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Assessing the impact of pesticides on lumbricid populations: an individual-based modelling approach

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Summary

1. In an ecological approach to risk assessment, population models may play an important role. Our population dynamical models take into account the complex life history of earthworms, as well as a particular ecological interaction (predation).

2. Sublethal impact of pesticides is quantified at the individual level in terms of impaired vital rates, i.e. growth, maturation and reproduction. A simple model for the energetic relationships underlying these vital rates quantifies toxic stress mechanistically through proportionality constants relating size to energetic costs of maintenance, growth, food intake and production of offspring.

3. Risk is defined at the population level. Risk resulting from chronic exposure relates to reductions in (equilibrium) density, changes in population size- and age-structure, and probability of surpassing an extinction threshold. Risk posed by a single or intermittent application of a highly degradable pesticide is defined in terms of extinction probabilities and recovery times, and related to pesticide decay and initial applied dose.

4. The models are individual-based and complementary. A deterministic partial differential equation model is used to derive equilibrium properties of the system analytically and to investigate the general dynamic behaviour. An individual-by-individual model shows how this behaviour is influenced by demographic and environmental stochasticity.

5. Results obtained for two species, *Lumbricus rubellus* and *L. terrestris*, indicate that both are sensitive to pesticides affecting the energy available for individual growth, as opposed to the amount of energy available for reproduction. Retarded growth impedes individuals in reaching adulthood. This juvenile delay regulation translates from individual performance to population demography.

6. Life-history characteristics appear to make *L. terrestris* more sensitive to toxic stress than *L. rubellus*, resulting in longer population recovery times.

7. The insights obtained from the models and the way results depend on model assumptions, are discussed, and compared to the little available observational and experimental evidence. Extensions enabling a full ecological risk assessment for pesticide use are identified. Establishing an explicit relationship between ambient concentration and individual performance seems mandatory prior to use of the models as predictive tools.

Key-words: ecotoxicology, *Lumbricus rubellus*, *Lumbricus terrestris*, population dynamics, population recovery.

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Introduction

To evaluate the risk posed by pesticide spraying to biological populations, laboratory experiments establishing a lethal concentration (i.e. lethal for 50% of the individuals: LC50) or a no observed effect concentration (NOEC) for individual vital rates, provide

insufficient information. The final outcome, in terms of the damage inflicted on real populations, depends on the life-history of the species concerned, its ecological relationships to other species, as well as the local physico-chemical properties of the site.

There is a need to incorporate ecological theory in risk assessment procedures (Jepson 1993). Ecological

insights become more important the farther we want to extrapolate individual level information beyond the direct effects on short time scales and small spatial scales. Ecological, mostly non-linear, processes involving predation, competition, dispersal, and local extinction and colonization, are the dominant factors determining how the deleterious effects of toxicants on individuals have an impact at the (meta)population level.

In this paper we use a combination of deterministic and stochastic modelling approaches for the ecological risk assessment of the sublethal effects of pesticide spraying on lumbricid populations. Earthworms were selected because of their important function in agro-ecosystems, and because members of this species group are established test species in standard ecotoxicological research (Greig-Smith *et al.* 1992). However, the approach is applicable to other substances and species. Our models are rooted in a description of individual life-history. A deterministic mechanism regulating population density is incorporated in the models.

The time-scale relating to population recovery and extinction and to the life-history characteristics of the species (high longevity, non-reproductive cocoon and juvenile stages of substantial duration), are well suited to a modelling approach taking into account the internal structure of the population. Models with this property are based on age, size or stage classifications. Klok & de Roos (1996) showed that a stage-structured matrix approach can determine the long-term impact of toxicants on the performance of lumbricid populations, interpreting the asymptotic growth rate as a measure of population fitness. We used a partial differential equation (PDE) to describe the dynamic and static consequences of toxic stress in a population with density-dependent regulation. In this model, the internal population structure is based primarily on a size classification, although some processes depend on age.

Extinction and recovery are essentially probabilistic processes, influenced by demographic stochasticity (erratic behaviour due to chance events in small populations) and environmental stochasticity (leading to fluctuating individual vital rates). We thus complement the continuous model with a stochastic individual-by-individual model. Although both models are individual-based models (DeAngelis & Gross 1992) we will refer to the former as the PDE, and the latter as the IBM.

Without a density-dependent regulatory mechanism (modelled) populations display either exponential growth or decline. Plausible density-dependent mechanisms operating within earthworm populations include food-limitation, predation and crowding effects. Crowding effects are mainly observed under rather unnatural conditions, involving unrealistically high densities. With no experimental results available, we aim to address food-limitation in a separate study. Predation is thus the mechanism

considered in this paper. Earthworms make up a substantial part of the diet of over 200 vertebrate species in north-west Europe (Granval & Aliaga 1988). The foraging behaviour displayed by foxes (Macdonald 1983) and thrushes (Smith 1974) leads us to expect density-dependent predation rates because earthworm populations show a patchy distribution, and detection of a patch will somehow be related to its local density, and because many predators tend to stay longer in high-density patches, visit them more frequently and attract other predators when foraging (e.g. Kruuk 1978). Feedback from local lumbricid density to predator density and performance is ignored, because most predator species do not feed exclusively on earthworms, operate on much larger spatial scales or are present only during a restricted period of the year.

Of two lumbricid species, *Lumbricus rubellus* and *L. terrestris*, experimental data on individual growth, development, reproduction and mortality were collected to obtain estimates of model parameters. In the model, we investigate the impact on population characteristics of a modification in these individual parameters—either constant or dynamic.

Model description

Energy budget models applied in an ecotoxicological context (Kooijman 1986, 1993; Hallam, Lassiter & Kooijman 1989; Nisbet *et al.* 1989; Calow & Sibly 1990; Hallam *et al.* 1990) are a convenient means of avoiding the complexity arising from substance- and species-specific low-level mechanisms. In general, these models describe how the energy available to an organism is allocated to its vital rates—growth, maturation and reproduction—under normal and stressed circumstances. We chose the Kooijman & Metz (1984) model because of its simplicity; lack of experimental data on *Lumbricidae* prevents a more detailed description, e.g. accounting for storage of energy (Kooijman 1993). Assuming food to be unlimited, we simplify the model by omitting the functional response for food intake in the original formulations.

INDIVIDUAL ENERGY BUDGET

The simplified Kooijman–Metz model is described below in condensed form; for a detailed description we refer to Kooijman & Metz (1984). Allocation of energy to basic requirements is size-dependent and described by the following rules. Size is defined as wet-weight (W) or as scaled length l ($= W^{1/3}$). Food (energy) intake is proportional to surface area ($W^{2/3}$), with proportionality constant v . Of the energy assimilated, a fixed fraction is routed to maintenance and growth respiration (κ); the remainder is available for reproduction ($1 - \kappa$). Maintenance respiration is assumed to be proportional to wet-weight (W), with proportionality constant ξ ; growth costs are assumed

Table 1. The relationship between the parameters for individual growth (γ , l_m) and reproduction (r_m), and the underlying parameters of the energy budget model

$\gamma = \frac{\zeta}{3\eta}$	$l_m = \frac{\kappa v}{\zeta}$	$r_m = \frac{(1-\kappa)v}{\omega W_b}$
Maintenance energy consumption rate per unit of weight	ζ (zeta)	Energy time ⁻¹ weight ⁻¹
Growth energy per unit of weight	η (eta)	Energy weight ⁻¹
Proportion of assimilation energy spent on respiration	κ (kappa)	—
Maximum energy intake rate per unit of surface area	v (nu)	Energy time ⁻¹ weight ^{-2/3}
Invested energy per unit of birth weight	ω (omega)	Energy weight ⁻¹

to be related to weight increase per unit of time, with proportionality constant η . Individual growth is thus governed by the equation:

$$\kappa v W^{2/3} = \zeta W + \eta \frac{dW}{dt} \quad \text{eqn 1}$$

Rewriting this equation for scaled length l , with γ (the measure of the growth rate) and l_m (the maximum attainable size of very old individuals) defined as in Table 1, yields individual growth rate:

$$g(l) = \frac{dl}{dt} = \gamma(l_m - l) \quad \text{eqn 2}$$

The fraction $(1-\kappa)$ of energy-intake is available for reproduction in adults and for maturation in immature individuals. Taking into account an energy-investment per offspring, proportional to weight at birth W_b with constant ω , the following balance-equation defines the weight-specific reproductive rate r_w :

$$(1-\kappa)v W^{2/3} = \omega W_b r_w \quad \text{eqn 3}$$

Defining r_m (the maximum reproductive rate per unit surface area) as in Table 1, this simplifies for length-dependent reproductive rate r_l to:

$$r_l = r_m l^2 \quad \text{eqn 4}$$

Maintenance takes precedence over growth; growth stops when energy allocated to maintenance plus growth is just sufficient to meet maintenance. If maintenance cannot be covered, requirements are met by respiration of structural body mass. As a consequence, reproduction may continue, even for individuals losing weight; an observed phenomenon (Ma 1984 for *L. rubellus*; Addison & Holmes 1995 for *Dendrobaena octaedra*). Assuming that no energy is lost in the transitions from available energy to structural body mass and back to available energy, equation 2 also applies to negative growth rates. Because this assumption is implausible, individual performance under stressed conditions will be slightly overated in the simulations. We will refer to the energy proportionality constants more briefly as energy intake v , maintenance energy ζ , growth energy η , and reproduction energy ω .

INDIVIDUAL LIFE-HISTORY

Stages in the life of *Lumbricidae* are cocoon, juvenile, subadult and adult (Edwards & Lofty 1977). We ignore the subadult stage where individuals already

have developed reproductive organs, but do not yet reproduce. We refer to adults as reproducing individuals and juveniles as non-reproducing individuals. Energy allotted to reproduction in juveniles is assumed to be used for the development of the reproductive apparatus (maturation). Experimental evidence for *L. rubellus* (Chuzeau & Fayolle 1989; Ma 1984, 1988) and others, e.g. *Aporrectodea caliginosa* (Springett & Gray 1992) indicates that the transition from juvenile to adult is triggered by size rather than age. We thus introduce l_j as the maturation-size threshold. Under stressed conditions reproducing individuals may shrink, such that $l < l_j$, and become non-reproducing.

Under constant environmental conditions, the growth equation 2 can be solved, yielding l as an explicit function of age x :

$$l(x) = l_m - (l_m - l_b)e^{-\gamma x} \quad \text{eqn 5}$$

Individual growth parameters l_b (scaled length at birth), l_m and γ are obtained by fitting this Von Bertalanffy (1969) equation to measured growth curves. The duration of the juvenile stage, τ , can be found by solving equation 5 for the age at which size l_j has been reached. The duration of the cocoon stage, τ_0 , is assumed to be fixed. During this stage no mortality is assumed to occur (neither background mortality nor density-dependent mortality: see below).

POPULATION LEVEL

For a large population, with a continuous function describing the abundance of individuals over the range of possible body-sizes, the dynamics of the size-distribution can be described by a hyperbolic partial differential equation (Sinko & Streifer 1967):

$$\frac{\partial n_{(l,t)}}{\partial t} + \frac{\partial g_{(l)} n_{(l,t)}}{\partial l} = -\mu_{(l)} n_{(l,t)} \quad \text{eqn 6}$$

The size-distribution $n_{(l,t)}$ changes due to individual growth (given by equation 2) and mortality, given by the function $\mu_{(l)}$, which may depend on individual, population or environmental properties. Assuming all individuals to have the same birth, l_b , maturity, l_j , and asymptotic, l_m , sizes, reproduction appears as the boundary condition:

$$g_{(t)} n_{(t,t_0)} = r_m \int_{t_0}^t n_{(t,t)} dt \quad \text{eqn 7}$$

The mortality rate $\mu_{(t)}$ is assumed to consist of a constant background mortality rate μ_0 (or an age-dependent rate; see below) and a density-dependent mortality rate μ_1 . The *per capita* probability of density-dependent mortality (predation) is assumed to scale linearly with the total number of individuals in the population N (cocoons excluded). The combined mortality rate is thus:

$$\mu_{(t)} = \mu_0 + \mu_1 N_{(t)} \quad \text{eqn 8}$$

This simple representation of density-dependent mortality is justified because of the scarcity of data on preferential predation on certain stages or size-classes. For an unstructured population, this mortality rate would result in logistic population growth.

The PDE model described above is appropriate to study the dynamics of the population independent of the spatial scale (since its state-variables refer to densities). The IBM, based on an identical representation of individual behaviour (equations 2, 4 and 8), is used to study the dynamics of a finite number of discrete individuals. It differs from the PDE by imposing an explicit scale on the system, and in taking whole individuals as basic units. The two representations are expected to yield different results (DeAngelis & Rose 1992) when low population densities are considered and especially when stochastic processes are incorporated in the IBM. Because we consider extinction and recovery (and thus small-numbers population dynamics), we expect the use of discrete individuals and demographic stochasticity to affect the results. Demographic stochasticity is accounted for because mortality is an individual probability of death within a certain time interval. Environmental stochasticity ('natural' fluctuations in vital rates) is accounted for because the duration of the cocoon stage is taken as a normal distributed random variable with a coefficient of variation of 0.1. We

deliberately consider minimal stochasticity, because our primary aim is to test the robustness of results obtained under deterministic conditions. We do not include variability of individuals in the IBM, although we acknowledge its potential role in an ecotoxicological context.

The simulations of the PDE model are performed using a numerical integration method called the 'escalator boxcar train' (De Roos, Dickmann & Metz 1992). For the age-dependent mortality case we had to consider both age and size; thus the actual PDE solved was more complex than equation 6. The IBM is developed and run within the toolkit for ecological simulation 'EcoTalk' (Baveco & Lingeman 1992; Baveco & Smeulders 1994). For the IBM, we use a 1-day timestep to update each individual's state; equivalent to performing an Euler Forward integration of equations 2 and 4 with a 1-day timestep.

Parameter values

GROWTH, DEVELOPMENT AND REPRODUCTION

The energetic parameters themselves are near impossible to measure (Kooijman 1993). However, growth curve analyses yield estimates for the compound parameters b , l , l_m , γ , and r_m . No study was found from which a complete and consistent description of individual life-history of earthworms could be constructed. Consistency here refers to growth and reproduction, as well as hatchling weight and maturation size being measured on the same individuals.

For *Lumbricus rubellus*, information on individual growth was obtained from Cluzeau & Fayolle (1989) and Ma (1984, 1988). The estimated growth parameters γ and l_m show a considerable spread (Table 2). Maximum reproduction rate r_m was estimated from reproduction data obtained from the same individuals. As a consistent set of default values, parameters obtained from Ma (1984, 1988, and unpub-

Table 2. Estimates of growth parameters for *Lumbricus rubellus* and *L. terrestris*, obtained by least-squares fitting experimental data on a Von Bertalanffy growth curve. W_m = maximum asymptotic weight (mg); γ = growth time-constant (day^{-1}); r_m = max. reproductive rate per unit surface area (cocoons $\text{mg}^{-2/3} \text{day}^{-1}$); W_f = maturation weight (mg). The W_m of 6.0 g (unpublished experiment) for *L. rubellus*, is exceptionally large (conditions were optimal with respect to food and density)

Reference	W_m	γ	r_m	W_f	Comment
<i>L. rubellus</i> :					
Ma (1984, 1988)	1865	0.014	0.0010	779	15°C; 3 ind. per pot (1 L)
Cluzeau & Fayolle (1989)	2744	0.021	0.0006	1000	17.5°C; 5 ind. per pot (1 L)
Own experiment (unpublished)	6000	0.0123	0.0030	1600	15°C; 1 ind. per pot (1 L)
<i>L. terrestris</i> :					
Butt <i>et al.</i> (1992); Fig. 4	7271	0.020			20°C; 1 per pot 200 g soil
Butt <i>et al.</i> (1992); Fig. 4	7128	0.0157			15°C; 1 per pot 200 g soil
Butt (1993); Fig. 1	7109	0.0214			20°C; 1 per pot 200 g soil
Butt <i>et al.</i> (1994); Fig. 2	7498	0.0144			20°C; 2 per pot 200 g soil
Butt <i>et al.</i> (1994); Fig. 2	6699	0.0214			20°C; 1 per pot 200 g soil

Table 3. Reproductive rates r_m (cocoons $\text{mg}^{-2/3} \text{ day}^{-1}$) for *L. terrestris* are calculated from experimental data on monthly reproductive rates R (cocoons $\text{ind}^{-1} \text{ month}^{-1}$), combined with estimates of average individual fresh weight W (g)

Reference	R	W	r_m	Comment
Butt <i>et al.</i> (1994); Fig. 3	2.4	5.36	0.00026	20°C; 2 ind. per pot (0.4 L)
Butt <i>et al.</i> (1994); Fig. 3	4.4	5.59	0.00046	20°C; 2 ind. per pot (0.75 L)
Butt <i>et al.</i> (1994); Fig. 3	3.6	4.98	0.00041	20°C; 2 ind. per pot (1.2 L)
Butt (1993); Fig. 2	3.17	6.6	0.00030	20°C; 4 ind. per pot (2.5 L)
Butt <i>et al.</i> (1992); Fig. 2	4	6.6	0.00038	15°C; 2 ind. per pot (1 L)
Butt (1991); Fig. 1	2.8	± 5	0.00032	15°C; 5 ind. per pot (2.5 L) (field collected)

lished data) were selected, including values for maturation size (0.779 g), the size of the hatchlings (0.014 g) and duration of cocoon stage (42 days). The default values apply to a temperature of 15°C, and are identical to values used by Klok & de Roos (1996).

For *Lumbricus terrestris*, growth parameters were estimated from growth curves reported by Butt, Frederickson & Morris (1992, 1994) and Butt (1993) (Table 2). In the field, Lakhani & Satchell (1970) estimated maximum weight at 5–6.25 g; in the laboratory they found values ranging from 8 to 11 g liveweight. Our estimate is inbetween: we use the values obtained at 15°C as a default. In neither study was maximum reproductive rate r_m measured on the same experimental animals. A monthly average was estimated from curves presented in these publications (Table 3). We preferred parameter values obtained under identical experimental set-up, and thus defined default maturation size as 4.2 g (Butt 1991) instead of 3.0 g (Lofs-Holmin 1982; Daniel 1990), hatchling weight as 0.053 g (Butt *et al.* 1992) instead of 0.1 g (Lofs-Holmin 1982) and cocoon incubation time as 91 days (Butt 1991; Meinhardt 1974) instead of 263 (± 114 SD) days (Daniel 1990) (see Table 4).

MORTALITY

Values for cocoon survival for *L. terrestris* at 15°C are given in Butt (1991) and Daniel (1990), 71 and

84%, respectively. For this species, cocoon survival is thus relatively high (under laboratory conditions). Since for *L. rubellus* no values were found, cocoon mortality will be ignored in the model analyses for both species. For *L. terrestris* juveniles and adults, Lakhani & Satchell (1970) estimated the survival curve under laboratory conditions and found age-dependence. The age-dependent mortality function $\mu_{(a)}$ is obtained from the survival function $S_{(a)}$:

$$S_{(a)} = \left[\frac{1 - x_1 a}{1 + x_2 a} \right]^k \quad \text{eqn 9}$$

$$\mu_{(a)} = - \frac{d}{da} \{\ln S_{(a)}\} = \frac{k(x_1 + x_2)}{(1 - x_1 a)(1 + x_2 a)} \quad \text{eqn 10}$$

with parameter values $x_1 = 0.0004$, $x_2 = 0.005$ and $k = 0.4$. Maximum age ($A_{\max}$) is the reciprocal of x_1 . For these values, an average mortality rate can be calculated, amounting to $c. 0.001 \text{ day}^{-1}$. Population behaviour is also studied for constant background mortality rate μ_0 of this magnitude. The associated survival function related to constant mortality is $S_{0(a)} = \exp(-\mu_0 a)$. Other observations that can be related to mortality rates are given by Daniel (1990) who mentions a 10–15% mortality at 16°C during the juvenile stage (of 102–112 days); this would also lead to a μ_0 of 0.001 day^{-1} .

For *L. rubellus* no data on survival were found. We

Table 4. Set of default parameter values, used in model analysis and simulations. Values in parentheses refer to size as fresh weight (W , in mg)

Symbol	<i>L. rubellus</i>	<i>L. terrestris</i>	Definition	Dimension
Variables:				
l			Scaled length ($W^{1/3}$)	$\text{mg}^{1/3}$
Parameters:				
l_b	2.41 (14)	3.76 (53)	Size at birth	$\text{mg}^{1/3}$
l_j	9.2 (779)	16.13 (4200)	Size at maturation	$\text{mg}^{1/3}$
l_m	12.31 (1865)	19.25 (7128)	Maximum attainable size	$\text{mg}^{1/3}$
γ	0.014	0.016	Time constant of individual growth	day^{-1}
r_m	0.00100	0.00038	Max. reproductive rate per unit surface area	$\text{mg}^{-2/3} \text{ day}^{-1}$
μ_0	0.001	0.001	Constant mortality rate	day^{-1}
μ_1	1.87 or $1.94 \cdot 10^{-4}$	1.69 or $1.75 \cdot 10^{-4}$	Dens.-dep. mortality rate (reference pop. with age-dep. or constant backgr. mortality)	$\text{ind}^{-1} \text{ day}^{-1}$
τ_0	42	91	Duration of the cocoon stage	days
x_1	0.0004	0.0004	Reciprocal of longevity	days^{-1}
x_2	0.005	0.005		days^{-1}
k	0.4	0.4		—

have no indication that longevity and survival differ substantially for this species, compared to *L. terrestris*. Thus, we use the same formulation for both species.

PREDATION

Little is known about mortality by predation. In an experimental plot in a calcareous beech forest exclusion of 'macro-predators', i.e. vertebrates (shrews) and carabids, appeared to have less impact than the noise of small-scale spatial variation (Judas 1989). The author concluded that the possible effects of macro-predators are small. From microcosm experiments of chilopod-earthworm predator-prey systems, Judas (1989) concluded that chilopod predation may be responsible for an increase in earthworm mortality (from 31 to 64% over a period of 56 days) of the small and medium size-classes. While chilopod densities in the experiments were comparable to their natural densities in the study area, the juvenile earthworm densities were about twice as high.

Other empirical information are data obtained from Bengtson *et al.* (1976) for an earthworm population consisting mainly of *L. rubellus* and *Aporrectodea caliginosa*. The (high) bird predation rate of 4–5 ind m^{-2} day $^{-1}$ at a standing stock of c. 200 ind m^{-2} , leads to an upper estimate for μ_1 of $5/(200 \cdot 200) = 0.000125$ ind $^{-1}$ day $^{-1}$. In our analyses, the density-dependent mortality rate is treated as of unknown magnitude, with a value that can be adjusted in order to obtain stationary population densities at approximately the densities observed in the field. Bengtson *et al.* (1978) found in the same field experiment some size-selectivity in predation: medium-sized lumbricids made up a larger portion of the stomach contents of plovers. In the absence of additional information, we assume that the predation pressure exerted by the complete spectrum of predators affects all size-classes in the same way.

Risk-assessment methods

Estimates of l_m , l_{m^*} , γ and r_m obtained from analyses of growth and reproduction under stressed conditions, provide relationships between ambient toxicant concentration and individual performance that can be extrapolated from individual to population level impact. However, use of an energy budget model allows for more explicit assumptions about the working mechanism of the stressor and about the interdependence of the compound parameters (Table 1). For instance, identifying the stressor as acting mostly on the maintenance energy consumption rate (ζ) will lead us to expect that both growth coefficient γ and maximum length l_m will be affected.

We define stress as a modification of an energetic parameter, in a negative way. Although we consider a single stressed parameter at a time, the impact of

interacting parameters can be deduced qualitatively from single parameter results, as long as all energetic effects work in the same direction, i.e. increase energetic costs. In case of an instantaneous equilibration of internal and external concentration, a linear relationship between these two concentrations, and a linear relationship between internal concentration and impact on energetic parameters, the abstract stress can be linked to an external toxicant concentration $[tox]$. Stress is thus quantified, for stressed maintenance energy constant ζ , as $\zeta_{stressed} = \zeta_{unaffected} (1 + c[tox])$ (c will be set to one in the following). Results for a population of stressed individuals are compared to a reference population, at equilibrium at 100 ind m^{-2} , with μ_0 of 0.001 day $^{-1}$ (or the default age-dependent mortality rate) and μ_1 (Table 4). This density is moderately high for *L. terrestris* (Daniel 1990), and moderately low for *L. rubellus* (van Rhee & Nathans 1973; Bengtson *et al.* 1976).

CONSTANT STRESS

Long-term constant stress provides insight into long-term (asymptotic or equilibrium) population consequences. Population extinction is certain when no individual reproduces, a trivial condition that is met when the adulthood size-threshold cannot be reached:

$$l_{m(stressed)} \leq l_j \quad \text{eqn 11}$$

This condition involves energy intake constant v or maintenance energy constant ζ both affecting the asymptotic size l_m . Taking into account mortality, a less trivial condition for extinction is derived from Lotka's (1924) integral equation, relating individual properties to population growth rate. For a stationary population, the total offspring produced by an individual over its entire lifespan should average one. In case of a population experiencing density-dependent and density-independent mortality, this condition is given, for constant and age-dependent background mortality, respectively, by:

$$1 = \int_{\tau}^{\infty} e^{-\mu_1 N^* a} S_{0(a)} r_m [l_m - (l_m - l_b) e^{-\gamma a}]^2 da$$

$$1 = \int_{\tau}^{A_{max}} e^{-\mu_1 N^* a} S_{(a)} r_m [l_m - (l_m - l_b) e^{-\gamma a}]^2 da \quad \text{eqn 12}$$

Given a single stressed energy constant modifying one or two of the parameters l_m , γ and r_m , we can solve this equation for the equilibrium density N^* and calculate a stress threshold beyond which mortality is no longer compensated for by reproduction (when N^* becomes zero). This threshold value, calculated for each of the energetic constants, will be referred to as $[tox]_{thr}$. Furthermore, we study how stress, increasing from zero to $[tox]_{thr}$, affects other population level characteristics like average age and weight. Equation

12 and similar equations in the following sections were solved numerically with MathCad (MathSoft 1995).

DYNAMIC STRESS

Pesticides are usually characterized by a short half-life. An equilibrium or asymptotic approach is thus less relevant. Spraying results in initially high, quickly declining concentrations. Actual bio-availability to earthworms is determined by many processes in the soil, including transport and conversion. Although models which describe the fate of pesticides in considerable detail are available (Boesten & Van der Linden 1991), we assume exponential decay, with rate constant δ . For a dynamic stress scaling linearly with environmental concentration of the pesticide, stressed maintenance and reproduction energy constants ζ and ω would have the following dynamic values:

$$\zeta_{\text{stressed}(t)} = \zeta_{\text{unaffected}} \cdot (1 + [\text{tox}]_0 e^{-\delta t})$$

and

$$\omega_{\text{stressed}(t)} = \omega_{\text{unaffected}} \cdot (1 + [\text{tox}]_0 e^{-\delta t}) \quad \text{eqn 13}$$

Here $[\text{tox}]_0$ refers to the initial stress magnitude ('applied dose'). We evaluate whether or not the population persists under different initial doses and degradation rates. Proposed admission criteria in the Netherlands relate to effects or residues detectable a few years after application; thus, the relevant time scale to consider stress impact is of at least this magnitude. Focusing on sublethal effects, we try to answer the following three questions.

First, when will the population go extinct as a result of exposure to a single sublethal dose? In the age-dependent mortality case (with a maximum age), the population is bound to collapse if ambient concentration prevents (almost all) reproduction for the duration of the cocoon stage plus the maximum longevity of adults. Hence, a necessary condition for persistence is that degradation must proceed fast enough to ensure that, after the period $(\tau_0 + A_{\text{max}})$, the stress level will allow reproduction to resume:

$$\delta > (\tau_0 + A_{\text{max}})^{-1} \ln \frac{[\text{tox}]_0}{[\text{tox}]_{\text{thr}}} \quad \text{eqn 14}$$

The condition for persistence stated above is necessary but not sufficient. To establish the persistence-limit more precisely, simulations are performed with the PDE and IBM for a set of $(\delta, [\text{tox}]_0)$ combinations—including one on the calculated borderline to see whether the population will actually recover. The stress is applied to the reference population of *L. terrestris*. With the PDE, only age-dependent mortality is considered; with the IBM both cases are addressed. For the IBM, an area of 4 m² is assumed, implying an equilibrium population size of 400 individuals.

Secondly, how long will it take the population to

recover from a single application? Recovery implies a return to nominal density and size-age distribution. Population dynamics for *L. terrestris* are simulated, with age-dependent mortality, $[\text{tox}]_0$ equalling $[\text{tox}]_{\text{thr}}$ and an initial small number of individuals (2 ind m⁻²) of identical body size l_i . Recovery time is defined as the time required for the total population density (juveniles plus adults) to reach 50 or 90% of the reference equilibrium density (thus, in this context, 50 or 90 ind m⁻², respectively). Results are compared to the population's capacity of increase, as defined by the exponential population growth rate r , in the absence of stress and of density-dependent mortality. This r is calculated from the characteristic equations (for constant and age-dependent background mortality, respectively):

$$1 = \int_{\tau}^{\infty} e^{-r(a+\tau_0)} S_{0(a)} r_m [l_m - (l_m - l_b) e^{-\gamma a}]^2 da$$

$$1 = \int_{\tau}^{A_{\text{max}}} e^{-r(a+\tau_0)} S_{0(a)} r_m [l_m - (l_m - l_b) e^{-\gamma a}]^2 da \quad \text{eqn 15}$$

We contrast the results for recovery to the time T_{rec} required for the stress to decrease to a level $[\text{tox}]_{N^* = 50\%}$ that would, in case of constant stress, permit the population density to establish itself at either 50 or 90 individuals m⁻²:

$$T_{\text{rec}(N^*)} = \delta^{-1} \ln \left(\frac{[\text{tox}]_{\text{thr}}}{[\text{tox}]_{N^* = 50\%}} \right) \quad \text{eqn 16}$$

The values of $[\text{tox}]_{N^* = 50\%}$ and $[\text{tox}]_{N^* = 90\%}$ are calculated by solving (12) for $N^* = 50$ and $N^* = 90$ ind. m⁻², respectively.

Thirdly, what are the additional effects of repeated spraying? Will this lead to a new, semi-equilibrium state, or—depending on frequency of application and the characteristic frequency of the population—to complex patterns of interference and resonance? For *L. terrestris* (age-dependent mortality case) simulations are performed with the IBM, exposing the reference population to a stressor with a short half life (50 days) and a considerable impact on the maintenance energy constant ζ , at application intervals ranging from 400 to 100 days. Each application has the same initial impact on the stressed parameter.

General model results

The sustainable *per capita* loss rate in equilibrium is uniquely defined by life-history parameters. This follows from eqn 12, for age-dependent as well as age-independent mortality (for a detailed calculation of equilibrium model properties, see the Appendix). For the age-independent mortality case, the total removed fraction ($\mu^* = \mu_0 + \mu_1 N^*$) amounts to 0.020 day⁻¹ for *L. rubellus* and 0.018 day⁻¹ for *L. terrestris* (from equation A2). From equation A11 for the total biomass it follows (by dividing the result by N^*) that

the corresponding average individual weight amounts to 405 and 1943 mg, respectively, while average individual lifespan (the reciprocal of μ^*) would be 49 and 54 days. In this case, μ^* also represents the fraction of biomass removed or produced, and is thus equivalent to the population's production/biomass (P/B) ratio, on a daily base (μ^* times N^* times average weight divided by total biomass yields μ^*).

Combining the different estimates for *L. terrestris* of γ and W_m (Table 3), with a r_m ranging from 0.00025 to 0.00050 yields a μ^* ranging from 0.015 to 0.025 day⁻¹. For *L. rubellus*, data sets (Table 2) from Cluzeau & Fayolle (1989) and our own experiments yield additional estimates for μ^* of 0.025 and 0.037 day⁻¹, respectively. Thus, although μ^* for *L. rubellus* may be higher, its value does not differ substantially between species. The sustainable *per capita* loss rate, and therefore average lifespan and the population's P/B ratio, are approximately equal for both species, while average individual weight is five times heavier for *L. terrestris*. For a stationary population at a density of 100 individuals m⁻² the number of individuals removed by density-dependent predation amounts to 100($\mu^* - \mu_0$), almost 2 individuals m⁻² day⁻¹.

The juvenile/adult number ratio is 5.4 for *L. terrestris* and 4.4 for *L. rubellus* for the default constant background mortality case. The cocoon density, in equilibrium equal to $\mu^* N^* \tau_0$, amounts to ≈ 84 cocoons m⁻² for *L. rubellus*, and more than twice this figure for *L. terrestris*.

Transient dynamics (Fig. 1), for a dynamic stress, show that, as in most structured population models incorporating delays in development (Kooijman, van der Hoeven & Van der Werf 1989; De Roos *et al.* 1992), an equilibrium state is reached through a phase of damped oscillations (Fig. 1). For the situation depicted, in the phase of decline and initial recovery, the PDE and IBM yield identical behaviour. For the IBM, fluctuations remain in the equilibrium phase. They result from (mainly) demographic stochasticity acting on adult density and are thus closely related to the scaling of the system. In other simulations (not shown) we observed that initial oscillations disappeared faster in the IBM, due to the variability in cocoon incubation times leading to a faster spreading out of successive birth peaks.

Risk-assessment

CONSTANT STRESS

The curves relating equilibrium density to increased stress levels (Fig. 2a), are either concave (with increased maintenance energy constant ζ and decreased energy intake constant v) or convex (with increased growth energy constant η and increased reproduction energy constant ω). The x-axis in Fig. 2a is relative, scaled on respective values of $[tox]_{thr}$. Applying the same absolute scale (Fig. 2b), the popu-

lation density reacts more to changes in maintenance energy constant ζ and especially in energy intake constant v . This also applies to the other population demographic parameters including average weight (Fig. 3a), age and biomass flux (not depicted). However, assuming that a linear increase in stress actually reflects a linear increasing internal toxicant concentration (e.g. in mg g⁻¹), the total toxicant load transferred to the next trophic level (Fig. 2c) reaches a maximum much sooner for stressed maintenance energy constant ζ and energy intake constant v , due to the 'compensating' effect of a quickly decreasing earthworm density.

The calculated values of $[tox]_{thr}$ (Table 5) consistently show that each population will go extinct with only a 20–40% change in maintenance energy constant ζ and energy intake constant v , or a 20–100 fold change in growth energy constant η and reproduction energy constant ω . Furthermore, with respect to the two most influential parameters (ζ and v), *L. terrestris* appears twice as sensitive to stress at the population level than *L. rubellus*. This result is not affected by background mortality being formulated as constant or age-dependent. Only for stressed growth energy constant η do we find a significant change (halving) in critical threshold level in the case of age-dependent mortality. This is the result of an increase in the proportion of older and smaller individuals in the population (see below), in combination with a maximum age limit.

Average individual lifespan increases from $1/\mu^*$ in the unaffected population, to $1/\mu_0$ in populations near the critical threshold value. The proportion of older individuals thus increases with increasing stress. The size-distribution of the reference population is relatively flat. Stress increases the proportion of large individuals in the population (Fig. 3b) until in the limit case all individuals have the maturation size. For stressed maintenance energy constant ζ and energy intake constant v , l_m is decreased, and thus the size-range will shrink. Only for stressed growth energy constant η , do smaller size-classes become dominant (not depicted).

The chain of effects through which constant stress acts on the population level are a decreased maximum attainable size, a decreased fraction of mature adults and a lowered average birthrate. This, in turn, reduces N^* and hence (density-dependent) mortality. Toxic impact is thus buffered to some extent by density-dependent predation; the remaining individuals benefit by living longer, although they do not reach the same asymptotic size. Proportionally, the larger size-classes dominate.

EXTINCTION AS A RESULT OF A SINGLE APPLICATION

Addressing both a concave and convex response of population density to stress, we focus on the main-

Fig. 1. Dynamics of a *L. terrestris* (model) population, subject to an initially large, but exponentially decaying sublethal stress, applied at time 100. Population divided into cocoons (C), juveniles (J) and adults (A). Age-dependent mortality. Results shown for PDE (smooth lines) and IBM (4 m²) simulations. (a) Stress acting through the maintenance energy constant ζ . Initial stress $[tox]_0 = 0.45$; half-life $T = 1680$ days ($\delta = 0.000413 \text{ day}^{-1}$). (b) Stress acting through reproduction energy constant ω . Initial stress $[tox]_0 = 5500$; half-life $T = 200$ days ($\delta = 0.003466 \text{ day}^{-1}$).

Fig. 2. Equilibrium properties of a *L. terrestris* population under increasing stress ([tox]). For [tox] = 0, the results relate to a reference population with age-independent mortality. (a) Number density (individuals m⁻²) for stress acting through maintenance, and reproduction energy constants ζ and ω , scaled on [tox]_{su}. (b) Idem, for all types of stress, on an absolute scale. (c) Toxicant flux to the next trophic level (mg m⁻² day⁻¹), assuming a linear relationship between internal concentration and stress impact (arbitrary numbers on y-axis).

tenance energy constant ζ and the reproduction energy constant ω . For both species, for stressed maintenance energy constant ζ , Fig. 4 shows the area of extinction for a range of values for half-life T ($= \ln 2 / \delta$) and initial applied dose [tox]₀. The difference between the two species in susceptibility to changes in maintenance costs is reflected in this curve; *L. terrestris* populations will go extinct at a lower stress level and shorter half-life. For increased reproductive costs, a similar curve results (not depicted), though on a much enlarged [tox]₀ scale; the population impact is approximately identical for both species.

Results for dynamically stressed maintenance energy constant ζ (Fig. 1a) show that shortly after application all individuals are non-reproductive (i.e. individuals with size less than l_j). In the absence of reproduction, the population declines. The longer the period of decline takes, the more the population is

made up of equally sized individuals. On the border of the extinction area (Table 6) this decline leads, as expected, to extinction for the age-dependent mortality case, for the PDE with a deterministic death rate, as well as for the IBM with stochastic death probabilities. The assumed maximum age—in both models a deterministic parameter—is apparently the main factor determining extinction, and the condition stated in equation 14 is approximately sufficient. For stochastic simulations with age-independent mortality, persistence is found for the same (T , [tox]₀) combinations as for the age-dependent case (Table 6). However, the absence of a fixed age limit means that in a large number of simulations the population survives a considerably larger stress, because of the (demographic) stochasticity in death rates under conditions of low population density.

The results for stressed reproduction energy con-

Fig. 3. Average size and size-structure in an equilibrium population, with age-independent mortality, of *L. terrestris*, under increasing toxicant stress acting through maintenance and reproduction energy constants ζ and ω . (a) Average weight of an individual (mg), for stress on an absolute scale. (b) Size-structure of the population in the absence of stress (thick line) and for stress at 90% of the threshold level $[tox]_{thr}$ (relative scale). On the y-axis the relative numbers per size-class (size as $W^{1/3}$): equation (A8) divided by N^* . l_m refers to the maximum size in the absence of stress.

Table 5. Stress threshold levels ($[tox]_{thr}$), for *L. rubellus* and *L. terrestris*, with age-dependent $\mu_{0(\omega)}$ and age-independent μ_0 mortality, for stress acting through each energetic parameter

	ζ	η	ν	ω
<i>L. terrestris</i> $\mu_{0(\omega)}$	0.193	22.68	0.193	119.1
<i>L. terrestris</i> μ_0	0.193	45.84	0.193	124.0
<i>L. rubellus</i> $\mu_{0(\omega)}$	0.338	27.50	0.338	128.7
<i>L. rubellus</i> μ_0	0.338	55.28	0.338	135.1

Fig. 4. Persistence boundaries for *L. rubellus* and *L. terrestris*, in the initial dose ($[tox]_0$) – half-life (T) plane, as deduced from equation 14, for the age-dependent mortality case and stress acting through maintenance energy constant ζ .

stant ω are qualitatively identical (Fig. 1b). However, the gradual decrease in reproductive energy costs does not lead to a reproductive outburst (as for decreasing maintenance costs); thus, no oscillations occur and the population increases smoothly.

RECOVERY TIME AFTER A SINGLE APPLICATION

For the age-dependent mortality case, in the absence of any stress (half-life approaching zero), the time required for growth to 50 and 90% of the equilibrium density amounts to c. 350 and 570 days, respectively (Fig. 5). These values specify minimum recovery times of almost a year, after a severe reduction in density. Independent of the half-life of the imposed stress factor, we will always observe such a delay in recovery. Given that, as a rough estimate, 200 model days under constant and fairly optimal conditions better approximate a real year, we would expect recovery times of 2 and 3 years. The exponential population growth rate for *L. terrestris*, in the absence of stress and density-dependence, amounts to 0.0111 day^{-1} . A population with a stable age- and size-structure and in the absence of any growth deceleration due to density dependence, would take 291 days to grow from a density of 2 individuals m^{-2} to a density of 50 individuals m^{-2} and 344 days to reach a density of 90 individuals m^{-2} . For *L. rubellus* corresponding values are 0.0146 day^{-1} , and 220 and 261 days, respectively.

For stress acting through maintenance energy constant ζ , recovery in population density again reflects the on/off switch in reproduction, inherent to our energy budget definitions. Once the maturation-size has been attained, a reproductive burst takes place. For recovery to 50%, only for large half-lives will the decay rate of the stressor become a limiting factor; recovery to 90% is more quickly restricted by the decay rate. For stressed reproduction energy constant ω , recovery more closely follows the exponential

Table 6. Population recovery for *L. terrestris*, for different combinations of initial dose $[tox]_0$ and toxicant decay rate δ (day^{-1}), as in Fig. 4. Stressed maintenance proportionality constant ζ , T = half-life in days; PDE $\mu_{(a)}$ = deterministic simulation with age-dependent mortality; PDE $\mu_{(a)}$ (threshold) = idem, with quasi-extinction threshold; IBM $\mu_{(a)}$ = stochastic simulation with age-dependent mortality; IBM μ_0 = stochastic simulation with age-independent mortality. Deterministic results: 1 indicates persistence; stochastic results: number of surviving populations out of 100 replicates

$[tox]_0$	δ (T)	PDE $\mu_{(a)}$	PDE $\mu_{(a)}$ (threshold)	IBM $\mu_{(a)}$	IBM μ_0
0.45	0.0004125 (1680)	1	1	100/100	100/100
0.50	0.0003750 (1848)*	1	0	0/100	93/100
0.55	0.0003375 (2054)	0	0	0/100	72/100
0.60	0.0003000 (2310)				38/100
0.65	0.0002625 (2641)				21/100

* Borderline value.

Fig. 5. Time required for recovery to 50 and 90% of the reference density for *L. terrestris*, with age-dependent mortality. The stress factor is decaying exponentially from an initial value of $[tox]_{0, \text{ref}}$. Initial population density is 2 ind m^{-2} . For stressed maintenance energy constant ζ , initial individual size was l_j ; for stressed reproduction energy constant ω it was the size corresponding to the age of the individuals. Dotted lines show the time required for the stress to decrease to a level that actually allows this density of 50 or 90 ind m^{-2} to exist as an equilibrium density.

decline in the stress. These results provide a dynamic complement to the static relationship between N^* and the amount of stress depicted in Fig. 2a. A proportional decrease in the amount of stress, moving from right to left in Fig. 2a, will, in case of maintenance energy constant ζ , lead to a large increase in N^* , while in the case of reproduction energy constant ω initially hardly any increase in N^* will be observed. Figure 5 shows that only when stress decay is the limiting process, can we obtain an indication of recovery time from the static picture in Fig. 2a.

REPEATED APPLICATION

Results for *L. terrestris* (Fig. 6) show oscillations in stage-specific densities, with the same frequency as the applied stress. The oscillations have their largest amplitude at an interval of c. 300 days. Apparently, this frequency coincides with the characteristic frequency of the population (see Fig. 1a). Applying the

stress more frequently results in oscillations with a smaller amplitude, but also a lower average. Further increasing the frequency results in population extinction, when stress never declines enough within the application interval to permit any reproduction. With respect to population composition, the most pronounced effect of increasing application frequency is the decreasing proportion of cocoons.

Discussion

Our study shows that populations of *Lumbricidae* are especially sensitive to toxicants affecting the amount of energy available for growth in individual size, as opposed to toxicants affecting the energy available for reproduction. Changes in the proportionality constants for maintenance or energy intake have far more dramatic consequences for population density, population biomass and mean individual weight than changes in the proportionality constants for growth and repro-

Fig. 6. Repeated application of a stressor acting on maintenance energy constant ζ , for *L. terrestris* (age-dependent mortality case). Stress magnitude at application $[\alpha\alpha]_0 = 0.5$, half-life $T = 50$ days ($\delta = 0.014 \text{ day}^{-1}$). First application at time = 1000. Application interval: 400 days (day 1000–3000), 300 days (day 3000–5000), 200 days (day 5000–7000), 150 days (day 7000–9000) and 100 days (day 9000–11000).

duction. Considering the parameter equivalences in Table 1, these findings suggest that the maximum individual size (l_m under unstressed conditions) is crucial to the performance of the population. Three main processes determine population dynamics: (i) individual maturation; (ii) individual reproduction; and (iii) individual mortality. Gurney *et al.* (1996) investigated the equilibrium properties of four different size-structured population models and showed a clear distinction between juvenile delay regulation and adult fecundity regulation. Given that in our model maturation always occurs at a fixed size l_j , our results point to a large influence of juvenile delay regulation. We also believe that this conclusion is relatively robust against changes in the assumptions underlying the energy budget model. The observed, natural fecundity of individual *Lumbricus* is so high that reproduction is almost never a limiting factor. The most sensitive step is therefore reaching this adult stage, that is, the process of individual maturation. Any stress that impedes individuals in reaching adulthood is consequently going to have a noticeable influence. Pesticides affecting individual development may thus be potentially more dangerous than substances affecting reproduction. An indication that pesticides may indeed reduce individual growth rate and thereby lead to retarded maturation, was found in laboratory experiments by Springett & Gray (1992), with *Aporrectodea caliginosa*. However, laboratory studies on *Eisenia andrei* by Brunnering, Viswanathan & Beese (1994)

indicated that terbutylazine and carbofuran mainly affected cocoon production, and not individual growth. Laboratory results from Gunn & Sadd (1994) showed that ivermectin in low doses seriously affected cocoon production of *Eisenia fetida*, but, at higher doses, also inhibited individual growth.

In light of the above arguments, our second major finding, that *Lumbricus terrestris* is more sensitive to toxic stress than *Lumbricus rubellus*, can also be interpreted. Examining the life-history parameters it follows that a newly-matured individual of *Lumbricus terrestris* will have spent c. 91 days in the cocoon, and subsequently c. 100 days in the juvenile stage. Immediately after maturation it will produce c. 0.1 cocoons per day. In contrast, for *Lumbricus rubellus*, the cocoon and juvenile stage will last c. 42 and 83 days, respectively, while a newly matured individual produces c. 0.085 cocoons per day. These values indicate that *Lumbricus terrestris* is relatively more constrained by the duration of its pre-adult stage and less by its adult fecundity, when compared to *Lumbricus rubellus*.

The longer duration of the pre-adult stages in *L. terrestris* is balanced by a larger daily reproductive output after maturation. As a result both species have comparable maximum population growth rates. In an equilibrium situation induced by predation regulation (top-down control of the earthworm population), this growth potential of single individuals has to be balanced by an equally strong predator-induced mor-

tality rate. Hence, in predator-controlled equilibrium situations the expected lifespan for both species is necessarily similar. The density dependent mortality rate induced by predation acts like a buffer for stress with contrasting influences on the individual and the population level: the model predicts that individual performance in terms of growth and reproduction will decrease, leading to the establishment of a new dynamic equilibrium in which the *per capita* mortality will be reduced equally. The population density will also decrease due to the stress, but the life expectancy of a single individual will increase. Consequently, the average individual weight of the individuals in a stressed population will increase also (Fig. 3a). Due to feedback of a predator-induced mortality rate, the negative toxic impact on individual growth and development will lead to a positive change in its outcome, the average individual weight in the stressed population. The reduction in individual growth is, nonetheless, the important factor threatening persistence of the population.

To earthworm predators, toxicants affecting earthworms may have different consequences, depending on the sensitivity of earthworm individual vital rates (Fig. 2c). Either earthworm individual rates are severely affected, reflected in a decreased availability of prey (with a relatively low body-burden) or individual rates, and thus prey availability are relatively unaffected, but prey individuals are highly contaminated. In the latter case, more of the toxicant is transferred to the next food-chain compartment—as long as the predator itself is unaffected by the toxicant.

Following a single application of a toxicant the population will move to a state in which it consists mainly of individuals that are too small to reproduce. Under these circumstances, the (decreasing) concentration of the toxicant is the main determinant of the individual size. Persistence of the population depends critically on the relationship between individual survival and the time it takes for the toxicant to decay to a level where reproduction starts again. The population will perish directly or drop below a pseudo-extinction threshold if the toxicant concentration stays too high for longer than the maximum lifespan of the individual earthworms (either determined deterministically or stochastically). Because we have concentrated on strictly sublethal toxic influences, the last conclusion is very conservative. Once the toxicant concentration drops to levels where individuals can attain reproductive sizes again, *per capita* cocoon production is high and population recovery rapid. The latter is in line with our previous findings that individual reproduction is not a limiting factor.

The recovery time of a population is determined by the decay rate of the toxicant and by population dynamic processes. In the case of a toxic substance affecting the reproductive capacity of individual earthworms (the parameter α), individual growth in size is still rapid, and the development delay between the

production of a cocoon and the maturation of the offspring is short. As a consequence, the recovery period will be closely related to the half life of the toxicant (Fig. 5). In contrast, when the toxicant is affecting individual growth, it will cause a considerable delay in individual development. This increased developmental delay will largely determine the population recovery period. For rapidly decaying toxicants the recovery period is independent of the half-life of the toxicant, and set by the time scale of earthworm growth and development. Recovery may then take many times longer than expected on the basis of NOEC's and pesticide half-lives, as in van Straalen, Schobben & Traas (1992). For slowly decaying toxicants, the half-life of the toxicant is again the main determining factor. The half-life of the toxicant and the developmental delay of the earthworms involve two different time scales of importance for population recovery. The slower of the two always exercises the largest influence. These results suggest that, depending on the affected vital rate, recovery after pesticide application for some pesticides will depend mostly on initial dose, while for others it will be mostly related to half-life.

Senapati *et al.* (1992) investigated sublethal effects of malathion on a rice field earthworm (*Drawida willsi*, Michaelsen). The pesticide was presumed to affect maintenance. Application led to a slight decrease in average worm density and to a marked dominance of adults, whereas non-adults dominated in the untreated plots. This conforms to our model predictions. However, their experiment lasted for 90 days; too short a period to understand the transient internal dynamics of the population fully. Edwards & Brown (1982) found that the total number of earthworms recovered within 12 months, following annual spring application of benomyl. The *Lumbricus terrestris* population showed no recovery at all within this period. This conforms well to the insight obtained from our model study, that the life history of *L. terrestris* necessarily implies slow recovery. In general, however, results from field studies focusing on the population level (e.g. Kula & Kokta 1992), are difficult to interpret with our individual-based framework, unless sufficient details on individual performance are provided.

The validity of the Kooijman–Metz model to represent the behaviour of single individuals is crucial for the robustness of our conclusions. Gurney *et al.* (1996) showed that, although the predictions of four different models of individual behaviour, including the Kooijman–Metz model, were similar at the individual level, their predictions differed markedly at the population level. In equilibrium situations, the control over population demographic characteristics was exerted by different individual properties in the models. We expect population level results to diverge even more under dynamic conditions affecting individual performance, making the appropriate choice of individual level model even more decisive. Our analyses

indicate that crucial elements in the model of Kooijman & Metz (1984) relate to the assumptions on individual growth and maturation under increasingly stressful conditions, i.e. the relationship between l_j and l_m while the latter is decreasing. At present, data on life-history aspects are scarce, such as how maturation is triggered in different earthworm species, how much plasticity a parameter like maturation-size shows, and how earthworms deal with conditions such as starvation in terms of energy allocation priorities. Furthermore, the l_j measured in the laboratory may be considerably lower than its value in the field (Daniel 1990). Experimental studies by Ma (1984, 1986) indicate that individual size plays a major role in maturation, while other studies attest the high reproductive capacity of individual earthworms even under adverse conditions. Hence, we are confident about the outcome of the model that individual growth and development are the main regulating factors in lumbricid populations.

Our approach incorporates more 'ecology' in risk assessment. Besides leading to the insights discussed above, our models can be of practical use in (exploratory) risk assessments. Given experimental data on individual growth, maturation, reproduction and mortality, under a range of toxicant exposure conditions, the models provide 'order of magnitude' estimates of effects on population density and structure, as well as indications of recovery times. For a complete assessment, an explicit exposure and uptake model would be indispensable (Hallam *et al.* 1989). Although we do not expect the general pattern in our results to change from such an extension (e.g. as in Kooijman & van Haren 1990; or Hallam *et al.* 1990), it would facilitate dealing with delayed effects, biomagnification, food-chain effects, as well as lethal toxicant impact, within the same model framework. In contrast, extending the models by addressing alternative regulatory mechanisms, for instance food limitation, may change results dramatically (Kooijman & Metz 1984; Kooijman *et al.* 1989). Unfortunately, little is known about earthworm feeding ecology. To account for food regulation, extensive data on growth and reproduction under different feeding regimes would be required (Daniel 1990). A complete ecological risk assessment should also evaluate population results in a spatial context, and consider recolonization perspectives (Marinissen & van den Bosch 1992; Stein *et al.* 1992), taking into account dispersal characteristics and local spatial distribution (Sherratt & Jepson 1993). Finally, one should try to interpret results on single-species population dynamics in the context of the embedding food-web relationships and nutrient-cycles. By linking population dynamics models to less detailed food-web and carbon/nutrient-cycling models (e.g. de Ruiter, Neutel & Moore 1994) we may obtain a better insight into the ecological consequences of pesticide usage.

The structured-population approach, using infor-

mation on individual life history, can become the skeleton of an ecological risk assessment procedure. The use of partial differential equation and individual-by-individual models side by side, proved fruitful. Both applied individual-based model formalisms are amenable to apparently useful extensions mentioned above. The ease with which realistic details can be added and stochasticity can be accounted for makes the individual-by-individual approach an ideal vehicle for quantitative risk assessment in specific situations. The partial differential-equation approach on the other hand proved very effective in obtaining insight into the general behaviour of the population—including existence and position of equilibria—and in understanding the relationships between population demographic characteristics and individual properties.

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Appendix: equilibrium properties

CONSTANT BACKGROUND MORTALITY

An implicit equation for the relation between the life history parameters and the density-dependent mortality at equilibrium can be derived from Lotka's integral equation (Lotka 1924):

$$\int_{\text{reproductive age}}^{\text{maximum age}} e^{-\text{population-growth-rate} \cdot a} \cdot \text{Maternity-function}(a) \cdot \text{Survival-function}(a) da = 1. \quad \text{eqn A1}$$

For a stationary population (population growth rate of zero) we need to solve equation

$$\int_0^{\infty} r_m [l_m - (l_m - l_b) e^{-\gamma a}]^2 e^{-\mu^* a} da = 1$$

with:

$$\tau = a_{(l)} = \frac{1}{\gamma} \ln \left(\frac{l_m - l_b}{l_m - l_i} \right) \quad \text{eqn A2}$$

to obtain the total mortality rate in equilibrium μ^* , and, indirectly, the equilibrium density N^* , because

$$\mu^* = \mu_0 + \mu_1 N^*$$

The total biomass of the earthworm population depends on the equilibrium number N^* and the size-distribution at equilibrium. For a constant background mortality rate, independent of age and size, the number of individuals of age a , in equilibrium, is given by

$$n_{(a)}^* = n_0 e^{-\mu^* a}. \quad \text{eqn A3}$$

From

$$\int_0^{\infty} n_0 e^{-\mu^* a} da = N^* \quad \text{eqn A4}$$

it follows that the flux into the first age-class is given by

$$n_0 = \mu^* N^* \quad \text{ind age}^{-1} \text{ m}^{-2}. \quad \text{eqn A5}$$

To convert the age-distribution into the size-distribution, we use

$$\int_{a_1}^{a_2} n_{(a)}^* da = \int_{l_{(a_1)}}^{l_{(a_2)}} n_{(l)}^* \frac{da}{dl} dl$$

with

$$a_{(l)} = \frac{1}{\gamma} \ln \left(\frac{l_m - l_b}{l_m - l} \right) \quad \text{eqn A6}$$

and thus the size-distribution is given by

$$m_{(l)}^* = \frac{n_{(a)}^*}{g_{(l,a)}} = \frac{n_0}{\gamma(l_m - l)} e^{-\mu^* a_{(l)}} = \frac{n_0}{\gamma(l_m - l)} \left(\frac{l_m - l}{l_m - l_b} \right)^{\mu^* / \gamma} \quad \text{eqn A7}$$

The influx of newly hatched juveniles into the first size-class (individuals size⁻¹ m⁻²) is given by

$$m_{(l_b)}^* = \frac{n_0}{\gamma(l_m - l_b)} = \frac{\mu^* N^*}{\gamma(l_m - l_b)} \quad \text{eqn A8}$$

The number of juveniles and adults is calculated from

$$\int_{l_b}^{l_i} m_{(l)}^* dl \quad \text{and} \quad \int_{l_i}^{l_m} m_{(l)}^* dl. \quad \text{eqn A9}$$

The total biomass of the population is found by solving

$$\int_a^{\infty} l_{(a)} n_{(a)}^* da, \quad \text{eqn A10}$$

resulting in a general equation for biomass made up by individuals of age a and older:

$$\left[\frac{l_m^3 e^{-\mu^* a}}{\mu^*} - 3l_m^2 (l_m - l_b) \frac{e^{-(\mu^* + \gamma)a}}{\mu^* + \gamma} + 3l_m (l_m - l_b)^2 \frac{e^{-(\mu^* + 2\gamma)a}}{\mu^* + 2\gamma} - (l_m - l_b)^3 \frac{e^{-(\mu^* + 3\gamma)a}}{\mu^* + 3\gamma} \right] \mu^* N^* e^{\mu^* a}.$$

Including individuals of all ages, equation A10 simplifies to:

$$\left[\frac{l_m^3}{\mu^*} - \frac{3l_m^2 (l_m - l_b)}{\mu^* + \gamma} + \frac{3l_m (l_m - l_b)^2}{\mu^* + 2\gamma} - \frac{(l_m - l_b)^3}{\mu^* + 3\gamma} \right] \mu^* N^*. \quad \text{eqn A11}$$

AGE-DEPENDENT BACKGROUND MORTALITY

Proceeding in the same way for the age-dependent mortality rate, we calculate the equilibrium size of the population again by solving Lotka's equation for N^* :

$$\int_0^{A_{\text{max}}} r_m [l_m - (l_m - l_b) e^{-\gamma a}]^2 S_{(a)} e^{-\mu_1 N^* a} da = 1. \quad \text{eqn A12}$$

From

$$\int_0^{A_{\max}} n_0 S_{(a)} e^{-\mu_1 N^* a} da = N^* \quad \text{eqn A13}$$

it follows that

$$n_0 = \frac{N^*}{\int_0^{A_{\max}} S_{(a)} e^{-\mu_1 N^* a} da} \quad \text{eqn A14}$$

The age-distribution in equilibrium is given by

$$n_{(a)}^* = n_0 S_{(a)} e^{-\mu_1 N^* a} \quad \text{eqn A15}$$

and the size-distribution by

$$\begin{aligned} m_{(i)}^* &= \frac{n[l_{(i)}]_{(a)}^*}{\sum [l_{(i)}]} = \frac{n_0}{\gamma(l_m - l)} S_{(a(i))} e^{-\mu_1 N^* a_{(i)}} \\ &= \frac{n_0}{\gamma(l_m - l)} S_{(i)} \left(\frac{l_m - l}{l_m - l_b} \right)^{\mu_1 N^* / \gamma} \quad \text{eqn A16} \end{aligned}$$

with the influx in the first size-class given by

$$m_{(0)} = \frac{n_0}{\gamma(l_m - l_b)} = \frac{N^*}{\gamma(l_m - l_b) \int_0^{A_{\max}} S_{(a)} e^{-\mu_1 N^* a} da} \quad \text{eqn A17}$$

RELATIONSHIP BETWEEN CONSTANT AND AGE-DEPENDENT MORTALITY RATES

The average lifespan of an individual, in the absence of density-dependent mortality, is in the constant background mortality case simply given by

$$\int_0^{\infty} e^{-\mu_0 a} da = \frac{1}{\mu_0} \quad \text{eqn A18}$$

while for the age-dependent mortality case it is given by

$$\int_0^{1/x_1} \left(\frac{1 - x_1 a}{1 + x_2 a} \right)^k da. \quad \text{eqn A19}$$

Solving the latter for the default parameter values, it follows that the average age-dependent mortality rate can be approximated by a μ_0 of 0.001.

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