A quest for the role of habitat quality in nature conservation

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3 Population level consequences of toxicological influences on individual growth and reproduction in *Lumbricus rubellus* (Lumbricidae, Oligochaeta)

Abstract

The effects of increased environmental concentrations of copper on the population dynamics of *Lumbricus rubellus* are investigated. A size-structured matrix model is used to translate sublethal effects on individual growth and reproduction into their population dynamical consequences. Laboratory data on growth and reproduction under different, sublethal conditions of copper stress are used to parameterise the model. An estimate for the critical threshold concentration of copper (critical in a sense that the population growth rate at this concentration equals zero), obtained from the model analysis, agrees well with observations on field populations of *L. rubellus*.

Introduction

The influence of chemical stress on a population as a whole can be assessed by carrying out toxicity tests on the population itself. Alternatively, these population consequences can be inferred using mathematical models that incorporate information on survival, reproduction and growth during the entire life cycle of an individual organism. Next to being a laborious, costly, and time-consuming approach, toxicity tests performed at the population level are sometimes difficult to interpret. For example, Edwards and Brown (1982) studied the effects of pesticides on earthworm populations living in grassland plots. Following the inflicted mortality, repopulation of the plots in their study was observed. It was unclear whether this recovery was due to surviving earthworms, hatching cocoons, or re-invasion. Most important of all, however, experimental studies to assess the toxicity effects on populations in their natural environment might be ethically not justifiable.

In this paper a mathematical model is employed to assess the consequences of increased concentrations of toxicants in the natural environment on the population dynamics of *Lumbricus rubellus*. The focus is on sublethal concentrations of chemical compounds that modify growth, development, and/or reproduction of the individual organism. Experimental studies with individuals of *L. rubellus*, living under different concentrations of copper in sandy loam soil, clearly reveal inhibition of all life processes
due to the induced copper stress (Ma 1983, 1984; see also Figs. 3.4 and 3.5). The important ecotoxicological question is how these influences translate into a consequence on the level of a population, given that this population is dynamic and in tight interaction with other biotic and abiotic factors (food resources, predators, etc.) as well.

Ecological studies on earthworms have primarily focused on the effects of abiotic factors, such as soil humidity and temperature, and less so on the effects of biotic factors, such as the availability of food or predation (Lavelle & Meyer 1983; Reinecke & Venter 1985; Reinecke et al. 1992). However, only biotic factors can be responsible for the regulation of earthworm populations through density dependence. A model, which is targeted at investigating changes in population densities due to toxicants, can, therefore, hardly be based on available biological information. As a useful alternative, the maximum population growth rate was adopted as a measure of population performance and investigates how copper stress on individuals of *L. rubellus* induce changes therein.

Causal relationships between mechanisms on the individual level and population level consequences can be investigated using ‘structured population’ or ‘individual-based’ models that basically adopt the biological individual as the central unit in the modelling process (Caswell 1989; DeAngelis & Gross 1992). Using a description of the behaviour of a single individual (growth, development, reproduction and mortality) under a range of biotic and abiotic environmental conditions, these models employ bookkeeping-like operations to specify a model for the entire collection of individuals, i.e. the population. Using a size-structured matrix model (Caswell 1989) the observed toxic influences reported by Ma (1983, 1984) were translated into changes in the maximum population growth rate in order to estimate the critical threshold concentration for copper (critical in a sense that the population growth rate at this concentration equals zero). The results are compared with observations on natural situations. To assess where in the range between unstressed and extinction conditions a field population is actually living, the applicability of the population structure (composition in terms of juvenile, subadult and adult individuals) was investigated.
Model formulation

Individual growth, development, and reproduction of *Lumbricus rubellus* can be successfully represented with a simple model for the individual energy budget introduced by Kooijman and Metz (1984). The observed changes in individual behaviour due to copper stress are then translated into changes of the parameters of this model. Individual survival was modelled phenomenologically on the basis of experimental data reported by Lakhani and Satchell (1970) for *L. terrestris*. To yield an estimate of the maximum population growth rate a matrix model (see Caswell 1989) was formulated that incorporates all information on the life cycle of *L. rubellus*. The life cycle of an individual was assumed to be subdivided into four distinct developmental stages, i.e. the cocoon, juvenile, subadult and adult stage, based on size criteria, following the experimental data of Ma (1983). The rate of progression through these developmental stages was derived from the energy budget model.

![Energy channelling diagram](image)

**Figure 3.1**

Schematic representation of the energy channelling in the model of the individual behaviour of *L. rubellus* (after Kooijman & Metz 1984).
A model for the individual behaviour of *L. rubellus*

The central assumption in the Kooijman and Metz energy budget model is that growth and maintenance are more directly competing for available energy with each other than with reproduction. Assimilated energy is allocated in a fixed proportion $K$ to growth and maintenance, and a proportion $1-K$ to reproduction and development (see Fig. 3.1). Energy requirements for maintenance always take precedence over growth and reproduction. Food intake is taken to be proportional to surface area and growth and maintenance are proportional to wet weight ($W$). These assumptions lead to an attenuating growth curve under constant food conditions. The model furthermore assumes that individuals with different sizes have the same allometric relations, so that surface area is proportional to $W^{2/3}$. Reproduction is assumed to start only after reaching a threshold size, referred to as the adult size. Smaller individuals are assumed to spend the energy channelled to reproduction on developing reproductive organs. For a complete derivation see Kooijman & Metz 1984.

The model assumptions imply that under constant food conditions the individuals will grow according to the von Bertalanffy growth curve:

$$ l(a) = l_m - (l_m - l_b) e^{-\gamma a} $$  \hspace{1cm} (3.1)

where $l(a)$ refers to the individual length, $l_b$ equals length at birth, and $l_m$ equals maximum attainable length, $\gamma$ the growth rate in weight per unit of time, and $a$ is age. Although reference is made to the quantity $l$ as length, it should be kept in mind that $l$ actually refers to wet weight to the power of one-third. Because of the allometric relations, $l$ is only proportional to the real individual length.

Given the von Bertalanffy growth curve, the assumptions that food intake is proportional to surface area $I^2$ and that a constant fraction of the assimilated food is channelled into reproduction imply that the reproduction rate of an individual of age $a$ equals:

$$ m(a) = r_m[l_m - (l_m - l_b) e^{-\gamma a}]^2 \quad \text{for} \quad l(a) \geq l_{ad}, $$  \hspace{1cm} (3.2)

where $r_m$ equals the maximum reproduction rate per unit surface area, i.e. $r_m l_m^2$ equals the reproduction rate of an individual with the maximum length, and $l_{ad}$ equals the size of a maturing individual. Individuals with a size smaller than $l_{ad}$ use the energy channelled to reproduction and development for the formation of reproductive organs only, therefore, their reproduction rate is zero. The assumption that the onset of reproduction is triggered by reaching a threshold size is in close agreement with the observations by Ma (1983).

The relations above, linking the weight and the reproductive rate of an individual to its age under a specific set of conditions, were fitted to the experimental data from Ma (1983, 1984).
To complete the description of the individual life history, a model of individual survival has to be formulated. Although *L. rubellus* is a well-studied species, it was not possible to locate any data on individual mortality of *L. rubellus* in literature. Therefore, mortality data of *L. terrestris* were used to derive an estimated survival curve for *L. rubellus*. Lakhani and Satchell (1970) proposed the following survival curve for a population of *L. terrestris* living under optimal, laboratory conditions:

\[
S(t) = \left( \frac{1 - at}{1 + bt} \right)^k
\]  

(3.3)

Parameter values for *L. terrestris* are estimated as \( a = 0.0004 \), \( b = 0.0056 \) and \( k = 0.369 \). The parameter \( a \) can be clearly interpreted as the inverse of the maximum life span of an individual *L. terrestris*. To describe the survival of *L. rubellus* the same functional form was used as derived by Lakhani and Satchell (1970). The parameters that involved the unit of time (both \( a \) and \( b \)) were scaled by the ratio of the maximum life span of *L. terrestris* and *L. rubellus*, respectively. The maximum life span of *L. rubellus* is set to 750 days (Ma, pers. comm.). Hence, \( a = 0.0014 \), \( b = 0.02 \) and \( k = 0.369 \) were used as reasonable parameter values for *L. rubellus*. Figure 3.2 presents the resulting survival curve for *L. rubellus* that was applied for the population dynamical model, investigated in this paper.

![figure 3.2](image-url)

**Figure 3.2**
Survival curve for *L. rubellus*, as inferred from Lakhani & Satchell 1970.
A matrix model for the population dynamics of *L. rubellus*

To translate the copper-induced changes in individual behaviour of *L. rubellus* into population level consequences, a size-structured matrix model was used that incorporated all relevant aspects of the life history. In this model the life cycle of an individual is subdivided into four distinct developmental stages: cocoon, juvenile, subadult and adult. Given the number of individuals in each of these developmental stages at some time $t$, the population model determines the size and composition of the population one time step later at time $t+1$ (as basic unit of time a week was adopted). All individuals within each developmental stage are assumed to be identical. Within one time step a single individual can (1) survive and stay in the same developmental stage with probability $P_i$, (2) survive and move to the next developmental stage with probability $G_i$ (provided it was not an adult), and (3), if in the adult stage, produce a certain number of viable cocoons, of which the average number produced per adult individual per unit time is indicated by the quantity $F_i$. Figure 3.3 summarizes the life cycle of an individual and the relevant population dynamical processes. The values of the transition probabilities are completely determined by the model for the individual behaviour, described above.

Let $c(t)$, $j(t)$, $s(t)$ and $a(t)$ be the number of cocoons, juveniles, subadults and adults constituting the population at time $t$. On the basis of the life cycle graph in

![Figure 3.3](image-url)

*Figure 3.3*

Graph representing the life cycle of an individual *L. rubellus*. 
Figure 3.3, it is possible to derive the values of \( c, j, s \) and \( a \) one time step later by simple bookkeeping

\[
\begin{align*}
    c(t+1) &= P_1c(t) + F_4a(t) \quad (3.4) \\
    j(t+1) &= P_2j(t) + G_1c(t) \quad (3.5) \\
    s(t+1) &= P_3s(t) + G_2j(t) \quad (3.6) \\
    a(t+1) &= P_4a(t) + G_3s(t) \quad (3.7)
\end{align*}
\]

These equations specify that the number of cocoons at time \( t+1 \) (\( c(t+1) \)) is equal to the number of cocoons at time \( t \) that survived, but did not hatch during the time interval \( t \) to \( t+1 \) (\( P_1c(t) \)), plus the number of viable cocoons produced by the adults present at time \( t \) during the time interval \( t \) to \( t+1 \) (\( F_4a(t) \)).

The number of juveniles at time \( t+1 \) (\( j(t+1) \)) is equal to the number of juveniles at time \( t \) that survived and stayed in the juvenile class during the time interval \( t \) to \( t+1 \) (\( P_2j(t) \)), plus the number of cocoons that developed into juveniles during the time interval \( t \) to \( t+1 \) (\( G_1c(t) \)). Equations 3.6 and 3.7 can be interpreted analogously.

Let \( n(t) \) be a vector denoting the number of individuals in the different developmental stages at time \( t \) ('the population vector'):

\[
n(t) = \begin{pmatrix} c(t) \\ j(t) \\ s(t) \\ a(t) \end{pmatrix} \quad (3.8)
\]

Using the population vector, \( n(t) \), equations 3.4, 3.5, 3.6, and 3.7 can be rewritten in matrix notation as:

\[
n(t+1) = Mn(t) \quad (3.9)
\]

in which

\[
M = \begin{pmatrix} P_1 & 0 & 0 & F_4 \\ G_1 & P_2 & 0 & 0 \\ 0 & G_2 & P_3 & 0 \\ 0 & 0 & G_3 & P_4 \end{pmatrix} \quad (3.10)
\]

The matrix \( M \) is usually referred to as the population projection matrix and can be
interpreted as a mathematical representation of the life cycle graph. Caswell (1989) provides an extensive introduction to the theory of matrix models, including their formulation, analysis, and application. Of special relevance for the current study is the fact that the long-term behaviour of \( n(t) \) depends on the eigenvalues of the population projection matrix. If the environment remains stable, the population will grow with a rate equal to the largest eigenvalue of \( M \). The largest eigenvalue of \( M \) is directly related to the maximum population growth rate: \( \lambda_m = \rho \), where \( \rho \) equals the maximum population growth rate, and \( \lambda_m \) the largest eigenvalue.

Formulas for individual growth, reproduction and survival (equations 3.1, 3.2, and 3.3) described in the previous section were used to derive expressions for the life cycle parameters \( P, G, \) and \( F \). The relations between the model of the individual behaviour and the life cycle parameters of \( L. \) rubellus are derived in Appendix 3.1.

![Figure 3.4](image)

Figure 3.4
Effect of copper on the growth and development of \( L. \) rubellus in sandy loam soil (after Ma 1983). Open arrows indicate the mean age and size at which individuals entered the subadult stage (defined as individuals that show the first signs of a clitellum), filled arrows indicate the mean age and size at which individuals become adult (that is, reproductively active).

- control, ○ Cu 60 mg kg\(^{-1}\), ▼ Cu 145 mg kg\(^{-1}\), and ▽ Cu 362 mg kg\(^{-1}\).
Experimental data and parameterisation

Experimental data from Ma (1983, 1984) clearly indicate sublethal effects of copper on the individual behaviour of *Lumbricus rubellus* raised in the laboratory under otherwise optimal conditions. Figures 3.4 and 3.5 summarize these toxic effects on individual growth and reproduction, respectively. Figure 3.4 indicates that the growth rate and maximum size of an individual *L. rubellus* decrease in the presence of increased copper concentrations. The data indicate that individuals reach the subadult and adult stage at fixed weights of 500 mg (open arrow) and 780 mg (solid arrow), respectively. These weight thresholds are equivalent with a length at reaching subadulthood and adulthood of $l_s=7.9\text{mg}^{1/3}$ and $l_{ad}=9.2\text{mg}^{1/3}$ (Ma 1983). These threshold values are not influenced by the increased copper concentration.

The energy budget model offers a mechanistic link between physiological processes, such as maintenance and food consumption, and individual growth and reproduction. The term 'scenario' is used to indicate the specific mode of action of a toxic substance on one or more of the physiological processes that are accounted for in the energy budget model.

![Figure 3.5](image)

Figure 3.5

Effect of copper on the reproduction of *L. rubellus* in sandy loam soil (Ma 1984).
On the basis of the data reported by Ma (1983, 1984), three possible scenarios of toxic influence were identified. The reductions in individual growth in the presence of increased copper concentrations (see Fig. 3.4) could possibly be caused by (1) a decrease in the assimilation of energy or (2) increased maintenance requirements for detoxification. These possibilities constitute the first two scenarios. In the energy budget model the first scenario also directly causes a reduction of the reproductive output, for which a fixed fraction $1-K$ of the assimilated energy is invariably used. The second scenario, increased maintenance requirements, directly leads to a decrease in growth (maintenance and growth compete for the fraction $K$, see Fig. 3.1), but only indirectly to a reduction of the reproductive output, because individuals will reach smaller maximum sizes (reproduction is a function of size, see equation 3.2). In the publication of Ma (1984) reductions in reproductive output are larger than can be explained on the basis of the two scenarios described above. Since the individuals in these experiments have not been stressed with the enhanced copper concentration throughout their entire life, these reproduction data are not entirely compatible with the individual growth data and do not reflect the long-term consequences of copper stress.

To cover the range of possible influences of the enhanced copper concentration, analysis was made of the first two scenarios to obtain a conservative estimate of the toxicity of copper. In addition, a third scenario was analysed, in which it was assumed that the enhanced copper concentration induced an increase in maintenance requirements for detoxification and an increase in the energy requirements to produce a single cocoon. This last scenario yields the best fit to the experimental observations on both individual growth and reproduction (Ma 1983, 1984). In the opinion of the authors, it therefore constitutes a stricter estimate of the copper toxicity.

The energy budget model of Kooijman and Metz (1984) has been succinctly summarised in this paper by two functions relating the individual length and reproduction to its age (equations 3.1 and 3.2). The changes in the individual growth curve and reproduction due to copper toxicity (Figs. 3.4 and 3.5) lead to different estimates of the parameters $l_m$, $\gamma$, and $r_m$ in these two functions. The parameters $l_m$, $\gamma$, and $r_m$ are actually composite parameters, made up by lower level quantities that refer to characteristics of the underlying energetic processes (for instance, the maintenance requirements per unit biomass) that were used in the original formulation of the energy budget model (Kooijman & Metz 1984). The composite nature of the parameters $l_m$, $\gamma$, and $r_m$ leads to interrelations between them that must be taken into account during the parameter estimation procedure. More details on this estimation are given in Appendix 3.2. The estimation results are presented in Table 3.1.
Figure 3.6
Effect of copper on the population growth rate per day. Dark bar: assimilation scenario, light grey bar: maintenance scenario, dark grey bar: best fit scenario.

Table 3.1
Values of the estimated energy budget parameters for *L. rubellus* under the assumption of three scenarios of toxic influence on individual performance. Indicated copper concentrations are expressed in mg Cu per kilogram sandy loam soil. Within brackets the relative change in the estimated parameter, as compared to the control situation, is given.
Copper stress and population growth reduction in *L. rubellus*

The maximum population growth rate can be determined from the matrix model following the methods discussed extensively in Caswell 1989. Figure 3.6 indicates the effect of increased environmental copper concentrations on the population growth rate in the three toxicity scenarios investigated in this paper. With a background copper concentration (13 mg copper per kg soil) a population of *L. rubellus* can attain a maximum growth rate of 0.012 per day. Obviously the absolute value of this estimate heavily depends on the precise experimental data that were used to formulate the population dynamical model. Relative comparisons between the different copper stress conditions are, however, more robust. From Figure 3.6 it can be concluded that the lower copper concentrations (Cu 60 and Cu 145), in the first and the second scenario, lead to similar population consequences. In all scenarios the model predicts that populations treated with 362 mg copper per kg soil achieve negative growth rates and will hence die out. This extinction of a population living at a copper concentration of 362 mg per kg of soil is the result of the severe reduction in individual growth under these conditions. The maximum attainable length $l_m$ (Table 3.1) at such high copper concentrations is smaller than the size at maturation $l_{ad}$. Hence individuals never mature and are incapable of reproduction. Whenever the toxic stress reduces the maximum attainable length to less than 75% of its normal, unstressed value, $l_m$ is smaller than the size at maturation $l_{ad}$. The critical threshold concentration for copper (critical in a sense that the population growth rate equals zero) can be obtained by plotting the relative decrease in $l_m$ (Table 3.1) against the ambient copper concentration and interpolating between the observations. In case of the assimilation scenario the critical threshold concentration equals approximately 300 mg copper per kg sandy loam soil. Both other scenarios yield estimates of zero population growth rates at copper concentrations of around 200 mg.

Apart from the copper stress, it was considered that the earthworms live under optimal conditions, i.e. in abundance of food and absence of predation. Under field conditions *L. rubellus* will face a combination of stress factors. Hence it was expected that the estimate for the critical threshold concentration of 200 to 300 mg copper per kg of sandy loam soil would be too high. Field studies reported by Ma (1988) showed a steep decline in the size of field populations when copper concentrations increased to 200 mg CuSO$_4$ kg$^{-1}$ of soil. These studies were carried out on grassland plots which were annually treated with copper sulphate. Five regimes of copper application were used, the highest of which, leading to around 200 mg kg$^{-1}$ copper sulphate in the upper 3 cm, had a drastic effect on the density of *L. rubellus* (three years after application the population density of the treated plots was less than 20% of the density of the non-treated plots). Although colonisation has not been excluded in these studies, the low densities of *L. rubellus* occurring at a copper concentration of around 200 mg kg$^{-1}$
Changes in the stable stage distribution due to increased maintenance requirements. Dotted line: percentage of adults; dashed line: percentage of subadults; solid line: percentage of juveniles. The relative increase in maintenance requirements is inversely proportional to the relative decrease in the maximum attainable length $l_m$.

Sandy soil, show that these populations are close to extinction.

Since the maximum population growth rate will scarcely be observable under natural conditions, other statistics on the population of interest should be exploited to assess where in the range between unstressed and extinction conditions the population is currently living. One of the possible candidates for this assessment is the relative composition of the population in terms of juvenile, subadult, and adult individuals. The stable stage distribution of the matrix population model corresponds to the relative composition that the population in the long run would attain. (Mathematically, this stable stage distribution is given by the right eigenvector pertaining to the largest eigenvalue of the matrix $M$; see Caswell 1989 for details.)

Figure 3.7 presents the stable stage distribution of the population as a function of maintenance requirements (scenario 2). For this scenario, plots of the relative changes in the energy budget parameters (Table 3.1) versus the applied copper concentration (not provided) suggest that increases in the environmental copper concentration lead to approximately proportional increases in the maintenance requirements. As Figure 3.7 reveals, substantial changes in the stage distribution only take place near to the point where the population achieved a negative growth rate (i.e. increase in maintenance requirements more than 25%). This result seems to suggest that for these earthworm populations the stable stage distribution is not a useful
statistic to deduce information on the toxicity of the environment. Figure 3.7 also indicates that near to the point of extinction, individuals get trapped in the subadult stage. Here the effect of copper stress on individual growth is so severe that the individuals will not reach the adult size and thus are incapable of reproduction. This observation strengthens the conclusion made by Klok et al. (1997) that the major danger for extinction of *L. rubellus* populations living under stress of sublethal toxicant concentrations resides in the fact that the individuals fail to reach the adult size within their life span.

**Discussion**

This paper exemplifies the application of structured population models to address ecotoxicological problems. The structured approach makes it possible to formulate predictions about the population behaviour, which are firmly based on individual biology. As demonstrated in this paper, these links between the individual and population level are not always straightforward and sometimes counterintuitive.

The practice of environmental risk assessment for toxic substances in The Netherlands is based on single species tests. Acceptable toxicant levels for ecosystems are estimated by applying safety factors to 'No Observed Effect Concentration' (NOECs) of toxicants, which are determined in laboratory experiments (Van Leeuwen 1990). NOECs result from either acute or chronic exposure tests, in which ecologically relevant parameters like survival, reproduction, and growth are monitored. Tests in which the individual is exposed during its entire life are, however, rare. Toxicity tests on *L. rubellus* are directed toward assessing the effects on reproduction. Compared to growth and mortality, reproduction, in most cases, is indeed the most sensitive effect parameter on the individual level. The individual level toxicity data analysed in this paper (Ma 1983, 1984), also reveal a larger effect of copper on reproduction than on growth (Figs. 3.4 and 3.5). However, the population model indicates that the large reduction in individual reproduction by far does not have the same impact on the population growth rate as the 'relatively' small reduction in growth. Therefore, if toxicity effects at the population level are of interest, tests on individual reproduction do not seem to be the appropriate measure. Given a size-dependent development and a maximum life span, it seems that tests on the duration of the preadult stages, i.e. growth through the juvenile stage, will be a better indicator of the population level consequences.

In the model it was unavoidable to make quite drastic assumptions especially about individual survival, because of the virtual absence of experimental observations. The maximum life span of *L. rubellus* was set to 750 days, which may be an underestimate. To consider the possible effects of a longer maximum and mean life
span on the results presented in this paper, a maximum life span of 2500 days was also investigated (this is the maximum life span for *L. terrestris* estimated by Lakhani and Satchell (1970)). The maximum population growth rate derived from the model increases as a result of a rise in the maximum life span. With a longer mean life, the total lifetime reproductive output of each individual will increase, which leads to an increase in maximum population growth rate of up to 20%. In contrast, the critical threshold concentration for copper does not change. This threshold is triggered by the fact that copper reduces growth to a level where the maturation size will not be reached. The individuals are assumed to grow according to the von Bertalanffy growth curve, an attenuating curve, which implies that when the maximum reachable size is smaller than the maturation size, the individuals will never reproduce, independent of their life span.

The matrix model used in this paper must be seen as a tool to consistently translate toxicological influences on the level of the individual into their population level consequences. As a consequence, the reliability of the model predictions is directly related to the amount and nature of the experimental data on which they are based. Parameterisation of the model is one of the major bottlenecks in population dynamical model studies. For *L. rubellus* it was not possible to find a consistent data set in literature, with which reference is made to a set of data that completely documents all relevant aspects of individual biology (growth, reproduction, and survival) for the same cohort of organisms under a controlled set of environmental conditions. The authors emphasize that they see here an interesting field of interplay between experimental and theoretical biologists, which will have a considerable payoff to both. If hierarchical levels of biological organisation must be spanned, as is done to understand the effects of stress on the population, knowing the stress acts primarily on the individual level, this interplay is without doubt a necessity.

**Conclusions**

This model study indicates that the major danger for extinction of *L. rubellus* populations, under stress of sublethal toxicant concentrations, resides in the fact that the individuals fail to reach adulthood within their life span. The critical threshold concentration for copper for populations of *L. rubellus* living in sandy loam soil, derived from the model, is in the range of 200 to 300 mg copper per kg of soil, which is in reasonable agreement with data from field studies. Furthermore, the population structure reveals no substantial changes up to copper concentrations only slightly below the critical level, which makes it virtually impossible to detect copper stress in observations of the population structure (that is its composition in terms of juvenile, subadult and adult individuals).
References


Ma, W. 1984. Sublethal toxic effects of copper on growth, reproduction and litter breakdown activity in the earthworm Lumbricus rubellus, with observations on the influence of temperature and soil pH. Environmental Pollution (Series A) 33: 207-219.


Appendix 3.1

Derivation of life cycle parameters

If the environmental conditions (e.g., food, temperature, and humidity) that the individuals experience were constant, the distribution of individual states in the population, such as age, would stabilize while the numbers grow exponentially (Kooijman & Metz 1984). This rate of exponential growth or intrinsic rate of population growth will be denoted by $r$. To derive formulas for the entries $P$, $G$, and $F$ in the population projection matrix $M$, it is assumed that the population has attained such a stable age distribution.

The stable age distribution of the exponentially growing population can be obtained from the continuous-time version of the Euler-Lotka equation:

$$1 = \int_0^\infty m(a)F(a)e^{-ra} \, da \quad (A3.1.1)$$

where $F$ equals the survival curve, i.e. $F(a)$ the probability for an individual to survive up to age $a$; $m(a)$ represents the reproduction rate of an individual of age $a$; and $r$ equals intrinsic rate of population growth per time unit.

The stable age distribution of the exponentially growing population is given by the function $F(a)e^{-\mu a}$. For computational reasons approximation is made of the survival curve of Lakhani and Satchell (1970), which was introduced in the main text with an exponential function $F(a)e^{-\mu a}$ within each individual life stage of $L.\ rubellus$. This assumption implies that all individuals in a single life stage experience the same, constant mortality rate while in that stage, indicated by the parameter $\mu$. The choice of the exponential function for $F(a)$ allows to obtain explicit expressions for the matrix entries $P$, $G$, and $F$ below. The individual death rate $\mu$ for each single life stage (juvenile, subadult, and adult) is chosen such that the probability of an individual to survive up to the end of the life stage is equal to the value given by the survival curve of Lakhani and Satchell which describes the survival of hatched individuals. This is equivalent to computing an average, constant mortality rate for every life stage, which is subsequently used in the exponential survival function. The same functional form was used to describe the cocoon survival. The percentage of viable cocoons equals 94% (Ma, pers. comm.), leading to $F(a)e^{-\mu a}$ for the cocoon stage.

Using the stable age distribution we can derive the matrix entries $P_i$, $G_i$, and $F_4$. $P_i$, the proportion of individuals that survive and remain in the same stage $i$ during a time step $\Delta$, can be described by:
The numerator in equation A3.1.2 is proportional to the number of individuals that stay in stage $i$ during a time step, while the denominator is proportional to the total number in stage $i$ at time $t - \Delta$ with identical proportionality constants. Multiplying this fraction with the probability to survive during the time step ($e^{-\mu\Delta}$) yields the complete expression for $P_i$.

$G_p$, the proportion of individuals that survive and move to the next stage during a time step $\Delta$, can be described by

$$G_i = \frac{\int_{A_2}^{A_1} e^{-(r+\mu)a} da}{\int_{A_2}^{A_1} e^{-(r+\mu)a} da} e^{-\mu\Delta}$$

The numerator in equation A3.1.3 is proportional to the number of individuals that move to stage $i+1$ during a time step, while the denominator is proportional to the total number in stage $i$ at time $t - \Delta$ with identical proportionality constants. Multiplying this fraction with the probability to survive during the time step ($e^{-\mu\Delta}$) yields the complete expression for $G_i$. The reproductive output of the adults per time step $\Delta$, represented by the matrix entry $F_4$, will be equal to the product of the average adult reproductive rate (that is the total reproductive output of all adults in the population divided by the total number of adults present) and the time step:

$$F_4 = \frac{\int_{A_2}^{A_1} e^{-(r+\mu)a} m(a) da}{\int_{A_2}^{A_1} e^{-(r+\mu)a} da} \Delta$$

In the expressions for $P_i$ and $G_p$, $A_1$ and $A_2$ correspond to the boundary sizes which must be reached to move to the next stage. In case of the cocoon stage, the stage duration is set to a period of six weeks (Ma, pers. comm.). In case of the juvenile, subadult, and adult stages, the corresponding sizes can be obtained using the weight-age relation, given by the von Bertalanffy growth curve.

According to the energy budget model, $L. \ rubellus$ grows following a von Bertalanffy growth curve after leaving the cocoon stage:
\[ W(a)^{1/3} = W_\infty^{1/3} - (W_\infty^{1/3} - W_b^{1/3})e^{-\alpha a} \]  
(A3.1.5)

where \( W \) refers to the individual weight, \( W_\infty \) the maximum attainable weight, \( W_b \) the weight at birth, \( \gamma \) the growth rate in weight per unit of time, and \( a \) age. Equation A3.1.5 can be written more compactly if the symbol \( W^{1/3} \) is substituted by \( l \):

\[ l(a) = l_m - (l_m - l_b)e^{-\alpha a} \]  
(A3.1.6)

where \( l(a) \) refers to the individual length, \( l_m \) to the maximum attainable length, and \( l_b \) equals length at birth.

This relation between weight, or rather length, and age will be used to calculate from the size thresholds \( l_s \) and \( l_{ad} \) the corresponding ages at which an individual reaches subadulthood and adulthood, respectively.

In equation A3.1.4 \( A_{ad} \) equals the age at which an individual reaches the adult length \( l_{ad} \), and \( A_m \) the maximum individual age. The function \( m(a) \) is defined in the discussion of the energy budget model in the main text and represents the individual reproduction rate at age \( a \).

The stage duration of stage \( i \) (for example the subadult stage) will be equal to the time it takes individuals of \( l_i \) to grow to \( l_2(l_{ad}) \).

The expressions for \( P_i \), \( G_{ij} \), and \( F_i \) relate the entries in the population projection matrix \( M \) to the functions and parameters in the energy budget model that were adopted for the basic individual description. With the parameter estimates discussed below, the matrix elements are specified up to the value of the intrinsic rate of population growth. As stated in the main text, this intrinsic rate of growth is directly related to the largest eigenvalue of the matrix itself. An iterative procedure, as is discussed by Caswell (1989), was used to find the final value of the intrinsic population growth rate.

Appendix 3.2

Estimation of the energy budget parameters

The parameter values of the energy budget model were estimated by fitting the von Bertalanffy growth curve (equation 3.1) to the experimental growth data (Ma 1983) and the function relating the individual reproduction rate to the individual size (equation 3.2) to the experimental reproduction data (Ma 1984) using non-linear regression.

First, the energy budget parameters of individual \( L. \ rubellus \) growing under optimal conditions with a background concentration of copper (13 mg per kg of soil,
indicated by Cu 13) were estimated. The maximum reproduction rate per unit surface area $r_m$ was calculated by dividing the number of cocoons produced per day per individual by the square of the mean length of the reproducing individuals at the start of the experiment. From the data (Ma 1984) this individual length was estimated to equal 11.58 mg$^{1/3}$ in the experiments.

The manner in which the different copper concentrations effectuate in the energy budget parameters depends on the scenario chosen and hence the estimation procedures differ for the three scenarios.

The first scenario assumes that an increased copper concentration leads to a reduced assimilation rate of food. This would decrease one of the underlying parameters in the energy budget model, e.g. the maximum energy intake per unit of surface area (for details see Kooijman & Metz 1984). The composite parameters $l_m$ and $r_m$ that were used in the model description are both proportional to this maximum energy intake per unit of surface area and hence it is possible to estimate a multiplicative factor for both parameters from the experimental data under copper stress. The estimation of $l_m^{cu}$ and $r_m^{cu}$ (the values $l_m$ and $r_m$ under copper stress) is done by fitting the von Bertalanffy curve with a fixed $\gamma$ (equal to its unstressed value) to the experimental observations of individual growth under copper stress (Ma 1983). This yields a value for $l_m^{cu}$ that is a factor $m$ smaller than the $l_m$ of the control individuals. The $r_m$ value of the control is subsequently divided by this same factor $m$ to give the $r_m^{cu}$ of the stressed population:

$$
\begin{align*}
  l_m^{cu} &= \frac{l_m}{m} \quad \text{and } r_m^{cu} = \frac{r_m}{m}
\end{align*}
$$

The second scenario assumes that the toxic influence induces a higher maintenance requirement for detoxification purposes. The basic formulation of the energy budget model (Kooijman & Metz 1984) uses a parameter $\xi$ which represents the maintenance requirements per unit of individual weight. In the second scenario this underlying parameter would be increased due to copper stress. The composite parameter $l_m$ that is used here is inversely proportional to $\xi$, while the growth rate $\gamma$ is proportional to it. The value of $r_m$ will not be affected in this scenario. The estimation of $l_m^{cu}$ and $\gamma^{cu}$ under copper stress is done by fitting the von Bertalanffy curve to the experimental data, assuming a multiplicative factor $n$ in $\gamma^{cu}$, which turns up inversely in $l_m^{cu}$:

$$
\begin{align*}
  l_m^{cu} &= \frac{l_m}{n} \quad \text{and } \gamma^{cu} = \gamma \cdot n
\end{align*}
$$

Figure 3.8 provides the resulting von Bertalanffy growth curves fitted to the experimental weight data of *L. rubellus* living under a copper stress of 145 mg kg$^{-1}$ soil.

In the third scenario it is assumed that in addition to an increased maintenance,
the energy requirements to produce a single cocoon also increase. This results in reproduction and growth to be not correlated. The values for \( l_m^{Cu} \) and \( \gamma^{Cu} \) are hence equal to the estimated values of the second scenario. In addition, \( r_m^{Cu} \) is estimated from the experimental observations under copper stress (Ma 1984) using the expression relating the reproduction rate to individual size (that is, the individual reproduction rate which equals \( r_m^{Cu} l(a)^2 \)). The individual size \( l(a) \) here equals the mean length of the reproducing individuals at the start of the experiment.

![Graph](image.png)

**Figure 3.8**

The von Bertalanffy growth curves fitted to the experimental weight data of *L. rubellus* living under a copper stress of 145 mg kg\(^{-1}\) (Ma 1983). ■: experimental observations; thick solid line: maintenance scenario; thin solid line: assimilation scenario.