricultural practices, in which the introduction of *P. corethrurus* might be a means of improving soil fertility (Rose and Wood 1980; Swift 1984; Lavelle and Barois 1987).

Materials and methods

These results are part of a research programme begun in 1980−1982 in the humid tropical part of Mexico (states of Veracruz and Chiapas). Monthly sampling of field populations was carried out over a 12- to 15-month period in three sites: a pasture at Laguna Verde (Veracruz) with a vertisol-type soil, and two forest sites at Boca del Chajul (Chiapas), one with alluvial nutrient-rich soils (Entisols, USDA classification system), the other on ferralitic soils (Ultisols) with a low nutrient status. Details of site characteristics and sampling methods are given in Lavelle et al. (1981) and Fragoso (1985). Complementary field data were taken from a 2-month sampling project in forests and savannas of the Mayombe forest in the Congo (P. Lavelle and M. Montadert 1984, unpublished data).

Laboratory experiments were conducted to determine the effect of soil moisture, temperature and organic matter contents on demographic parameters of *P. corethrurus* populations. The culture technique developed by Lavelle (1978) allows simultaneous measurement of soil ingestion, individual growth, cocoon production and

mortality. Details about the individual experimental conditions are available in Pineda and Hernandez (1983: effect of temperature and soil organic matter). For the soil-moisture experiments, newly hatched *P. corethrurus* were raised over a 250-day period in the soil of tropical pastures of Laguna Verde, where they would normally live, at a mean temperature of 27 °C and eight different moisture contents, ranging from 27.5% to 60%, with three sets of five worms cultured at each moisture content; in this soil the moisture content was 35% at pF 2.5 and 20% at pF 4.2. The culture boxes contained about 200 g dry soil each and the culture medium was changed every week. The assimilation rate of soil organic matter was determined by comparing the C content of the soil before and after its digestion by the worm.

Finally, the digestive system was studied, using a set of biochemical, microbiological and microrespirometric methods as detailed in Lavelle et al. (1983) and Barois and Lavelle (1986).

Results

Natural populations

P. corethrurus populations are generally concentrated in the upper 10 cm of the soil, but may go deeper into the soil during dry periods (Fragoso 1985). The mean annual depth of activity at Chajul was 5.8 cm in the alluvial soils and 10.9 cm in the ferralitic soil.

Diet is strictly geophagous; this species can thus be classified between the polyhumic and mesohumic endogenic categories, since the casts often have a greater organic matter content than the bulk surrounding soil (Lavelle 1981, and 1985, unpublished data).

P. corethrurus normally lives near villages and other areas disturbed by human activities, such as induced pastures and savannas, secondary forests and re-growth and also cropland and tree plantations. It is generally absent from undisturbed ecosystems, although populations already settled in a disturbed area may sometimes colonize neighbouring undisturbed environments in a limited way (Fragoso 1985; P. Lavelle and M. Montadert 1984, unpublished data). Populations are generally spread by man, when planting gardens or trees or transporting soil (e.g. as ballast for sailing ships up to four centuries ago; Gates 1970; Lee 1985). *P. corethrurus* populations tend to have rather high densities and biomasses by tropical standards: 100−350 individuals/m² and 35−128 g fresh

weight. They generally constitute 80%−100% of the total earthworm biomass (Table 1).

The populations are generally dominated by young individuals, and there may be many cocoons all year round, since reproduction occurs whenever the soil is moist. In the forests near Chajul the proportion of adults varied from 3.1% to 37%, with a mean of 21%, and the mean density of cocoons was 34/m². Density and biomass fluctuations are very much dependent on the water regime of the soil (Fragoso 1985; P. Lavelle et al. 1982, unpublished data).

Range of tolerance to soil physico-chemical characteristics

P. corethrurus seems to tolerate a wide range of physico-chemical conditions. In the Laguna Verde area (Mexico), Lavelle et al. (1981, and 1982, unpublished data) found them in soils with a rather wide pH range (6.2−8.1), clay content (4%−41%) and organic matter content (1.0%−9.9%). In the Rio Grande do Sul province (Brasil), Knäper and Pinto Porto (1979), found *P. corethrurus* in sandy soils (<20% clay) with low pH (<5.5) and low organic matter content (<2%). In the tropical rainforests of Chajul (Mexico), rather large populations have been found in ferralitic (Ultisols) and alluvial (Entisols) soils with pH ranging from 4.8 to 5.5, organic matter contents from 6.1% to 6.6% in the upper 10 cm and clay content from 10% to 16% (Fragoso 1985). The soil of the induced savannas of Dimonika (Congo), where large populations are found, has an acid pH (4.7), a low organic matter content (3%) and a loamy texture.

Sweet potato gardens in Wari (Papua New Guinea) had high organic matter contents (7.5%−21.5% organic C), low pH (4.0−5.4) and high nutrient contents. In India, Kale and Krishnamoorthy (1980) found that *P. corethrurus* populations were more abundant in soils with high C/N and low humic to fulvic acid ratios; the populations they sampled in Bangalore lived in soils with organic matter contents of 3.9%−12.6% and neutral pH (7−7.2).

Table 1. Mean annual abundance of populations of *P. corethrurus* in different environments (Dimonika and Piwa: wet season only). 1, Lavelle et al. (1981); 2, Lavelle and Montadert (unpublished data); 3, Fragoso (1985); 4, Rose and Wood (1980)

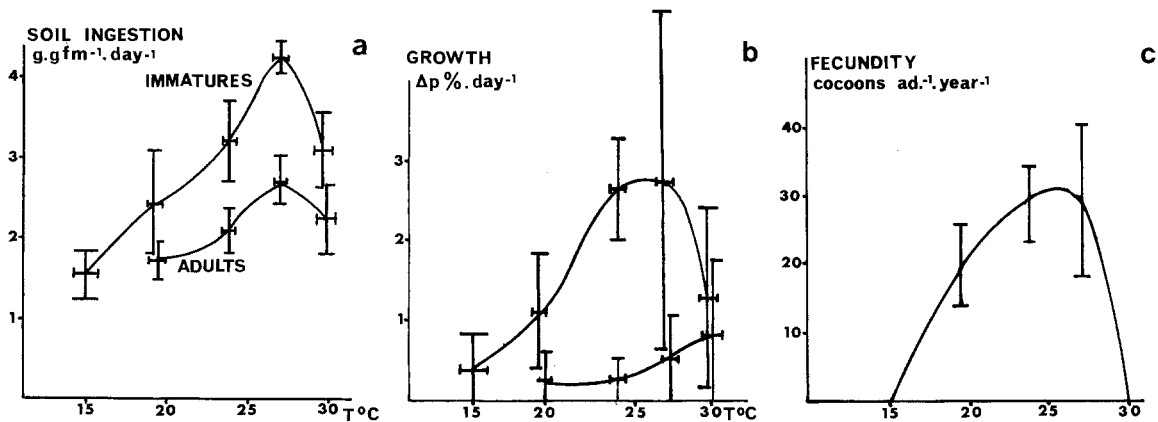|	Density (per m²)	Biomass gfw/m²	Earthworm biomass (%)	Vegetation type
Laguna Verde (1) (Veracruz-Mexico)	121.5	35.0	85.4	Pasture
Dimonika (2) (Congo)	349.0	66.7	99.5	Savanna
Dimonika (2) (Congo)	5.7	1.3	44.4	Primary forest
Chajul (3) (Mexico)	101.7	35.5	83.2	Secondary forest
Chajul (3) (Mexico)	33.3	12.1	35.4	Primary forest
Piwa (4) (Papua New Guinea)	93−302	47−128	99.5	Sweet potato

Fig. 1. Effect of temperature variations on **a** soil ingestion, **b** growth rate (Δp%, percentage change in individual weight) and **c** fecundity of *Pontoscolex corethrurus* in a Mexican Vertisol (*ad.*, adult)

Range of tolerance to temperature

Laboratory cultures of immature and adult worms from the Mexican tropical pasture of Laguna Verde were successful at temperatures ranging from 15 °C to 35 °C, with soil moisture about 38% (pF 2.5). The rates of mortality, soil ingestion, daily growth and the fecundity of adults were measured in soil taken from the upper 10 cm, where they normally live (Pineda and Hernandez 1983).

Young worms ingested more soil than the adults; their ingestion rate increased progressively with temperature, reaching a maximum of 4.2 g dry soil/g fresh weight at 28 °C and decreasing sharply at 30 °C (Fig. 1a). The maximum adult ingestion rate was 2.6 g/g fresh weight at 28 °C.

The growth rate of the young worms was very low, though positive, at 15 °C; it increased with temperature, reaching a maiximum at 25 °–28 °C, and then decreased at 30 °C (Fig. 1b). Adult growth was much slower and showed a rather different pattern, with a maximum at 30 °C.

The adults did not produce cocoons at 15 °C or at 30 °C. Fecundity was maximum at 23 °–28 °C (Fig. 1c).

Range of tolerance to soil moisture

Newly hatched *P. corethrurus* were raised for 250 days, under the conditons previously described. Mean temperature was 27 °C and cultures were carried out at eight different moisture contents, ranging from 27.5% to 60%, with 15 worms in each culture set.

Life expectancy of young worms at birth was shortest (1.2 months) at 27.5% moisture content; it increased with rising moisture to 5.5 months (40%), then remained more or less constant up to 50% (6.0 months) before decreasing gradually to 4.6 months at

55%, and then falling sharply to 1.3 months at 60% moisture content.

Soil ingestion increased regularly with soil moisture up to 45%. For technical reason it was impossible to measure this parameter at higher moisture contents. Young worms consistently ingested more soil than adults per unit of weight: 5.4 g soil/g fresh weight for young worms and 2.7 for full-grown ones (Fig. 2a).

The growth rate of immature worms was negative at 27.5% moisture content, increased to a maximum of 7% at 55% and then decreased at 60%. Adults had a much lower growth rate than immature worms at any moisture content, with a maximum at 60% (Fig. 2b).

At moisture contents below 35%, the worms had not reached the adult stage at the end of the experiments (250 days). At 35%, the first cocoon was produced at 108 days, and with increasing moisture this generation time decreased to 80 days at 50%, increasing again in moister soils (Fig. 2b).

The fecundity of adults varied greatly with moisture, increasing between 35% and 55% moisture content, then decreasing (Fig. 2c). The maximum was about 100 cocoons/adult per year.

Assimilation of soil organic matter

Together with soil microorganisms, *P. corethrurus* has developed a mutualistic system of digesting soil organic matter. In the anterior part of the gut, large amounts of water (approx. 130% of the dry weight of the soil) and intestinal mucus (16%), a rich and readily assimilated energy source, are secreted and mixed well with the ingested soil. As a result, pH increases, and the soil microflora, being strongly activated, becomes able to digest the complex organic compounds of the soil (Barois and Lavelle 1986; Fig. 3). Simple organic solutes are released and reabsorbed in the posterior part of the gut.
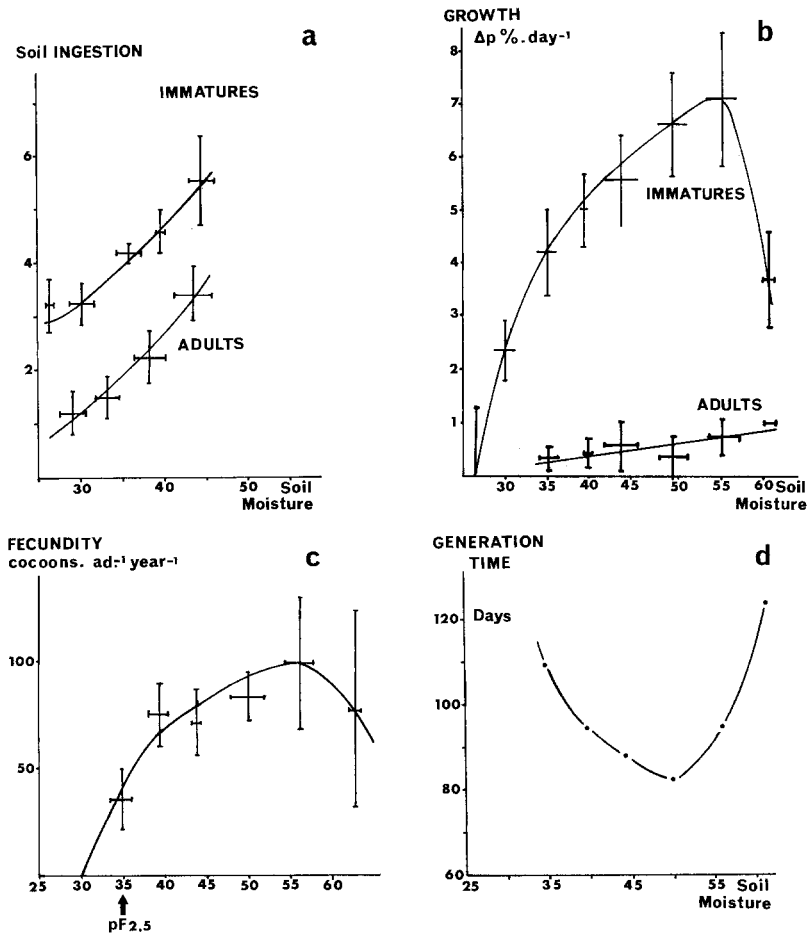
Fig. 2. Effect of soil moisture variations over a soil ingestion, **b** growth rate, **c** fecundity and **d** generation time of *Pontoscolex corethrurus* in a Mexican vertisol

The efficiency of this joint digestion system is very high, since in 2−4 h, the duration of a gut transit, up to 19% of the soil organic matter was digested, while the mineralization rate in the absence of earthworm stimulation is only 0.6%−0.8% a week (Barois and Lavelle 1986). This difference was significant at the 99% level (Student's *t*-test).

In addition, a potential for free N fixation has been demonstrated in the gut (Barois et al. 1987).

Demographic profile

The demographic profile of earthworm populations may be described by three parameters: the fecundity of adults (F = number of cocoons produced per adult per year), the generation time (C = time of growth until the first cocoon is produced) and the life expectancy of newly hatched worms (E_v). These parameters may be combined in the index $D = \log 10^3 \ (F/C \cdot E_v)$, which describes the demographic profile of earthworm species (Lavelle 1979).

Values of these parameters calculated from the laboratory cultures of *P. corethrurus* are compared with

values for native earthworm species of African savannas in Table 2.

In the earthworm communities of Lamto (Ivory Coast), values of the D index are closely related to an ecological index, $E = \log W \cdot p$, where W is the maximum weight of the adults and p the mean depth at which the individuals are found over an annual cycle (Lavelle 1979). This index represents a mathematical description of the adaptive choices made by any earthworm species: the worms may be small (and have a high metabolic rate and high maintenance expenses) or large; and can live close to the surface (with high quality nutritive resources but unpredictable microlimatic conditions) or deep in the soil. The E index was calculated for *P. corethrurus* from field data taken from two sites in the Chajul forest. E was 0.92 in the secondary forest ($W = 1.2$ g; $p = 6.9$ cm; Fragoso 1985). At Laguna Verde, E was 0.95 ($W = 1.5$ g; $p = 3$ cm; P. Lavelle et al. 1982, unpublished data). A similar calculation was made for the Indian species *Lampito mauritii*, using data from Dash and Patra 1977). Comparisons with these species are shown in Fig. 4.
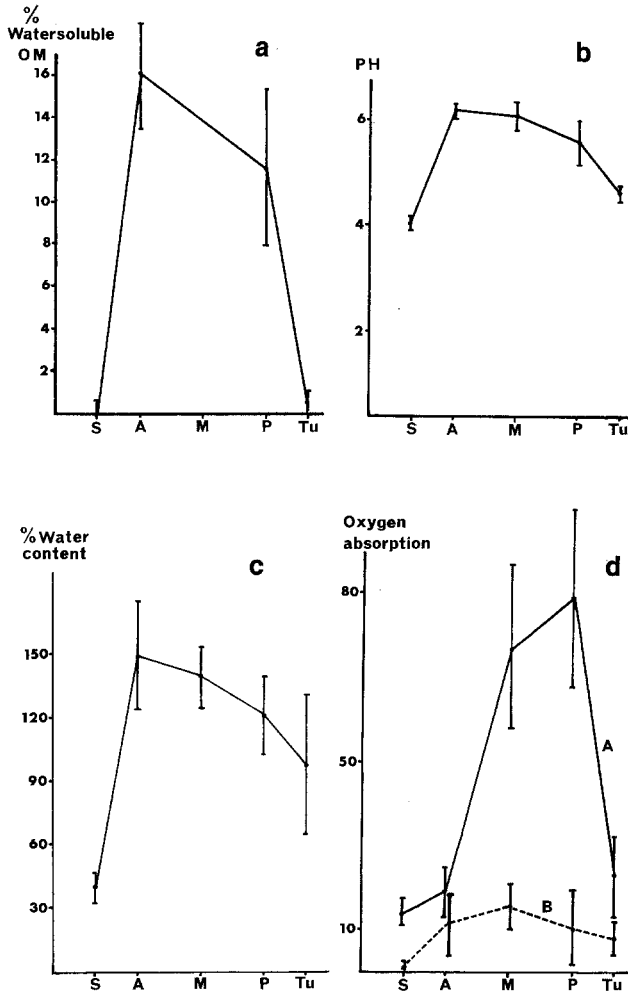
Fig. 3a–d. Variations in some soil characteristics during transit in the gut of *Pontoscolex corethrurus* (A, anterior; M, middle; P, posterior parts; S, control soil; Tu, casts). **a** Water-soluble organic matter (% dry soil); **b** pH; **c** water content of the soil (% dry weight); **d** oxygen uptake (A) and control (B) when microbial activity is inhibited by NaN_3 (nl/mg per h)
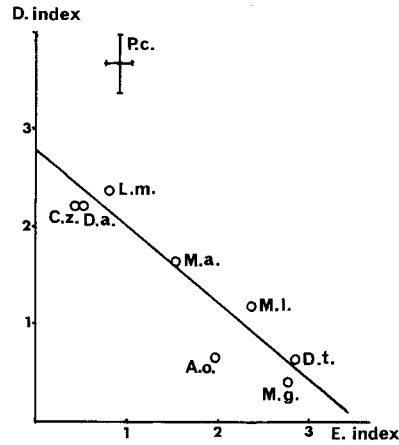

Fig. 4. Relationship between the demographic index ($D = \log 10^3$ $F/C \cdot E_v$) and ecological index ($E = \log W \cdot p$) for seven species from the Lamto savannas (Ivory Coast), *Lampito mauritii* (*L. m.*) in Indian pastures and *Pontoscolex corethrurus* in a Mexican tropical pasture (Lavelle 1979; Dash and Patra 1977; present study)

Discussion

The few studies on natural populations of *P. corethrurus* seem to demonstrate that this species is rather eurytopic. Populations have been found in sandy or clayey soils, with basic or acid pH, low to high organic contents, in pastures, savannas, tree plantations or secondary forests (Knäper and Pinto Porto 1979; Lavelle et al. 1981; Fragoso 1985; P. Lavelle and M. Montadert 1984, unpublished data). All these sites are situated in disturbed land with humid tropical climates.

The ability to colonize such a wide range of humid tropical soils is probably due primarily to a high ability to utilize soil organic resources as an energy source. The mutualistic digestion system in association with soil microflora is very efficient, since up to 19% of

Table 2. Demographic parameters, demographic index ($D = \log 10^3$ ($F/C \cdot E_v$) and ecological indexes ($E = \log W \cdot p$) for *P. corethrurus* (at 27°C, with 35% – 60% soil moisture at pF 2.5: 35%) and the native species of an African savanna and Indian pastures (field data)

Species	F	C	E_v	D	E
Pontoscolex corethrurus	35 – 99	2.7 – 4.4	1.3 – 6.0	3.4 – 4.1	0.92 – 0.95
Chuniodrilus zielae	13.0	18	3.3	2.3	0.56
Dichogaster agilis	10.7	15	3.4	2.3	0.48
Millsonia anomala	6.2	20	6.2	1.7	1.68
Millsonia lamtoiana	3.1	24	7.5	1.2	2.35
Dichogaster terrae-nigrae	1.9	36	11.6	0.7	2.81
Agastrodrilus opisthogynus	1.3	24	11.1	0.7	2.06
Millsonia ghanensis	1.3	42	10.6	0.5	2.76
Drawida calebi	8.7				
Lampito mauritii	9.3	12	3.8	2.4	0.92
Octochaetona surensis	15.5				

F, Fecundity adult per year; C, duration of growth in months; E_v, life expectancy of immature worms at birth in months (Dash and Patra 1977; Lavelle 1978; Senapati 1980; present paper)

total organic C may be digested in 2−4 h, the duration of a gut transit (Barois and Lavelle 1986). By comparison *Millsonia anomala*, a native African species with an ecological niche close to that of *P. corethrurus*, has an assimilation rate of about 9% and *Aporrectodea rosea*, an endogeic Lumbricidae, 0.9%−1.3% (Lavelle 1978; Bolton and Phillipson 1976).

Comparative studies suggest that the greater efficiency of *P. corethrurus* is due to the great production of intestinal mucus in the anterior part of the gut, followed by strongly induced microbial activity (Lavelle et al. 1983; Barois and Lavelle 1986; Martin et al. 1987).

The efficient use of soil organic matter, even at very low concentrations, may be further enhanced by the activity of free N-fixers in the gut, which might benefit the worm (Barois et al. 1987).

P. corethrurus has no special tolerance for a wide range of temperature or moisture conditions. Populations are only found in environments where the annual mean temperature is well above 20 °C. Growth to the adult stage is only possible in temperatures of 20°−30°C, reproduction being restricted to the 23°−27°C range. In comparison, *M. anomala*, and even the epigeic lumbricid *Eisenia fetida*, have a wider range of tolerance to temperature variations (Lavelle 1978; Kaplan et al. 1980).

Growth of *P. corethrurus* begins, and the adult stage is attained, within a reasonable length of time at moisture values of about 35%, close to pF 2.5. The optimum values for growth, survival and reproduction are 50%−55%. This species is much less adapted to drought than native species from the Lamto savannas (Ivory Coast): young immature *M. anomala*, for example, become active and grow at pF 3.0, with a maximum at pF 2.5, while at higher moisture levels growth gradually decreases (Lavelle 1978).

The demographic profile of *P. corethrurus* is typical of a fast colonizer, compared with the native African and Indian species (Lavelle 1979). Parthenogenesis reduces the time from sexual maturity to cocoon deposition since there is no need to seek a partner in the same physiological state, and no risk of remaining unfertilized in situations of very low density.

The hatching rate of cocoons is very high, as is usual in earthworms (Lavelle 1978; Senapati 1980), varying from 78% to 97% in moist soils according to temperature. Growth is very rapid, and individuals bred in optimal conditions may produce cocoons after as little as 82 days, which is much less than has been observed previously in tropical species (10−36 months for the species of the Lamto savannas). Values of the same order have been recorded only for the fastest growing Lumbricidae, such as *E. fetida*, which can

produce cocoons after 42 days in optimal conditions (Kaplan et al. 1980). Fecundity of adults is also exceptional compared with that of the Lamto species. Fecundity values of more than 50 cocoons/adult per year are common in moist soils, and the maximum recorded value was about 100 cocoons/adult worm per year at 27 °C and 55% moisture (i.e. about 1.6 times the value at pF 2.5), while at Lamto, fecundity of adults in natural populations ranged from 1 to 13 cocoons/adult worm per year and at Berampuhr (India) values of 8.7 to 15.5 were recorded (Senapati 1980).

Life expectancy of young individuals at birth seems to be quite low, especially in field conditions, as natural populations always have very low proportions of adults (P. Lavelle et al., unpublished data; Fragoso 1985). Even in favourable laboratory conditions, the mean life expectancy of young individuals at birth was no greater than 1.2−6 months. Such numbers are low compared with those measured for the African and Indian native species (3.3 to 11.6 months under field conditions).

Thus, the demographic index $(D = \log 10^3 \ F/ C \cdot E_v)$ has remarkably high values (3.4−4.1) compared with the African species studied at Lamto (0.5−2.3 in natural conditions, Lavelle 1979). These high values probably account for the extraordinary colonization capacity of this species even if, under field conditions, the measured value might be lower; at Lamto, the D index for *M. anomala* might be as high as 2 under favourable field conditions while laboratory results indicate that the D index would not exceed, even in the best (and quite unrealistic) case, 2.4 $(F = 14; \ C = 9; \ E_v = 6)$ (Lavelle 1978).

At Lamto, the very close relationship between the D index and the ecological index $E = \log W.p$ suggests that the demographic profiles are highly dependent on size (W is the maximum weight of adults) and feeding habits as related to the mean depth of activity (p). Data for *Lampito mauritii* from Dash and Patra (1977) also conform to this pattern. *P. corethrurus* is clearly out of the range of these species (Fig. 4), indicating that only part of its extraordinary ability to colonize new environments is due to the limited size of individuals and the location of populations in the upper, organic rich, horizon of the soil. The difference appears to arise from a more efficient and adaptable use of soil organic matter, thus ensuring a higher energy input, if other factors remain constant. The allocation of a great part of this energy to reproduction and the parthenogenetic mode of reproduction would then explain the outstanding ability to colonize new environments.

This ability to colonize environments with a large range of edaphic if not climatic conditions would explain why this species has been able to invade newly

disturbed environments after having been introduced accidentally by man. In such soils, native species usually disappear, most often because they are stenoecic species that cannot adapt to the savanna-like conditions of clearcut areas. Our results, however, do not explain why *P. corethrurus* is rare or absent in undisturbed lands. In some cases, its poor adaptation to drought might make it a weak competitor with native species. This seems to be particularly true in many rainforest soils, which have extreme seasonal water regimes. In other apparently favourable ecosystems, such as the moist Guinean savannas or tropical rainforests with an annual rainfall of up to 2–3 m, *P. corethrurus* may be excluded by competition with local well-adapted species or simply may not yet have been introduced.

Introduction and systematic use of *P. corethrurus* could strongly influence the future of sustained low-input tropical agriculture, because it could help in maintaining or in improving soil structure through mechanical activity and because it appears to have an influence on free N fixation and microbial activity (Lavelle and Barois 1987). The worm might also be used as a source of protein, since it is able to convert poor quality soil organic matter to fresh tissues with a 60% – 70% protein content with great efficiency. In New Guinea, Rose and Wood (1980) showed that *P. corethrurus* has become an indispensable component of the diet of pigs after having been introduced in the early 1960s.

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