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The subterranean behaviour of the earthworm

ABSTRACT

The earthworm behaviour could be, directly in nature, observed mostly in night *on* the soil. This visible behaviour has been rather well described since Darwin (1881) who founded this knowledge.

Conversely, *in* the soil we are more or less obliged to assume hypothesis or to use indirect experimental devices which give results reflecting more our simplistic ideas than actual facts.

A series of qualitative observations and quantitative measurements made in field leads us to a better understanding of the subterranean behaviour versus main vital stresses: food, temperature, humidity and physiological adaptations (diapause, reproduction, ...).

Key words: Earthworms, behaviour.

1. Introduction

When Darwin (1881-82) focused attention on the role of earthworms in the economy of nature, regarding the formation of vegetable mould, he included data on the *visible* behaviour of these animals. This description of the surface activity has since been augmented by many qualitative and quantitative studies conducted, under laboratory conditions, on the flight or shift reactions to some isolated factors (light, electric shock, alimentary choice of substances) and after Vejdovsky (1892) by many data on lethargy (anhydrobiosis, quiescence, diapause). The recent or foreseeable progress, in quantifying the role of the earthworm, indicates that studies in this field require a good knowledge of earthworm activity, which in turn is largely dependent on subterranean behaviour, itself a function of physical factors.

This subterranean behaviour, which is a result of a long unseen adaptation, is not well understood and has not yet been described. The aim of this article is to provide a concise description of the subterranean behaviour of earthworms. Here hall not deal with details observed below the soil or under artificial conditions, but with qualitative and quantitative data obtained *in situ*, and with

the experiments related to the natural phenomena. Some of the data we shall describe are defined below:

— *lethargy*: arrest of motor activity under endocrine control (= diapause) or not (= quiescence), the latter are only simple refuges with a relevant loss of water (anhydrobiose) or control of the body water level (= paradiapause);

— *activity*: this is relative, with no dimension, it is expressed by comparison; it is minimal during lethargy (a certain metabolism subsists when motor activity is absent) and then it increases (maximal) under optimal environmental conditions;

— *temperature*: this is obtained by making a clear distinction between *body* temperature and *soil* temperature. At the present state of knowledge, we accept that body temperature may be the same as the temperature of the soil where the animal lies, if it remains long enough to achieve a thermic balance. Nevertheless, we shall distinguish the saccharosic temperature in $°S$ ($\simeq °C$), which is the only method used to determine the body temperature at equilibrium;

— *moisture*: the same applies as for temperature, with the difference that we ignore *in situ* body moisture: we can only determine it in the laboratory (in % of the dry mass of earthworms).

The soil water potential, exercising a nil or strong effect over the body water (in pF = logarithm of the osmotic pression expressed in cm of water $/cm^2$) is measurable beginning from the ground, but it is not directly linked to the animal's position, as regards these measurements;

— *photoperiod*: we know today the importance of photoperiod at least for the anecic of central and southern Europe (see below);

— *tropho-tonic stresses*:
— trophic: search and choice of food;
— tonic: regulation of the metabolism;
— predatism: risk caused by exposition to predators
— demographic: reproduction;

— *ecological categories*: we shall deal with (since we cannot examine in detail the relations of the subcategories) the epigeic, the epianecic (= they are large *Lumbricus ssp.*, since, information is limited on them), anecic and endogeic. Some adaptative variants can be evoked at the species level.

2. Lethargy, photoperiod, and survival

This point has been already analysed in several articles (Bouché, 1972, 1985).

2.1 *Quiescence:* Anhydrobiosis is an arrest of motor activity owing to desiccation that may be followed by death. Before this, the animals often curl up together. The species, with this form of resistance only are closely related to muddy soil (limicoles) or to constantly damp soil (hygrophils). They are endogeic or/and epigeic.

Two groups overcome the limits of these species, either by resistance via a cocoon (in particular epigeic: *Lumbricus castaneus, Lumbricus rubellus rubellus,* and so on...) or by boring deep galleries to reach a damp horizon: these are hypohygrophils, all epianecic (*Lumbricus terrestris, Lumbricus friendi, L. centralis, L. rubellus friendoides...*).

2.2 *Paradiapause* (Saussey, 1966) is a well known activity arrest of *Allolophora icterica,* but it is probably general to the endogeic. The animals remain in small individual cavities under the effect of desiccation, with their digestive duct empty and with minimal water loss. They curl up until the paradiapause is interrupted by the rehumectation of the soil.

2.3 *Diapause:* this is the result of endocrine regulation that is under photoperiod control. The influence of photoperiod, tested unsuccessfully by Galissian (1971) has been experimentally described starting from soil data, by Heidet and Bouché (in prep.). In the laboratory Saussey and Debout (1984) have demonstrated this mechanism; that explains why Michon (1954), working with breeding stoves, has denied the obligatory diapause in species that have regular diapauses *in situ* (Avel, 1929). I have checked the opacity of Michon's stoves and have found that all the animals were in fact in «long night». The threshold found by Heidet and Bouché (in prep.) at the ground explains the diapause which is obligatory under French latitudes for *Nicodrilus longus, N. giardi, N. nocturnus* and several *Scherotheca.* On the contrary, this mechanism does not exist in *N. longus* in Sweden (Nordström, 1975) where the summer days are very long. This is suggestive of either the genetic evolution of some local species, or a threshold of light intensity, under Swedish latitudes, that is ineffective in triggering the genetic-endocrine control process. The diapause, that seems to be generalised among the anecic of temperate and Mediterranean areas, appears to regulate the reproduction and lethargy cycle that allows an arrest of organized activity (preservation of body water, empty digestive duct, curling up in small bundles) with a reduced metabolism (50% decrease of breathing, Galissian, 1971) and a programmed sexual rest (Avel, 1929). In addition, diapause permits a «programmed eclipse» of the animals, in a period of relative famine (plants in growth, but that release only a low amount of dead organic substances) and exhaustion of the reserves of post-anal rations (see cp 5) with short periods of nourishment («short night») and probability of drought.

3. Moisture and behaviour during activity

Moisture is a very important factor in the regulation of earthworm activity. We have just examined its role in lethargy. Its quantitative study has been possible thanks to the mobility and activity indices, and is presented in Heidet and Bouché (in prep.) for an anecic *Nicodrilus longus longus*.

The behaviour of the anecic is regulated in relation to a narrow zone of suction (pF unit). Below the pF3 (measured on clods of earth, through dialysis with an osmotic solution) a water fraction is released and the earthworm goes through the aquatic phase. When the pF is too high the animal cannot retain its body water, it stops its activity and re-enters lethargy. In dry periods all earthworms tend to go first to the still damp areas, where they can group, as reported for the hypohygrophils, sometimes together with several mixed species. Futhermore, dryness and moisture are not limited to only one horizon for animals with vertical activity. Adjustment of the mobility rate to the pF (dialysis of clods) of two horizons (a = -10 cm, b = -30 cm) shows the opposition between the surface horizon, that receives the animals that are in good conditions, and the deep horizon, that serves as a refuge (pF at -10 cm and -30 cm of opposed signs).

$$pF_r = (0.61 \ pF_{-10} - 0.19 \ pF_{-30}) / 0.43$$

After the elimination of the «temperature» effect, there is in the sub-vertical burrows, a hygropreferendum for *N. longus*. In the autumn of 1969 we observed a remarkable activity when the soil at -10 cm is at pF > 4, which is a *lethal* value. In fact, occasional rain had wet the ground and the superficial layers were damp; *N. longus* is able to cross over dry layers of soil between the damp deep horizon (of refuge) and the wet surface (feeding). This ability is moreover facilitated by the relevant amount of mucus we have indirectly observed with [15]N *in situ* (Bouché and Ferrière, 1986). On the other hand, most of the anecics and epigeics have nephridial openings at various body levels («en solfège») which allow a temporary self-dampening of the animal (Bouché, 1972), defined of «transpiration» by El Duweini & Ghabbour (1971). At the other extreme, water excess may bring a «caudal respiration» behaviour (in spite of the risk of predatism): the earthworm's tail emerges from the soil to increase oxygenation with different variants. This behaviour, independent of the taxon and ecologic categories, takes different forms (Bouché, 1970): caudal scattering with important blood vascularisation (Beadle, 1933) in *Alma emini* (Mich. 1892) (Almidae); simple blood turgidity in the anecic *Scherotheca savignyi savignyi* (G. & H. 1893) var. *oligotheca* (lumbricidae); simple emergence in the water of flooded soils in the endogeic *Allolobophora leoni* (Mich. 1891) and with rotatory agitation

in the limicole *Criodrilus lacuum*, Hoofm. 1845 (Criodrilidae). There is a remarkable adaptation to clay soil (in which the water flows in excess at pF3 and offers only a slight range between excess and absence) in *S. savignyi*, which is adapted to the diapause dryness followed by quiescence, and to excess moisture through caudal respiration.

4. Temperature and activity

Laboratory data indicate that earthworm activity depends on temperature, following an exponential law (Q_{10}). However, there is some reserve regarding the very low values (which really affect the earthworms) and the high ones (which in nature is also linked to the dry period and equally to the choice in thermopreferendum, see below). Over all, this process *in situ* is best reflected by the logistic law, for *Nicodrilus*. Nevertheless, here again, it is important to investigate the animal's behaviour in connection with the heat gradient of the soil. We have direct information on this behaviour *in situ* (quantitative measurement of body temperature and of nitrogen metabolism and qualitative observations).

The measurement of body temperature in the soil, integrated in function of time, according to the kinetics of a chemical reaction ($Q_{10} = 4$) has been taken in *N. longus* by Ranc (1980) and interpreted by Bouché (1983): it demonstrates that in springtime, when there is high activity, to entering lethargy (from March to May, Heidet and Bouché, unpubl.) the animals tend to have a uniform average body temperature of 12-13°C. As these adult animals feed daily on top of the soil on litter debris and on incubated excrement, their behaviour, out of the period of feeding and defecation that may be superficial, (cf. defecation, chapter 6), leads them to a choice in the thermic gradient of the soil that compensates for periods of exposure to extreme conditions of heat or cold on the surface. This thermic regulation, through thermopreferendum in the soil gradient, is very important for the regulation of metabolic activity.

A second quantitative measurement has been the measurement of the nitrogen *in situ* in the same meadow, on the same species, from 13/04/83 to 23/05/83. The soil at -10 cm had a temperature of 8°C (range from 6.2 to 10.2°C) and some free water (for this soil pF 3). During this time, the release of nitrogen (marked) constantly renewed, for one g of body nitrogen, followed the formula:

$$y = e^{-0.218x+5,571} + e^{-0.064x+6.613}$$

thereby giving a daily production of corporal 105 mg/gN (Ferrière & Bouché,

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1985). In the laboratory, under controlled conditions (without gradient) at 15°C, this production was measured as corporal 149 mg/gN. If the earthworms Q_{10} is 2, the average body temperature *in situ* would be 10°C. As we have seen, *N. longus* selects the warmest zones of the thermic gradient, tending towards 12-13°C, during the spring when the most superficial layers are heated.

In fact, this estimation is only indicative since the experimental conditions in laboratory were higher (15°C) than the thermic optimum observed *in situ* (12°C), and outside the value where the exponential law in Q_{10} appears applicable to this species ($2°C < \theta < 12°C$) under natural conditions.

In spring there is, a precise behaviour regarding this point: the anecics warm themselves beneath large stones (evapo-transpiration having made the surrounding soil cold). Numerous burrows are found in the soil-stones contact, while this is not the case of stones buried in the soil (in this context the concentration of burrows against walls described by Jeanson (1968) appears to contain an incorrect calculation; in fact in this experimental work conducted under critical thermohydric conditions, the animals took shelter in the central part of the columns: 31 galleries against 19.5 peripheric for comparable volumes). The preferential contact with the stones is related to the thermopreferendum. In case of soil freezing the thermopreferendum inverts to values near to 0°C. In this situation, the anecics, the epiendogeics, and, if the ice penetrates deeply, almost all the endogeics, can no longer feed on the surface (anecics, epianecics) or in the horizons rich in organic substance (endogeics). Thus, many species enter «hibernation» (Bouché, 1972) rolling-up like some quiescent animals, or sometimes without rolling-up *just under the frozen soil layer*.

In these conditions of famine, these poikilothermes minimize their trophoenergetic needs. If the cold penetrates more deeply into the soil and a ice-crystal touches a hibernating earthworms, it wakes up and crawles toward the lower level, to avoid being trapped in the ice. This is easily verified by placing some earthworms in some water at 0°C with or without crystals of melting ice, as I observed in an unsuccessful attempt to obtain anaesthesia by cold. The hibernation is not total since some species can live in «positive» thermopreferendum on their reserves. As the periods of frozen soil are too short I have not been able to study the inversion behaviour among the species. It is easy to verify hibernation by breaking the frozen soil and observing the concentration of earthworms just under the level of frozen ground.

In summary, earthworms, particularly the anecic, use their vertical galleries for a thermopreferendum, that allow them to exploit the warm micro-habitats (superficial stones). In case of ice associated with famine, the thermopreferendum inverts: hibernation with its tropho-energetic saving takes place.

— *pre-oral incubation*: typical of the large *Lumbricus* epianecic, that bury in their burrow, in conditions of dampness and temperature favourable to micro-organisms the coriaceous leaves, not well decomposed on the surface, avoiding the «pasteurization» that affects the dead leaves on the surface exposed to daily evaporation-condensation rhythms. In this way they have a reserve of alimentary rations placed in pre-oral incubation;

— *post-anal incubation*: the ingestion of coarse elements, their digestive crushing results in enriched excrement that after undergoing microbic incubation in the soil (on the soil in faeces) are reingested. The food of *Nicodrilus velox* (Bouché, 1967) is mainly constituted by these post-anal rations (Bouché et al., 1983).

In which measure do the other elements of the community, especially the endogeics, not make use of these pre-oral and post-anal rations? The question is still without an answer. In both the above mentioned cases, there is the creation of an alimentary stock, with successive distribution in time. For the anecic, the important litter burial in autumn and winter is probably followed in spring by the use of some reserves, made of post-anal rations, until their exhaustion (vegetation produces little dead substance in this season). This would better explain the photoperiodical diapause of June.

6. Synthetic conclusions

To conclude, before attempting a general schematization we will deal with two typical behaviours of the true anecic: the vertical burrows and their organo-mineral feeding.

6.1 *Why do anecics dig deep open burrows?*

The first answer would be to estivate during dry periods. However this is true for the *Lumbricus terrestris* epianecics, but not for the anecics *stricto sensu*. The small lodges of diapause are found from -40 cm to -60 cm, sometimes a little below, in the Cîteaux meadow, for *N. longus*, *N. nocturnus*, *N. longus ripicola*, confirming Saussey's observations (1981) on *N. giardi* and my qualitative observations on *N. caliginosus meridionalis*, *Scherotheca savignyi*, *Scherotheca gigas mifuga* and *Scherotheca gigas rhodana*. This leads to the question: why do these animals dig burrows as deep as 1.5 to 2 m (*Nicodrilus ssp.*) and also 5 to 6 (some *Scherotheca*). These burrows appear to be an essential means to find in their thermic and hydro gradients the hygrothermopreferendum position the nearest the optimum.

This is a clear selective advantage considering the accumulation of surface

litter in the «dry season» and it also explains the renewal of productive surface casts activity in autumn (Fig. 1) starting from the re-ordering the burrow system at the end of the summer lethargy. Perhaps it is an element (together with the existence of litter, rich in sclerophylles) that would explain the gigantism of certain mediterranean anecics (*Allolobophora robusta, Scherotheca ssp.*).

6.2 *Why do earthworms ingest unassimilable mineral fractions?*

While it is evident that the endogeics and especially the oligohumics, that use dispersed food, ingest mineral soil to extract the assimilable organic fractions, it is not evident that the *Lumbricus*, which have some epigeic forms ingesting few elements of mineral layers, have some epianecic forms that ingest an important mineral fraction. This behaviour is partly explained by their need to dig subvertical burrows and by their feeding on substances derived from post-anal incubation. By ingesting and burying the superficial litter immediately after its emanation by plants, the anecics and epianecics subtract this food from the epigeic straminivore earthworms (*Dendrobaena rubida, Lumbricus rubellus rubellus*) or others (larvae of the *Bibionidae* and *Sciaridae* dipterans and even mushrooms (white putrefaction, capable of an effective degradation, Toutain, 1981).

The anecic worms soon collect all that can be immediately assimilated and place it in reserve, and thus, the post-anal food is available after a certain incubation. This, because of its concentration in micro-organisms of biogenetic elements, particularly nitrogen, favours bacteria growth and impedes competition from white putrefaction, insect larvae, mushrooms.

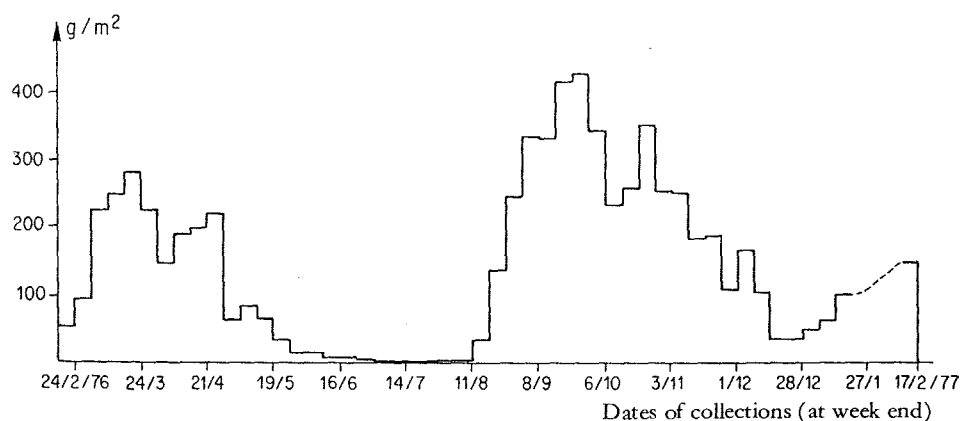The question is whether certain endogeics use this reserve of the anecics.

Fig. 1 - Weekly production of surface casts at Cîteaux (from 24/02/75 to 17/02/76) on the grounds of Beugnot (1978): notice the autumnal maximum.

7. Conclusions

Thanks to *in situ* methods of quantitative observations, on the body temperature, on element turnover, on the activity observed through mobility indices, on the directly observed distribution (qualitatively, considering the difficulties of such observations) and thanks to a knowledge of the causes of lethargy, we are now beginning to understand the subterranean behaviour of earthworms. Even if there is still much to learn, we can now address our research to a less arbitrary and more sure knowledge. I have said little about the subterranean horizontal movement of earthworms, still not well known, because it seems very reduced, and the first coloured markings (Mazaud & Bouché, 1980) in intercompetition environments, have confirmed an observation acquired with introductions on «free» environments (Stockdill, 1966).

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