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LIFE HISTORIES AND POPULATION DYNAMICS
OF THREE EARTHWORM SPECIES (OLIGOCHAETA:LUMBRICIDAE)
IN A NORTHERN MICHIGAN HARDWOOD FOREST

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Mark Timothy Thogerson

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LIFE HISTORIES AND POPULATION DYNAMICS OF THREE EARTHWORM SPECIES (OLIGOCHAETA:LUMBRICIDAE) IN A NORTHERN MICHIGAN HARDWOOD FOREST

By

Mark Timothy Thogerson

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in partial fulfillment of the requirements
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ABSTRACT

LIFE HISTORIES AND POPULATION DYNAMICS OF THREE EARTHWORM SPECIES (OLIGOCHAETA:LUMBRICIDAE) IN A NORTHERN MICHIGAN HARDWOOD FOREST

By

Mark Timothy Thogerson

Life histories of *Dendrobaena octaedra* (Savigny), *Lumbricus rubellus* Hoffmeister and *Aporrectodea tuberculata* (Eisen) are presented, based on transition matrix population models and original field observations. The matrix models are of a new type, being dynamic in nature and using environmental conditions as driving variables. The models themselves are intended to be adaptable to other earthworm species, and may be useful to both soil ecologists and vermiculturists.

Both *D. octaedra* and *L. rubellus* were found to have an approximate three-year maximum lifespan in northern Michigan, averaging a life cycle approximately two years in length. Small immatures hatching early in the warm season grow rapidly, some of them becoming reproductive near the end of their first summer. Most of the cocoon production takes place during the second year of life, with

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about 75% of the cocoons produced during this year. These species can be classified as r-adapted, with high juvenile mortality, rapid growth, relatively small adult size, high cocoon production and a short life cycle.

A. tuberculata grows more slowly, reaching maturity in its second year, with maximum cocoon production in the third year after hatching. Cocoon production continues for several years. The maximum lifespan is about seven years, with an approximate four-year average life cycle. This species tends toward being K-adapted, with substantially lower juvenile mortality, slower growth, a constant mortality rate throughout its adult life, lower cocoon production, larger adult size, and a longer lifespan with a noticeable proportion of individuals living to the maximum physiological age.

The *A. tuberculata* model is also used to explore possible population-level effects of extremely low frequency (ELF) electromagnetic fields associated with the operation of the United States Navy's ELF antenna in northern Michigan. Significant decreases in clitellate earthworm densities were found ($p = 0.001$) between observed field populations and predicted model values, given mean monthly temperature and moisture data; however, higher fecundities of those clitellates remaining may offset the lower clitellate densities.

A new technique for permanently marking earthworms and other soft-bodied invertebrates using tattoos is presented, as is a modified and automated technique for soil moisture determination via time-domain reflectometry.

This diss

This dissertation is dedicated to the memory of my father, Rev. D. D. Thogerson

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ACKNOWLEDGEMENTS

Ecological research of this scope is impossible without the assistance of many people. I wish to thank my graduate committee, Drs. Richard and Renate Snider, Thomas Burton, Ralph Pax, and Donald Dickmann for their support, guidance and patience throughout the years of this project. Renate Snider taught me many things about soil biology and ecology over the years of fieldwork, and Donald Dickmann made it possible for me to complete my field observations on cocoons by allowing me to place them in an experimental forest near campus.

Several undergraduates, technicians and high schoolers helped with fieldwork, but three stand out: Chad Schaedig, Amy Ottoson and Dana Feak assisted me with collection and processing of my bucket microcosms on many occasions.

Finally, I wish to acknowledge the love and support of my family and friends throughout my graduate study. Without the knowledge that they were behind me, I would not have made it.

TABLE OF CONTENTS

LIST OF TABLES

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.

LIST OF FIGURES

Figure 9.

Figure 10

Figure 11

Figure 12

Figure 13

Figure 14

Figure 15

Figure 16.

Figure 17.

Figure 18.

Figure 19.

Figure 20

Figure 21

Figure 22

Figure 23

Figure 24

Figure 25

Figure 26

Figure 2

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Figure 3

Figure 3

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Chapter 1

SYSTEMATICS, BIOGEOGRAPHY, BIOLOGY AND ECOLOGY OF EARTHWORMS

Systematics

Earthworms are probably among the oldest of the terrestrial animals. sils are uncommon, since earthworms are soft-bodied, decompose quickly, and terrestrial environment is not especially good for fossil preservation. Closely ed marine polychaetes are known from Australian pre-Cambrian strata some -570 million years old (Glaessner *et al.* 1969). An Ordovician fossil segmented m, *Protoscolex latus* (Bather 1920), has been placed in the Oligochaeta. It is known whether oligochaetes were derived from polychaetes, or had a similar stor (Lee 1972).

Annelids are segmented worms, divided into segments by septa creating a s of hydrostatically isolated compartments, each containing a pair of nephridia, paired ganglia, and a number of external setae used for locomotion. ntral, fused double nerve cord runs the entire length of the animal. The latory system is closed, with a ventral vessel in which the blood flows eriorly, and a dorsal vessel in which blood flows anteriorly.

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The Oligochaeta are set apart from other annelids by the presence of a small number of setae, usually eight (arranged in four pairs) per segment, and absence of specialized outgrowths of the body wall. Fertilization and embryonic development take place within a "cocoon" formed over the clitellum of the parent producing the ova. Oligochaetes are either terrestrial or aquatic, with only a few species able to withstand estuarine or intertidal habitats. Polychaetes, on the other hand, are almost entirely marine, the Hirudinea are strictly aquatic, and Branchiobdellids are commensal or parasitic on aquatic invertebrates.

Some confusion exists about the higher taxonomic groups of the Annelida. Ruppert and Barnes (1994) and Brusca and Brusca (1990) list three classes of annelids: Polychaeta, Oligochaeta, and Hirudinida. In contrast, Clark (1978) groups the last two into a single class, Clitellata, with three subclasses, as do Meglitsch and Schram (1991). Cladistic analysis of the major groups (Brusca and Brusca 1990) suggests that polychaetes diverged from the ancestral stock first, and a series of small changes from the basic annelid plan produced a proto-clitellate, which was essentially identical to the modern oligochaete. Polychaetes and oligochaetes then developed as sister clades, one in saltwater and the other in freshwater sediments.

There is similar confusion even within the most intensively studied family of oligochaetes, the Lumbricidae. For instance, several members of the genus *Dorrectodea* Örley were at times included in another genus, *Allolobophora* Eisen. This latter genus became a "catch-all" for many diverse species (Sims 1983), mainly because a type species was not designated. Omodeo (1956) rectified this

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oversight, thus forcing a revision of the genus *sensu stricto*. Gates (1975) resurrected the genus *Aporrectodea*, and designated the type species as *A. trapezoides* (Dugès). Other species now recognized as part of *Aporrectodea* were formerly placed in no less than six other genera, some of them now defunct. This count does not include *Nicodrilus* Bouché 1972, which is now considered a junior synonym of *Aporrectodea* (Reynolds 1977a). Within this genus, the "species" *Aporrectodea caliginosa* (Savigny) is considered by many to be a complex comprising *Aporrectodea trapezoides*, *Aporrectodea tuberculata* (Eisen), *Aporrectodea turgida* (Eisen), and *Aporrectodea nocturna* Evans, all of which have different diagnostic features, habits, and phenologies; nonetheless, the original name persists, especially in Europe, because the biology and ecology of this "species" have been widely studied and "*caliginosa*" has become established by usage (Easton 1983, Sims 1983).

Almost all taxonomic literature treating North American terrestrial oligochaetes up to the mid-1900s was penned by European workers: Beddard, Benham, Cernosvitov, Cognetti, Eisen, Pickford, Rosa, Stephenson, Ude and Vejdovsky (Gates 1982). As a result, many of the extant North American holotypes are in European collections. In the 1940's, Gates in the east, and MacNab and McKey-Fender on the west coast began to publish distributional information about terrestrial species in their respective areas. With Gates' appointment as a research fellow at Tall Timbers Research Station in Florida, and Reynolds' association with the same institution in the 1970's, much work was done by them to characterize the earthworm fauna of the eastern United States and

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Canada. Reynolds' primary contribution was to define the distributions of native and introduced species in the eastern U.S. and Canada. Gates worked on the systematics of North American oligochaetes during this time, and his final publication (Gates 1982) is a compendium of the known North American species, their ecology, biology, and distribution. Little systematics work has been done on North American endemics since.

The *caliginosa* Problem

Earthworm workers have, for many years, published investigations including the "species" *Aporrectodea [Allolobophora] caliginosa*. Despite quite convincing arguments by Reynolds (1977a) and Gates (1982), many workers, primarily those in Europe, continue to use this designation, although it is obvious by differences in cocoon morphology, adult size, coloration, external genitals, and behavior that there are actually four species (*A. nocturna*, *trapezoides*, *tuberculata*, and *turgida*). Three of these are sympatric in Upper Michigan forests (Snider and Snider 1988), lending further credence to the assertion that they are not merely ecological morphs of one species. Since many ecological studies have been done on this species group, it is important to define clearly what is meant when one refers to "*A. caliginosa*", especially since one of the species being examined in this work is *A. tuberculata*. When the species "*A. caliginosa*" is referenced here, a reasonable assumption using evidence presented in the cited literature is made that the species being treated is *A. tuberculata* sensu Reynolds (1977a) and Gates 1982). The former species designation is used only to preserve the historical

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reference. Generic and specific names within the text are spelled according to currently accepted usage (e.g., "*Octolasion*" and "*fetida*"); bibliographic citations retain original spellings.

North American Distribution and Zoogeography

The currently recognized taxa of native North American earthworms include 83 species in seven genera, all of which are endemic. These are contained in five families, three of which are only found in North America (Table 1). Seven other megadrile families (excluding the Enchytraeidae), all introduced, are also found in North America. All of these families have been only collected south of the Pleistocene glacial limit, in glacial refugia, or near large population centers (Reynolds 1995).

All other taxa are presumed to have been introduced to North America as a result of transportation by man. Reynolds et al. (1974) proposed his theory of post-Pleistocene introduction as the only rational way to explain the present distribution of earthworms in North America. Many species of Lumbricidae, whose center of radiation is in Europe, and many Megascolecidae, which are Australasian in origin, are found scattered throughout North America, wherever conditions permit them to maintain viable populations. Continental drift, proposed as a dispersal mechanism by Omodeo (1963) is too slow a process to have introduced these taxa to North America since the most recent glaciation, which ended approximately 11,000 years ago, since North America and Europe began to split approximately 190 million years ago (Smith 1973). There is also no evidence of a

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Table 1. Endemic North American earthworms, adapted from Gates (1972).

Family	Genus	Species count	Distribution
Acanthodrilidae	*Argilophilus* *	19	Extreme northwest US
	Diplocardia *	38	South and central US
Komarekionidae *	*Komarekiona*	1	southwestern Appalachia
Lumbricidae	*Bimastos* *	9	South-central US
	Eisenoides *	2	Southeastern US
Lutodrilidae *	*Lutodrilus*	1	Coastal Louisiana
Sparganophilidae *	*Sparganophilus*	13	Southeastern US

* Entire taxon endemic to North America.

land bridge across the north Atlantic since the last glaciation to allow the predominantly European Lumbricidae to cross (Wright and Frey 1965). Even had there been such a land bridge, the time necessary for earthworms to cross such an expanse and colonize American soils would surely have been long enough for differences to arise between the American and European populations. The absence of such differences alone is a convincing argument against natural colonization (Gates 1970).

The present distributions of all endemic taxa are closely associated with Pleistocene glacial refugia, either south of the limit of glaciation (Gates 1970), or slands adjacent to the Pacific coast of North America (McKey-Fender and Fender 1982). Glaciation extirpated all earthworms from the northern United States and ll of Canada, and the native species failed to recolonize (Table 2).

Undisturbed areas in the southern Appalachians tend to support earthworm aunas composed of a high percentage of endemics, while sites that have been

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Table 2. Distribution of introduced and native earthworm families, genera, and species in glaciated and unglaciated areas of North America.

	INTRODUCED			NATIVE			
LOCATION	FAM	GEN	SPP	FAM	GEN	SPP	REFERENCE
Glaciated							
Cape Breton	1	8	14				Reynolds 1975a
Ontario	1	8	17	2	2	2[1]	Reynolds 1977a
Nova Scotia	1	8	15				Reynolds 1976
Pr. Edward Island	1	6	11				Reynolds 1975b
Massachusetts	2	10	16	1	2	2[2]	Reynolds 1977b
Rhode Island	1	8	13				Reynolds 1973a
North Dakota	2	5	5				Reynolds 1978a
South Dakota	1	3	4				Gates 1979
Upper Michigan	1	5	10				Snider 1991
Lower Michigan	1	10	19	2	2	2[3]	Snider 1991
Unglaciated							
Delaware	1	6	10	2	3	4	Reynolds 1973b
Maryland	3	8	14	3	4	8	Reynolds 1974
Kentucky	1	1	1	3	4	6	Dotson and Kalisz 1989
Tennessee	2	9	23	3	4	14	Reynolds 1977c, 1977d, 1978b, Reynolds et al. 1974

[1] One endemic species known only from a botanical garden, the other is limicolous and restricted to the Great Lakes shoreline.

[2] Both species known only from arboretums or botanical gardens.

[3] Confined to southernmost tier of counties; largely untouched by Wisconsin glaciation.

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cleared, cultivated or otherwise severely disturbed have exotic earthworms, such as *Lumbricus terrestris* L., *L. castaneus* (Savigny), *L. rubellus* Hoffmeister, *Octolasion tyrtaeum* (Savigny), and *Pheretima* spp. (Kalisz and Dotson 1989). Of the native taxa, *Komarekiona eatoni* Gates and *Eisenoides carolinensis* (Michaelsen) seem the most susceptible to disturbance and competition with exotics, whereas the genus *Diplocardia* tends to persist.

Early settlers north of the limit of Pleistocene glaciation reported a lack of earthworms, yet lumbricids are now found widely throughout the northern United States and Canada (Table 3). Gates (1982) intercepted a variety of potential introductions from all over the world, demonstrating that it is indeed probable that earthworms were introduced to North America accidentally subsequent to European colonization.

It is not known why endemic species have failed to colonize the areas of North America affected by the Wisconsin glaciation. S.W. James (pers. comm.) has performed transplant experiments with native *Diplocardia* spp. and *E. carolinensis* in northern and western Minnesota, where frost annually extends to depths of 1.5 m. After three years the populations persisted, demonstrating that climate is not a factor in halting the northward expansion of their range into previously glaciated areas.

Earthworm Anatomy and Biology

The general body plan of the Annelida is cylindrical, consisting of two concentric tubes. The outer layer consists of the integument and outer

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musculature, and the inner is composed of the alimentary tract and its associated organs, as well as another muscle layer. These layers are separated by a coelomic cavity bounded by a peritoneum and divided longitudinally by a series of septa, creating fluid-filled compartments whose dimensions can be changed by sets of opposing muscles.

The body wall consists of four layers (Seymour 1978):

- The cuticle, consisting of laminated layers of collagen fibers, running roughly diagonal to the long axis of the worm and alternating left- and right-handed helices in adjacent layers. This gives strength and flexibility to the animal's hydrostatic skeleton.
- The epidermis, mainly a supportive layer of columnar cells that produce the collagen fibers.
- An outer layer of circular muscle fibers and an interior layer of opposing longitudinal muscle fibers. The gut is also surrounded by two layers of muscle, the inner layer of circular and the outer transverse muscle fibers.
- A peritoneal membrane that defines the inner boundary of the body wall.

The septa, which divide the coelom into segments, have pores with sphincters that can allow the passage of small amounts of coelomic fluid or completely isolate the segments. They consist of a layer of connective tissue between two layers of peritoneal cells (Stephenson 1930).

The typical earthworm has eight setae per segment (sometimes more), arranged in four pairs. The spacing of these setal pairs around the segment is used as a key character to distinguish species (Reynolds 1977a).

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Organ Systems and Function

Digestive System, Intestinal Flora and Enzymes

The lumbricid digestive system consists of a buccal cavity, pharynx, esophagus, crop, gizzard, and anterior secretory and posterior absorptive intestines. The anterior portion, from the buccal cavity through the crop, is used to procure and store food prior to processing; material is fragmented in the muscular gizzard and passed on to the intestine.

The intestine is basically a tube with a more or less convoluted typhlosole which, by nature of its increased surface area, aids in both enzyme secretion and absorption of nutrients. The anterior portion secretes an acid mucus and various enzymes that break down proteins, chitin and carbohydrates (Laverack 1963, Edwards and Fletcher 1988). Cellulase and chitinase are present in the gut of the litter-feeder *Dendrobaena octaedra* Savigny, but not in the geophagous species *A. caliginosa* (Nielsen 1962). As epigeic species feed on raw litter and little-decomposed humus, it seems reasonable that they would have a means of breaking down complex structural molecules; those feeding in the soil on well-decomposed organics would have less need for such enzymes.

Although a variety of extracellular enzymes have been found in the earthworm gut and surrounding tissue, many of these enzymes have specific pH optima that are not met in the earthworm gut (Laverack 1963). It seems that very little of the plant tissue and detritus ingested by earthworms is actually broken down and assimilated; indeed, the digestive processes of earthworms may enhance

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polymerization of aromatic compounds, resulting in more complex humins (Lee 1985).

The posterior portions of the intestine absorb the low molecular weight organics resulting from the chemical reactions in the anterior intestine. This part of the gut is also very important in osmoregulation, as it absorbs a variety of ions and water (Lee 1985), forming castings which are eliminated via the anus.

Much of the gut tract is surrounded by layers of chloragogenous tissue, which is similar in function to the vertebrate liver. It is able to store glycogen, and has been implicated in the ability of certain earthworm species to undergo resting stages (Semenova 1967). It has also been shown to absorb and sequester a variety of toxins, such as heavy metals, pesticides, and herbicides (Fischer and Molnár 1992). High levels of certain toxins can deplete the chloragogenous tissue. Individual cells become detached from the tissue as a whole, and these chloragocytes float free in the coelomic fluid. Senescent cells autolyze, liberating ammonia and other waste products into the coelom where they are eliminated via the nephridia and dorsal pores (Laverack 1963, Edwards and Lofty 1972).

Circulatory System and Respiration

The oligochaete circulatory system, unlike that of most invertebrates, is closed. It consists of two to five pairs of esophageal vessels which are strongly muscular and provided with valves and function as hearts, an efferent ventral vessel which distributes the blood via segmental branches to the somatic vessels,

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networks of capillaries in the gut and the body wall, and an afferent dorsal vessel which pumps the blood forward by peristalsis.

Blood is oxygenated in the subcuticular capillaries and is mixed with non-oxygenated blood from the gut in the dorsal vessel. Some species have particular areas of the cuticle modified for gas exchange. In *A. caliginosa*, the lateral regions of segments IX-XIII have a thinner than normal cuticle with flattened epithelial cells and numerous capillaries (Stephenson 1930). An East African glossoscolecid worm utilizes a similar modification together with specialized musculature in the caudal region to form a roughly conical "lung" which is protruded above the waterlogged, anoxic soils and sediments which it occupies (Beadle 1957).

Oxygen is carried in both the plasma and in the respiratory pigment erythrocruorin, analogous to vertebrate hemoglobin. Unlike vertebrates, this molecule exists free in the plasma instead of in erythrocytes. Erythrocruorin has a much lower oxygen binding potential than mammalian hemoglobin, and seems to act most efficiently at low oxygen tensions (Weber 1978).

As long as the cuticle remains moist, oxygen can be readily absorbed from the air or soil atmosphere. Oxygen uptake from water is also possible, as long as the water has sufficient surface area to permit adequate diffusion from the air above (Lee 1985). Immatures of *Aporrectodea turgida* can be kept in water at 5-6 °C for several months, although the worms do not grow or mature (pers. obs.).

Earthworms can tolerate very high CO_2 tensions, substantially higher than that normally found in the soil atmosphere (Lee 1985). Anaerobiosis can also be tolerated for short periods, energy being derived from glycogen stores (Weber

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1978). This is advantageous especially during periods of heavy rain, when burrows may become flooded and available oxygen depleted.

Excretory System

The typical earthworm has paired nephridia in each segment, save the first and last. These are true metanephridia, with the nephrostome opening into the coelom of the immediately anterior segment and the bladder opening to the outside on the ventral surface. In some earthworms (*Pheretima* s.l. group), several pairs of nephridia in the anterior portion of the worm open into the gut rather than to the outside. This may serve to decrease water loss, and probably changes the pH in the anterior portion of the gut (Edwards and Lofty 1972, Oglesby 1978, Lee 1972).

Nitrogenous wastes are eliminated primarily as ammonia, diluted in a copious amount of urine. Some species are able to produce urea when under water stress. Salts are resorbed as the urine passes through the nephridium, Na^+ being actively removed, while Cl^- as well as other ions passively diffuse out of the nephridial lumen.

Nervous System

The nervous system consists of a ventral nerve cord with ganglia in each segment, and three pairs of nerve branches per segment which innervate the muscles, epidermis, gut, and the posterior septum. The first two pairs form nearly complete nerve rings meeting at the mid-dorsal line (Edwards and Lofty 1972). The first four segments deviate from this: segment III contains the cerebral

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ganglion and is innervated from the ganglia of the fourth segment, the second segment nerves arise from the junction of the circumpharyngeal connectives in segment III, and the first segment is innervated by a pair of nerves arising from the subpharyngeal connectives in segment II. The prostomium is innervated by two nerves originating at the cerebral ganglion in segment III, and its epidermis contains many sensory organs capable of receiving light, chemical, and tactile stimuli (Laverack 1963).

Reproductive System

The typical earthworm is hermaphroditic and often possesses mechanisms to prevent self-fertilization, insuring amphimixis (Reynolds 1977a). However, parthenogenesis, together with reduction of the male reproductive organs has been observed in some species (Lee 1972). Pseudogamy, in which spermatozoa play no part in embryonic development other than as a stimulant, is also known from a few observations (Reynolds 1977a).

Generalized sexual organs are as follows:

Male: Paired testes in segments X and XI; seminal vesicles in IX-XII. Sperm transferred via sperm funnels and sperm ducts to a vas deferens which may extend posteriorly for several segments before opening to the outside via the male gonopore. A prostate gland is also generally present. Paired saclike spermathecae in segments ix and x are present to store transferred sperm. Spermatophores have been noted from several species (Lee 1972).

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Female: Paired ovaries in XIII. Oocytes travel through the coelomic fluid into ovisacs which lead into an oviduct to the female genital pore.

The clitellum (often segments XXX-XXXV in the Lumbricidae) produces a mucous sheath which slips forward, receiving at least one mature oocyte and some of the stored sperm. As the sheath slips off the prostomium, the ends are sealed and a nutritive substance fills this cocoon. The oocyte is fertilized and the embryo develops within the cocoon. Upon eclosion, the immature earthworm is fully functional.

Muscular System and Locomotion

Each segment has two sets of muscles. The outer circular muscle fibers provide the contractile force to make each segment longer and smaller in diameter. Interior to the circular muscles are opposing longitudinal muscle fibers which perform the opposite function. Each segment acts as a more or less sealed hydrostatic system in close coordination with adjacent segments. Worms move via a peristaltic wave of deformation (Dobrolyubov 1986) running retrograde to the direction of movement. The setae are extended as the segments contract longitudinally, providing a firm grip within the burrow, and are retracted as the segments extend. A similar set of muscles surrounds the gut, and acts synchronously with the muscles of the body wall.

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Life Cycle

The life cycle of lumbricids is termed semi-continuous by Olive and Clark (1978) because they produce several cocoons ("broods") over an extended breeding season, and may do so for several years. This differs from the polytelism exhibited by many polychaetes, which generally have only one intensive breeding event per year.

Specific life cycles for many earthworm species are poorly known, especially regarding life expectancy. Michon (1954, quoted in Edwards and Lofty 1972), found that *Dendrodrilus rubidus* (Savigny) became reproductive in 100-140 days, remained clitellate for 200-250 days, with death occurring at approximately 550-600 days. Reinecke et al. (1992), investigating the suitability of three epigeic species for vermicomposting, listed time to maturity for *Eisenia fetida* (Savigny) as ±70 days, for *Eudrilus eugeniae* (Kinberg) as ±60 days, and for *Perionyx excavatus* (Perrier) as ±46 days at 25°C. Maximum life expectancies for the latter two species in outdoor beds was 120 and 90 days, respectively.

Most earthworms mature in roughly one year (Evans and Guild 1948, Satchell 1967), although environmental conditions such as seasonally low temperatures or periods of drought may considerably lengthen this period, thereby causing increased mortality of immatures. Life expectancy for many species is believed to be 1½-2 years, although large anecics such as *Aporrectodea longa* (Ude) and *L. terrestris* may live as long as 10 years (Satchell 1967). A generalized earthworm life cycle diagram is presented in Figure 1.

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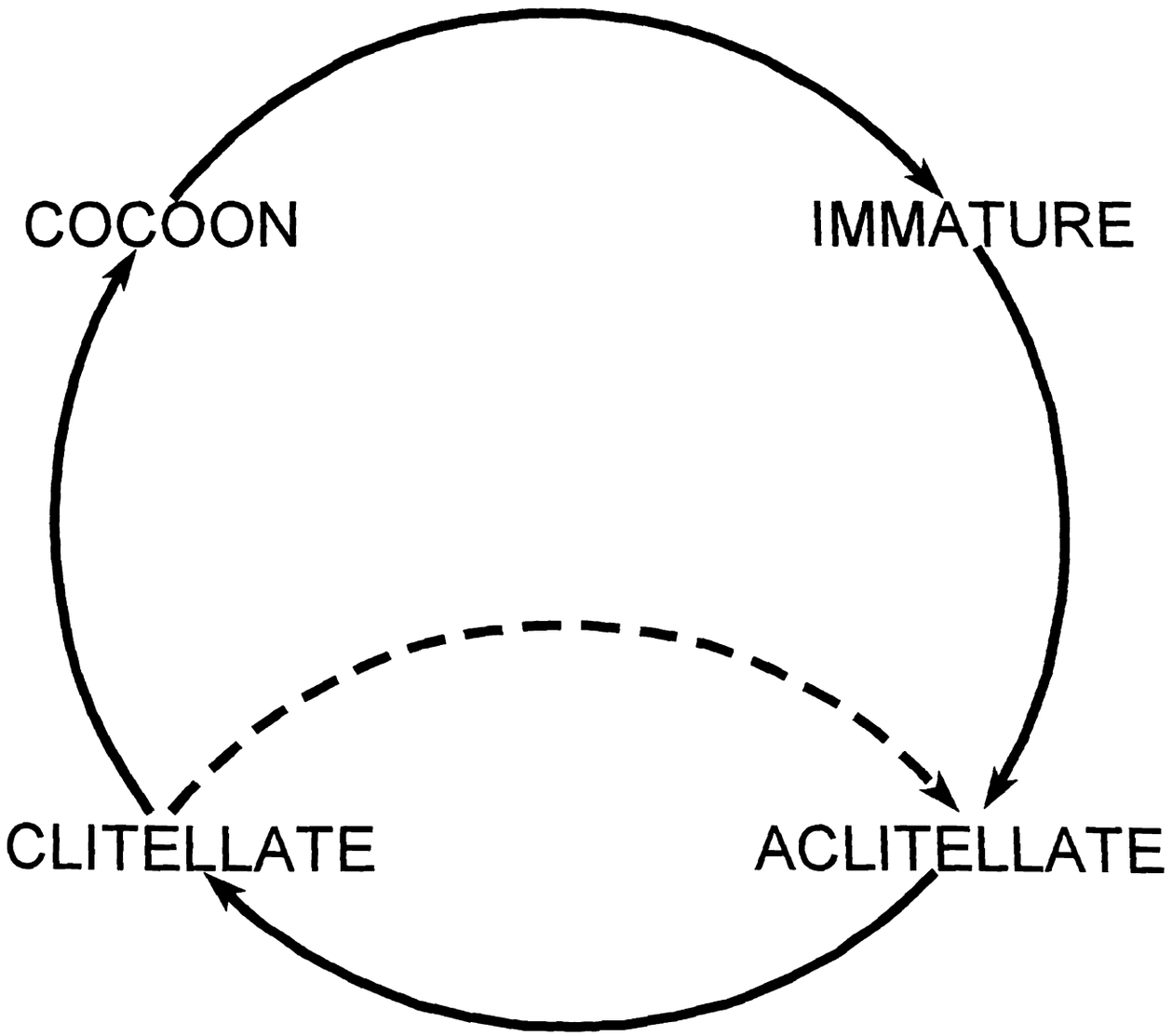

Figure 1. Generalized lumbricid life cycle. Some longer-lived species with resting stages alternate between reproductive and non-reproductive states (dashed arrow); others have only a single extended reproductive period.

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Evans and Guild (1948) found that cocoon production of several species of British lumbricids varied throughout the year, peaking with the maximum mean daily temperature in midsummer, except in species with an obligatory summer diapause.

There is great variation in the rate of cocoon production by different species. Satchell (1967), re-analyzing data from Evans and Guild (1948) noted that deep burrowers (anecics) produced 3 to 13 cocoons per year, topsoil-dwellers (endogeics) produced 25 to 27 cocoons each year, and litter (epigeic) species produced 42 to 106 per year. He suggested that these differences are related to the degree of environmental variation each species is likely to encounter; the greater the risk of early mortality, the higher the cocoon production.

External Causes of Mortality

Many animals utilize earthworms as prey. Among the vertebrates are amphibians of all orders, snakes, lizards, birds, and a variety of mammals, from shrews to bears. In the Upper Peninsula, animals which are known to eat earthworms include garter snakes (*Thamnophis* spp.) (Reynolds 1977a), woodcock (*Scolopax minor* Gmelin) (Liscinsky 1965, Reynolds 1977a), moles (Skoczen 1970), shrews (*Sorex* spp.) (Judas 1989), red foxes (*Vulpes vulpes* L.) (Macdonald 1980), and robins and blackbirds (*Turdus* spp.) (Granval and Aliaga 1988). In a review of vertebrate predators, as well as an exclusion experiment of his own, Judas (1989) concluded that vertebrates generally do not seriously reduce earthworm standing stocks, do not affect their vertical distribution, and are not an

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important factor in population control, although he did mention studies in which certain birds were shown to have a significant effect on earthworm populations.

Invertebrate predators include chilopods (Judas 1989) and large carabid beetles (Loreau 1988), which feed on earthworms on the soil surface or in the leaf litter. Judas (1989) found that chilopods are important earthworm predators (mortality was twice as high in chilopod treatments than in controls), but their effect was confined to small size classes.

Earthworms and their cocoons are hosts to a variety of parasites. *Histiosoma murchiei* Hughes and Jackson, an anoetid mite, is known to infest cocoons in Denmark (Gjelstrup and Hendriksen 1991) and northern lower Michigan (Oliver 1962). An unknown nematoceran fly larva has also been observed in cocoons of several earthworm species (personal observation). Immature and adult worms may become infested with monocystid gregarines, around which the worms form a fibrous capsule which eventually becomes calcified (Dales 1978). These white nodules are easily seen through the integument (personal observation). The cluster fly, *Pollenia rudis* Fabricius, lays its eggs on earthworms or in moist soil, and the larva parasitizes the mature earthworm. The attack is usually fatal (Yahnke and George 1972). At present, it is known to parasitize only *Eisenia rosea* (Savigny) in North America, but attacks other species in Europe.

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Earthworm Ecology

Guild Classification Systems

Several attempts have been made to group earthworm species into guilds which can be used in generalizations about how worms interact with their environment. Various workers have taken different tacks: grouping by life history characters, feeding ecology and internal anatomy, and by vertical stratification and ecological function.

Life History Characters

Satchell (1980), summarizing information from Evans and Guild (1947, 1948) and Graff (1953), developed a system of classification based primarily on life history characters, specifically, adaptation along the r-K continuum. **r-adapted** worms produce many cocoons, experience high mortality early in life, mature quickly, and are often small, whereas **K-adapted** species produce few cocoons, are generally large and mature more slowly, and have a longer life span.

A suite of other characters follow this dichotomy as well. r-worms generally do not aestivate, are red-pigmented, respond weakly to light, consume and/or live in the litter layer, have a thin cuticle and are not well suited to burrowing. K-worms, on the other hand, live in the mineral soil and have well-developed musculature for burrowing; they also possess a thicker cuticle which is not red-pigmented, although they may be dark brown or gray, particularly on the dorsal surface.

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Of the three species treated in this work, *D. octaedra* is an r-adapted species and *A. tuberculata* is K-adapted. *Lumbricus rubellus* Hoffmeister is intermediate, tending toward the former.

Feeding Ecology and Internal Anatomy

Perel' (1977) divided earthworms into morpho-ecological associations based on feeding habits, musculature and intestinal morphology. She distinguished between **humus formers**, those taxa which feed on largely undecomposed litter and roots, and **humus feeders**, species which ingest large amounts of soil, digesting well-decomposed humus and associated microbes.

Humus formers have a simple typhlosole and a moniliform gut tract, a closed epilobic or tanylobic cephalic lobe for grasping food items, and a complex pennate arrangement of longitudinal muscle fibers, to which Perel' attributed these worms' ability to respond quickly to external stimuli, but which are poorly suited for burrowing. Humus feeders, on the other hand, have a prolobic or epilobic prostomium, a highly convoluted typhlosole within a straight tubular gut, and bundled longitudinal muscle fibers which facilitate strong longitudinal contractions and are well suited for burrowing.

Dendrobaena octaedra and *L. rubellus* are considered humus formers, and *A. tuberculata* is a humus feeder under this method of guild classification.

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Vertical Stratification and Ecological Function

Bouché (1977) developed and defined the concept of classifying earthworms using a combination of morphological characters which indicate their ecological role, and their "preferred" placement in the litter/soil horizons. His three basic classifications were **épigées**, worms which live above the soil horizons and consume litter, **endogées**, those living and feeding within the mineral soil, and **anéciques**, which live in the mineral soil and come to the surface to feed on litter. He realized that each species may embody some characters of all three basic types, and visualized each species being placed within a triangular region with one of the three basic types at each vertex. Thus, each of the three basic types is divided into subgroups which are composites or adapted to specific habitats. He used not only vertical stratification, but also factors such as presence of "digging muscles", ability to keep the cuticle moist, reproductive rates, presence and type of resting stage, and gut transit time to delineate his groupings.

Épigées typically live in the litter layer of forests. True litter species are straminicoles, but there are also species which specialize in living in compost or other temporary surface organic accumulations (détritiphages), mammalian dung (coprophages), or under tree bark (corticoles). Due to wide ranges of temperature and moisture conditions at the surface, many of these species exploit rich temporary organic matter sources, are small, short-lived, and produce many cocoons (or several worms per cocoon); therefore, they fall into the same class as Satchell's r-adapted group.

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Endogées live within the mineral soil, constructing temporary to semi-permanent horizontal burrows, often with several surface openings. They feed on more or less enriched pockets of organic matter incorporated into the inorganic soil matrix. Subgroups include hypoendogées, living in the deep horizons, and epiendogées, which live closer to the surface. Members of the latter group which specialize on dead and senescent plant roots are termed saprorhizophages. Many of these earthworms are large and long-lived relative to épigées, and can be classified within Satchell's K-adapted guild.

Anéciques often construct deep, permanent vertical burrows, and some of them actually pull large leaf fragments down into the soil, where they feed on them. Some of the largest lumbricids, including *L. terrestris*, are members of this guild.

The three species studied in this work each fall into different classes under this scheme: *A. tuberculata* is a hypoendogée, *D. octaedra* is a straminicolous épigée, and *L. rubellus* switches from an épigée early in life to an epiendogée as an adult, remaining mostly within the A-horizon.

Satchell's r-K continuum is an interesting way of examining megadrile reproductive strategies, but is incorporated largely within the Bouché scheme. The humus former/ humus feeder dichotomy proposed by Perel' cuts across the other two schemes, largely because it depends more on functional feeding strategies and gut morphology. Of the three classifications discussed above, Bouché's is the most comprehensive, and is used most extensively in this text.

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General Requirements and Limiting Factors

Since earthworms lose moisture readily through their integument, urine and castings, sufficient substrate moisture is of primary importance. Similarly, because of their limited capacity for movement, they must live close to suitable food sources (Lee 1985). All ectotherms are more or less at the mercy of the ambient temperature regime to provide acceptable temperatures for metabolic activity. Megadriles have additional requirements including soil texture, pH, and presence of sufficient quantities of nutrients such as calcium.

Reynolds and Jordan (1975) postulated a conceptual model for megadrile activity, based on environmental and edaphic characters. Among the characters examined were landscape slope and aspect, elevation, physiographic position (bottomland, terrace, upland), soil pH, soil temperature, soil moisture, soil color (Munsell notation), soil texture (percent of various fractions), and vegetation palatability on a subjective scale. Absolute values of Pearson's correlation for all characters were low (below 0.2), but several were greater than 0.1. Among these were temperature (positive for aclitellates), soil color characters, percent sand (negative), percent silt (positive), and palatability (positive for aclitellates only). Soil texture correlations were the strongest, suggesting that soil composition is an important regulator of earthworm distribution. Since all earthworms were treated as a group, one would expect to see low correlation values. Had they divided earthworms into functional groups, or treated single species, correlations for some factors may have been substantially higher; nevertheless, their findings identify important factors determining earthworm activity.

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Fragoso and Lavelle (1992) found that species distribution and earthworm community structure were determined by a hierarchy of variables in tropical rain forests: temperature was most important, followed by edaphic (nutrient-related) factors; seasonal effects such as rainfall patterns comprised a third level. Given similar temperature regimes, nutrient-poor soils favor anecics and epigeics, both of which feed on surface litter, whereas rich soils of neutral pH favor geophagous endogeics.

Food

Food for earthworms consists of nonliving organic matter in various stages of decay and free-living microflora and fauna. Experimental evidence shows that microorganisms, particularly protozoa and fungi, are of major importance (Edwards and Fletcher 1988).

Richards and Arme (1982) have demonstrated that some earthworms are able to derive a small portion of their nutrition via transintegumentary absorption of amino acids, hexoses, and short-chain fatty acids. Uptake is by diffusion rather than any active transport mechanisms; therefore, concentration ratios cannot exceed equilibrium. Since absorption rates are low, the contribution to the earthworms' nutritional budget via absorption through the cuticle is probably insignificant.

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Soil Moisture and Water Relations

The cuticle is permeable to water, and selectively permeable to a range of ions commonly found in the soil environment (Laverack 1963). As a result, earthworms have only a limited ability to control the osmotic pressure of their body fluids, and are sensitive to changes in soil moisture and ionic concentrations in the soil solution. The cuticle, nephridia, calciferous glands, and gut wall all play a part in maintaining ionic and osmotic equilibrium. Most earthworms are confined to soil water tensions in the range of pF 2.0 to 4.7, approximately from soil field capacity to close to the wilting point (Lee 1985).

Because of the need to keep their cuticle moist to aid in respiration, earthworms tend to lose water to the environment except under conditions of high humidity. They also lose water via the copious hypotonic urine needed to flush away excreted ammonia. Total losses through the integument and excretory system are probably in the range of 10-20% of body weight per day, which must be replaced if the worm is to survive (Lee 1985). Moisture losses are greater for worms that are small, thin and active (juveniles and small species) than for those that are large, thick, and inactive (Piearce 1981).

Many earthworms will enter a quiescent state if they encounter conditions of extended low water availability. They form a ball, encase themselves in a chamber lined with mucus and castings, lose much of their body water and slow their metabolic activity drastically. Several workers (Schmidt 1918, Hall 1922, Grant 1955) have found that many species can lose 70% to 80% of their body water and still be revived.

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Aporrectodea longa, exposed to differing soil moistures, showed little decrease in body water until soil suction was increased to pF 2.78, somewhat less than field capacity (pF 2). Live weight decreased from that point as a function of increasing soil suction. At pF > 3.79, somewhat above the wilting point of plants, worms initiated diapause (Kretschmar and Bruchou 1991).

Production of cocoons also depends on soil moisture. The highest cocoon production occurs at high soil moisture (30-40% gravimetric). Cocoon mass, both fresh and dry, also increases with soil moisture (Evans and Guild 1948).

Temperature Ranges

The study of temperature effects on earthworms has traditionally followed one of two paths: (1) vital ranges or lethal limits, or (2) temperature preferences, usually determined by placing earthworms in a long soil-filled trough with a temperature gradient and allowing them to redistribute. There have also been a few studies which examined the effects of temperature on reproduction in field populations (Graff 1953, Satchell 1967).

Upper temperature limits may be either physiologically determined by the inability of gas exchange across the cuticle to keep pace with increasing metabolic requirements, or related to breakdown of the collagen fibers in the body wall (Rigby 1968). Lower limits are probably due to the freezing of fluids within the body, resulting in cell rupture.

Several factors may confound observations of minimum, maximum, and optimum temperature ranges in earthworms. Mangum (1978) suggested that there

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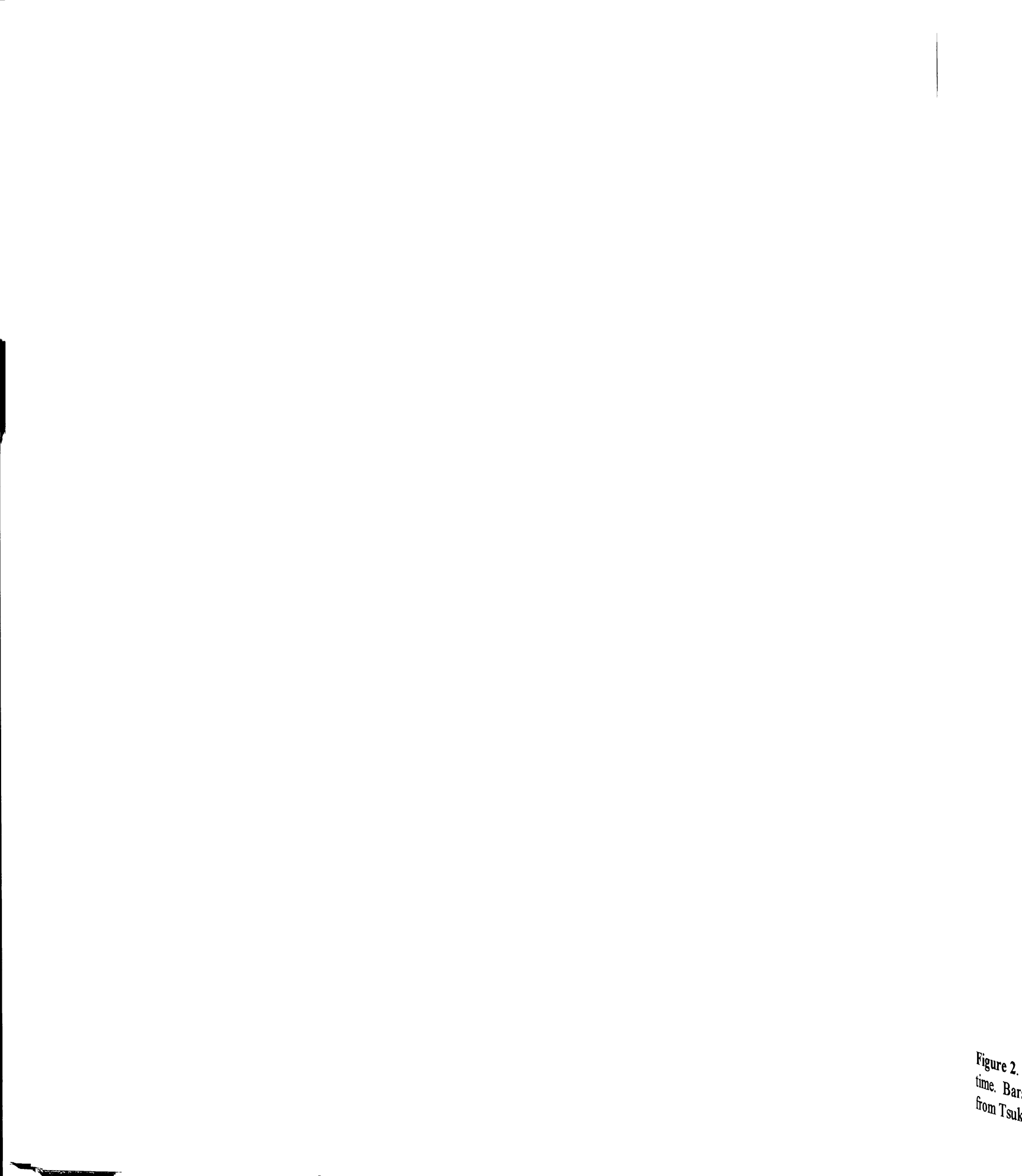
may be quantitative differences in oxygen consumption between worms acclimated to different temperatures because of qualitative differences in carbohydrate metabolism as regulated by neuroendocrine hormones. Soil moisture also seems to interact with temperature effects. Reinecke (1975) and Nordström and Rundgren (1974) have observed that preferred or optimum temperatures increased with increasing moisture content. Soil temperature and moisture were found to have a synergistic effect upon litter consumption rates in immature *L. terrestris*. Consumption, therefore assimilation and growth, increased roughly exponentially with both temperature and moisture until the optimum was reached (approximately 23°C and -9 kPa), above which it fell rapidly to zero (Daniel 1991).

Life history characters are strongly affected by temperature. Time from eclosion to mature clitellate worm often decreases markedly with increasing temperature, as does size at maturity (Frenot 1992, Viljoen and Reinecke 1992, Viljoen et al. 1992). Growth rate and activity increase with temperature (Nordström 1975). Cocoon production generally is highest in the upper temperature range for the species (Viljoen and Reinecke 1992, Butt et al. 1992).

Cocoon development is also affected by temperature. Butt et al. (1992) found that the optimum incubation temperature for *L. terrestris* cocoons was 15°C; mean incubation time at this temperature was 70 days, but it was 275 days at 5°C. *Eisenia fetida* cocoons showed significant change in incubation time, number of hatchlings per cocoon and percent hatchability with temperature (Figure 2). Time to hatching decreased as a negative exponential with respect to temperature,



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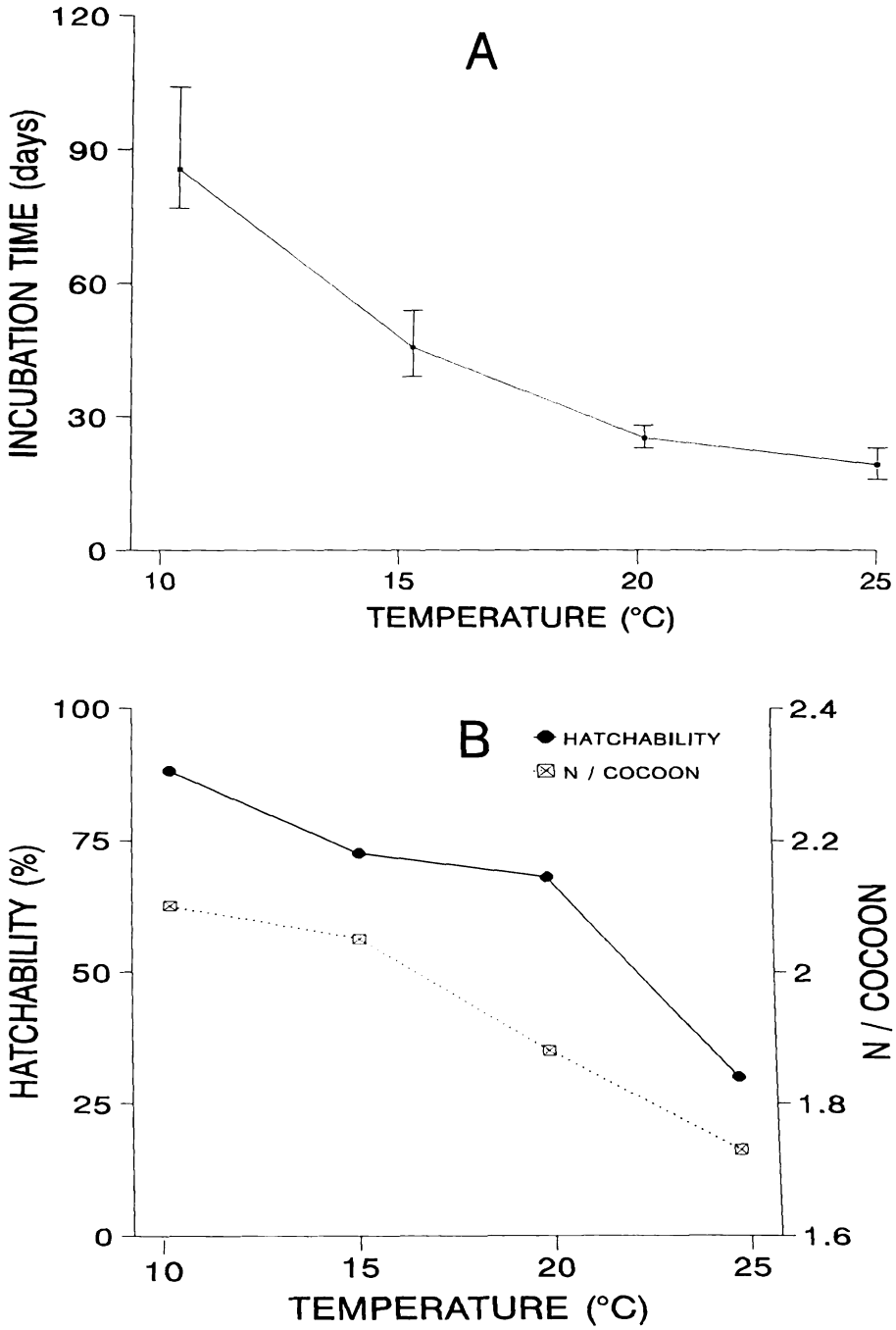

Figure 2. Changes in *Eisenia fetida* cocoon parameters with temperature. A: Incubation time. Bars indicate range. B: Hatchability and number of hatchlings/cocoon. Adapted from Tsukamoto and Watanabe (1977).

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and both hatchability and number of successful worms per cocoon decreased more or less linearly as temperature increased (Tsukamoto and Watanabe 1977).

Although most adult worms cannot tolerate freezing, cocoons of some species can survive frost. Among earthworm species found in northern Michigan, *A. caliginosa* (*tuberculata*, *turgida*, *trapezoides*), *A. longa*, and *Dendrodrilus rubidus* cocoons can survive mild frost, circa -1°C. A few of the latter two species can survive a moderate freeze, ca. -5°C, as can most cocoons of *L. terrestris*. About one third of *D. octaedra* cocoons can survive a hard freeze at -10°C (Holmstrup et al. 1990).

Embryonic development proceeds even at low temperatures, but there may be species-specific temperature thresholds below which hatching is inhibited. This would insure that hatchlings find a favorable environment for growth (Holmstrup et al. 1991).

Soil Properties

Organic Matter and Chemical Nutrient Composition

Carbon and nitrogen are the two nutrients most important to earthworm growth and survival. Although availability of one or the other occasionally limits populations, it is usually the C:N ratio which is most important. Animal and microbial tissue have a C:N ratio of about 5; as this ratio increases in food sources, organisms experience difficulty in extracting the nitrogen necessary for tissue production. Nitrogen availability appears to be one of the most important factors

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ffecting earthworm distribution, especially in tropical soils where its content is ow (Lee 1983).

Bouché (1972) examined the C:N ratios in the food of 67 French species, nd found that optima for 49 species ("eubiotic" forms) were < 13, and the emaining species ("mesobiotic" forms) had food C:N optima ≥ 13, including two pecies with optima > 17. Comparison of these groups with his guild classification ystem showed that almost all aneciques were eubiotics, as were most of the ndogeés; epigeés, adapted to living in substrates composed primarily of ndecomposed plant litter, fell into the latter group. Of the species Bouché xamined which are found in upper Michigan, *A. caliginosa* has the lowest C:N ptimum, about 11.7, and *D. octaedra* has the highest at 14.3.

exture, Porosity, Compaction, Water-holding Capacity, Clay Content and Other hysical Factors

Since the soil is the medium in which earthworms live, its physical texture id composition are extremely important factors in how earthworm populations re in a given location. Ease of movement, availability of suitable food, water lations and O_2/CO_2 tensions are all affected by the medium's physical nature.

Coarse-textured soils, due to their abrasive nature and susceptibility to ought, rarely contain substantial earthworm populations (Lee 1985). nversely, soils with high clay content in regions of high rainfall also have pauperate earthworm communities due to extended periods of oxygen deficit ee 1985).

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Soil type is more closely correlated with earthworm abundance than is litter ype. English beechwoods on mull soils support not only larger earthworm opulations than beechwoods on mor soils, but more species as well, whereas there s no significant correlation with litter type (Phillipson *et al.* 1978). Mean arthworm mass and total biomass per unit area, however, are tied to litter type Zajonc 1972, cited in Phillipson *et al.* 1978), since leaf litter is a major organic nput into the soil system and therefore the ultimate food of many earthworms.

Soil compaction is another important factor in earthworm distribution. It ot only affects the ease of burrowing, but also water-holding capacity and air ermeability. Field observations of earthworm communities and populations howed the highest activity and biomass in uncompacted arable soils, whereas the owest biomasses were recorded from wheel-rutted paths. Column experiments ith differentially compacted soils showed significantly more and longer burrows lighter substrates (Söchtig and Larink 1992).

H, Alkalinity and Other Chemical Properties

Soil pH is not generally limiting except in soils with a pH below 4.0. hloride content is probably a more significant factor, as is calcium ion ncentration (Lee 1985). Laverack (1961) demonstrated that *A. longa*, *L. rrestris* and *L. rubellus* would not burrow into soils with pH below their specific resholds, which ranged from 4.6 to 3.8. Bouché's (1972) study of French rthworms showed that the majority were found in soils with pH from 5.0 to 7.4; ly 26 of 67 taxa were found in soils with pH < 4.0, and four were found only in

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soils with pH > 6.6. Straminicolous species such as *D. octaedra* and *L. rubellus* predominate at lower pH levels (Nordström and Rundgren 1974).

Availability of Ca^{++} may also be very important to some endogeic species (Lee 1985). Calcium carbonate acts as a pH buffering agent, and is also necessary for proper functioning of the digestive system, particularly the calciferous glands.

Light

Earthworms avoid bright light when possible. Short wavelengths, ultraviolet light in particular, damage the cuticle and may be lethal. Generally, the more highly pigmented species which live in or eat surface litter are less susceptible to light damage (Lee 1985).

Effects of Earthworms on Their Environment

Soil macrofauna are generally believed to indirectly affect litter turnover and decomposition via comminution of larger debris and stimulation of soil microbial populations (Anderson 1988, Edwards and Fletcher 1988, Lee 1985, Petersen and Luxton 1982); however, moderately large populations of *L. terrestris* have been found to affect carbon cycling more directly by assimilation and digestion of plant remains (Daniel 1991). Other anecic or epigeic species with the capacity to digest plant structural molecules may do the same. Symbiotic interactions between earthworms and soil microorganisms comminute large detritus into successively smaller fragments, eventually incorporating them into

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water-stable aggregates and making their nutrients available to plants (Edwards and Fletcher 1988).

Litter Decomposition and Turnover

Earthworms are an important factor in degrading and cycling organic matter derived from leaf litter in North American floodplain forests (Knollenberg et al. 1985). Up to 93% of the annual litterfall in such forests was utilized by *L. terrestris* in a four-week period in field microcosms. Populations of this species in apple orchards buried $2 \cdot 10^6$ g·ha^{-1} leaf litter between leaf fall and the end of February (Raw 1962). Likewise, *L. rubellus* is important in incorporation of litter N into soil on permanent pasture systems (Syers et al. 1979). Presence of earthworms (*A. caliginosa*) also promotes incorporation of organic matter, increasing pasture production (Stockdill 1982).

Leaf burial by earthworms is followed by rapid decay, proliferation of microbial populations, and increased soil buffering (Hartenstein 1986). All this activity in turn increases the rate at which labile nutrients are made available to plants.

Soil Organic Matter Turnover and Nutrient Cycling

Endogeic and anecic earthworms consume a large amount of soil while tunneling. In laboratory rearing studies, Martin (1982) found that *A. trapezoides* and *L. rubellus* consumed 2 - 6 g dry soil g^{-1} live worm day^{-1}. Lavelle et al. (1989) estimated that up to 60% of the humic pool in the upper 10 cm of the soil passes

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through earthworms every year in African tropical savannas with soils that average 1.2% organic matter. Hartenstein (1986) calculated that up to 4% of the organics in the top 20 cm of soil in temperate areas are utilized by earthworms yearly, assuming only 6 months activity. This prodigious feeding activity by earthworms results in accelerated nutrient release and availability (Barley and Jennings 1959, Curry and Cotton 1983, Vimmerstedt and Finney 1983); mineral cycling and organic matter decomposition are thus enhanced by earthworms (Bouché 1972, Edwards and Lofty 1972).

Several studies in both field and laboratory have shown that earthworms positively affect N cycling and availability to higher plants. Earthworms processed about 50% of the nitrogen inputs due to plant litter in a Georgia agroecosystem (Parmelee and Crossley 1988), and enhanced biological activity and decomposition processes in the humus layer in a coniferous forest soil (Haimi and Einbork 1992). Haimi and Boucelham (1991) found that presence of *L. rubellus* in coniferous forests increases N mineralization and nitrification rates, as well as increasing available KCl-extractable N and P than did controls, making more of these nutrients available to plants. Pot experiments with *Octolasion lacteum* (Örley) and beech seedlings indicated that N availability was higher in worm-worked soils, increasing stem production by shifting the transfer of C and N toward the aboveground portion. It also increased the large:fine root ratio (Wolters and Stickan 1991). Pashanasi and Lavelle (1992) demonstrated significant increases in plant growth for two of three tropical fruit tree species when inoculated with *Pontoscolex corethurus* (Muller). Enhanced availability of soluble N and P may

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also be detrimental in the long run; R.W. Parmelee (pers. comm.) has found that increased soluble N and P coupled with increased permeability of soils due to worm activity may actually remove these nutrients from corn agroecosystems by percolation.

Effects on Soil Texture, Porosity, and Water-holding Capacity

Large-scale introductions of earthworms into areas previously lacking them or enhancement of depauperate earthworm faunas have shown that earthworms can have a profound effect on soil structure. Introduction of lumbricids into New Zealand pastures was shown to increase porosity, friability, soil moisture, and water-holding capacity, as well as reduce runoff (Stockdill 1982, Springett et al. 1992). Organic matter, lime, and agrochemicals are also mixed throughout the soil. This in turn provides a more favorable environment for both other soil invertebrates and microbial decomposer communities.

Earthworms have also been found to be important in the building and maintenance of soil structure via their burrowing and casting activities, which result in mixing the lower mineral layers with the organic surface layer (Nielsen and Hole 1964, Hoogerkamp et al 1983, Stewart and Scullion 1988, van Rhee 1977). Darwin (1881) estimated that surface-casting lumbricids may bury objects on the surface of a pasture about 3 cm in 10 years, moving as much as 18 T. soil per acre per year. Another important way in which earthworms affect the physical structure of the soil is by formation of water-stable aggregates. Worm-worked soils contain many more large water-stable aggregates than moist soils simply stirred with a

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glass rod (Piearce 1981). Soils with earthworms are more resistant to erosion due to the production of these water-stable soil aggregates in earthworm casts (FAO 1977, van Rhee 1977).

Water relations of earthworm-amended soils are often dramatically changed. Burrowing activity increases hydraulic conductivity, infiltration and percolation rates (Smettem 1992, Ehlers 1975, Germann et al. 1984, Lee 1985, Joschko et al. 1992), and can have a significant effect on the quality of soil water. Edwards et al. (1992) have demonstrated that presence of burrows increases the transport of soluble NO_3-N downward through the soil profile. Higher concentrations were seen after storms which followed prolonged dry periods, suggesting that the drilosphere contributes to nitrate infiltration.

Earthworm-induced changes in soil structure also affect plant production and carbon allocation. Introduction of earthworms into fruit tree plantations increased incorporation of organic matter, aggregate stability and air permeability. Density of thin roots as well as the ratio between thin:thick roots increased in the worm plots, and fruit production was 2.5% higher in worm plots than in controls (van Rhee 1977).

Modelling of Earthworm Populations

Several attempts to model earthworm populations and their effects on the soil/litter system have been made in the last 20 years. Some of the more notable efforts are discussed below.

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Reichle (1971) - Carbon Flux in a Deciduous Forest

Modelling of earthworm populations was not a primary concern of this study; its aim was to describe the ecological energetics within a forest ecosystem by modelling the flow of carbon through various compartments. Earthworms were one of the compartments; the model predicts ingestion, egestion, and respiration rates of the earthworm community as a whole.

Bouché and Kretschmar (1977), Bouché (1980) -- R.E.A.L., a Descriptive Model of Earthworm Population Dynamics in Agroecosystems

The "Ecological and agronomic role of Lumbricidae" is a compartmental conceptual model diagramming carbon and nitrogen flow, microbial activity, casting and burrowing activity, and attempts to explain the role of earthworms in agroecosystems.

This model delineates the effects of lumbricid communities on agroecosystems, by tracing nutrient flow through the system. As a descriptive model, it serves as a good framework with which to direct further research, but is not an end in itself. Being qualitative rather than quantitative, it cannot be used to directly test the effects of changes in one compartment on another.

Lavelle and Meyer (1977, 1982) - Allez les Vers, a Complex Population Dynamics Model of *Millsonia anomala* Omodeo, Based on Individuals

This population dynamics model of *Millsonia anomala* seems to have been constructed with extensibility to other species and environments in mind. It is

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quite complex, taking into account weight classes within developmental stages, burrowing behavior with respect to changing soil moisture profiles, food quality of the substrate in various soil horizons and the litter layer, and reproduction and mortality are keyed to the number of days within each period an individual increases or decreases in mass. The model was tested with an independent data set, but the environmental conditions in the second set were substantially different (much drier) from those of the first set. Even though the model performed satisfactorily, one should use validation data values which are found substantially within the bounds of the set used to build the model.

The primary drawbacks of the model are (1) cocoon incubation time is fixed, even though several studies have shown that it is often dependent upon environmental factors, particularly temperature; and (2) this model, just like the above model, works with discrete "individuals", and is subject to the same limitations as that of Mitchell (1983) discussed below.

Martin and Lavelle (1992) - an Elaboration of the 1982 Model, Taking Vertical Distribution into Account

DRILOTROP (in FORTRAN) is a model to simulate the functioning of the drilosphere (the soil surrounding earthworm burrows) in a tropical savanna. A submodel describes the vertical movements of *M. anomala* due to environmental conditions such as depth-specific temperature and moisture, and biotic factors such as individual behavior and depth-specific organic content (food quality).

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Mitchell (1983) - WORM.FOR, a Model of Production, Growth and Population Dynamics for *Eisenia fetida* in Sewage Sludge

This is a predictive model, the purpose of which is to investigate the effects of temperature and food type on population dynamics, biomass change, and waste conversion for *E. fetida*. I have obtained the program source code (in FORTRAN) from Dr. Mitchell, and translated it to Turbo Pascal for examination. It seems to be a tight model for *E. fetida* under controlled conditions, but it would have to be extensively reworked for use under changing natural conditions. It may not be adaptable for use with another earthworm species -- it is quite specific to the task for which it was designed.

Other possible barriers to adaptation to other species and systems include:

- It lumps all developmental stages, dividing individuals into mass classes alone. A large immature very likely behaves differently from an adult of similar mass -- a clitellate allocates more of its energy to reproduction rather than growth.
- It assumes a maximum mass, using a logistic equation to determine growth rates. In nature, environmental conditions such as temperature, moisture, and food quality may in part determine maximum mass and change parameters in growth rate equations, both of which are not considered in this model.
- Although it is a predictive model, validation with data sets independent of those used to create the model was not performed.
- Individuals are treated separately, even though the same growth equations and environmental state transitions affect all animals equally. From a computing standpoint, this approach uses extra computer memory and storage, especially if many weight classes are used, and takes a lot of computer time.

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Chapter 2

OBJECTIVES AND RATIONALE

Introduction

Detailed dynamics of natural earthworm populations, particularly those of species that are not economically important, are poorly understood, although these animals are important members of the soil community. Even for species studied extensively, only selected life history parameters have been observed, such as cocoon development time (usually at a single temperature), mean time to first reproduction, or fecundity. Little is known about life spans or life expectancies in the field; only a few notes have been made of life spans in laboratory situations (Edwards and Lofty 1972). Very little is known about interactions between multiple environmental variables, such as temperature, moisture, and food quality and availability.

Many studies have been done on the sensitivity of certain earthworms to various biocides and heavy metals, and on their ability to bioaccumulate some of these substances, thus passing them up the food chain. One environmental perturbation previously left unexamined is their possible sensitivity to small electric currents or fields within the soil. Earthworms must maintain a moist cuticle as a respiratory surface, rendering their bodies conductive. Because their nerve fibers

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are not insulated by a myelin sheath, they may be susceptible to electric fields induced in the soil. Edwards and Lofty (1972) describe earthworms' responses to an electric current: in water, they become U-shaped, with both ends pointing toward the cathode. Many earthworms come up to the soil surface when an electric current is applied, and this has been used as the basis for earthworm sampling devices (Rushton and Luff 1984).

The U.S. Navy's Extremely Low Frequency (ELF) radio antenna in Michigan's Upper Peninsula generates an alternating electromagnetic field similar in frequency to household line frequency (76 Hz nominal). Whenever a magnetic field contacts a conductive medium, it induces a current in the conductor. As the polarity of the magnetic field changes, the induced current also changes direction, producing an alternating current. Soil, especially if moist, can conduct electricity, so that the ground near the antenna is subjected to a weak alternating current, which is rapidly dissipated with increasing distance from the source.

One of the elements of the ELF ecological monitoring program in Michigan was designed to look for just such a localized EM effect on soil fauna, particularly earthworms (Snider and Snider 1987, 1988; Snider 1994). The first five years of this ten-year field study were used to obtain baseline data in a TEST site adjacent to the antenna and a CONTROL site removed from its influence before the antenna was activated; the second five years, the study areas were monitored for any population- or community-level changes that may have occurred due to a weak EM field induced by ELF antenna operation.

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Research Objectives

This study had three objectives:

(1) To develop dynamic structured population models of three species of lumbricids based on soil temperature and moisture regimes.

(2) To describe the life cycles of the three species and compare their success in different environmental regimes, ranking their responses and adaptations along the r-K continuum.

(3) To use this modelling approach to detect and describe any significant effects of induced EM fields on earthworm populations during the operational phase of the ELF project.

Results pertaining to the first two objectives are presented in Chapter 5 of this thesis; Chapter 6 details the application of one of the models to ELF data during the operational period to determine if and in which developmental stages the ELF EM field had an effect, and if so, what consequences it may have had for the fate of the population.

Species Studied

Three lumbricid species were chosen for examination because of their widely different lifestyles and their high abundance in the study area near the ELF antenna: *Aporrectodea tuberculata* (Eisen), *Dendrobaena octaedra* (Savigny), and *Lumbricus rubellus* Hoffmeister. They can be placed in three distinct sites along the r-K continuum (MacArthur and Wilson 1967).

Aporrectodea tuberculata was common at the ELF TEST site and occasionally collected at the CONTROL site. Twenty-five to 30% of the individuals collected on any given date were large adults (either clitellate or

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aclitellate) with masses up to about 1.0 g, and cocoon:clitellate ratios were low when compared to other species found in the ELF sites. Cocoons were also larger than those of most other species, averaging about 20 mg. The seasonally stable population structure, comparative size and frequency of cocoons suggests that this species tends toward K-adaptation.

Dendrobaena octaedra is a small species, rarely weighing more than 0.15 g at maturity. It was the most commonly found species at the CONTROL site, and much less common at TEST. Small immatures dominated the population during June and early July, shifting to large immatures and adults later in the summer. The number of cocoons found per clitellate was much greater than in *A. tuberculata*, and they were much smaller, averaging 3 to 4 mg. These factors indicated an r-adapted species with high juvenile mortality compensated by high fecundity.

Lumbricus rubellus was common at the TEST site, but uncommon at CONTROL. There were indications that it was in the early stages of population expansion at CONTROL (R.M. Snider, pers. comm.). The population structure was more skewed toward immatures than in the other two species, with clitellates becoming more common in the late summer and fall. No marked increase of immatures was evident at any time, unlike *D. octaedra*. The cocoon:clitellate ratio was nearly as high as in *D. octaedra*. The more seasonally stable population structure together with high cocoon production suggests a position on the r-K continuum somewhere between the other two species.

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Earthworm Population Modelling Approach

Both soil temperature and moisture affect the cocoon production, growth and developmental rates of earthworms (Laverack 1963, Edwards and Lofty 1972), but the combined effect of these environmental variables has not been quantified for many species. These effects will differ not only between species, but also between developmental stages within a population. Since earthworms can easily lose mass and may regress developmentally when stressed, a predictive model of population dynamics can quickly become complex.

Matrix projection models, such as those of Leslie (1945, 1948), are well suited to this type of modelling, as the matrix can be so arranged as to allow both growth and retrogression, and differential fecundity based on age or size. They are also sensitive to small changes in the behavior of individual age, size or developmental stage classes. The major disadvantage of this type of model as used in many biological or ecological studies is that it is static, and describes the behavior of a given population under specific conditions. If those conditions change, the behavior of the population will also change, requiring the generation of a new matrix. This means that a matrix produced from one year's data at one site is likely not an accurate predictor of the behavior of a population elsewhere, or even at the same place under different conditions. An example is Bierzychudek's (1982) work on Jack-in-the-pulpit: data collected during different seasons and within and between geographically separated populations produced matrices that indicated population increases in some instances, and declines in others.

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One way around this problem is to produce a stack of matrices from which to choose, depending upon the combination of conditions. This solution produces its own problems. How does one choose between several valid matrices? What if one encounters a particular combination of conditions for which no current matrix exists? A more elegant, but complex, way is to calculate predicted mean changes in size and developmental stage due to environmental influences, and place the results in a matrix. Standard matrix algebra can then be used to calculate an expected change in population size and structure, just as with the typical matrix model.

The structure of the model used in this work is more complex than a typical Leslie matrix because changing environmental variables are taken into account. This is not a "static" transition matrix -- a single matrix containing immutable transition probabilities. Instead, it is a "dynamic" matrix, one whose transition probabilities change with environmental conditions.

The aims of this model design are similar to those of Lavelle's (Lavelle and Meyer 1977 and 1982, Lavelle et al. 1989), where the production of a generic framework can be utilized for a variety of species under different conditions, possibly for monitoring effects of environmental changes. The difference between the two models is one of approach -- probabilistic versus deterministic. Instead of having a separate case for each individual, which winds its way through different states of a suite of environmental and biotic variables, a set of equations based on environmental conditions was used to determine probabilities of state change for all members of a given group of similar size and/or developmental stage, including cocoons. All that changes in consecutive periods is the number of individuals in

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each class -- parameters for each individual do not have to be changed and stored separately for the next iteration. Therefore, this model is more compact and faster, and as a result should be easier to test. It should also be more adaptable to other species and conditions; in fact, it was designed with this feature in mind, and will be tested in this work with multiple species.

Advantages of the transition matrix approach are:

- The ability to easily change parameters for response of particular classes (sizes, ages, developmental stages) by a small amount to test the robustness of the model as a whole to small changes.
- The possibility of testing the success of an introduction or the fate of an existing population, given a regime of environmental conditions.
- A way of pinpointing the classes that are most affected by a given environmental change.

The basic method has been used in a variety of applications, from life histories of individual species (Bierzychudek 1982, Crouse et al. 1987) and population growth projections to prediction of multispecies interactions (Woolhouse and Harmsen 1989), and also wildlife (Rosenberg and Doyle 1986) and forest management (Pakkala and Kolström 1988). As a result, a number of methods have been developed to test the validity of any model produced. Because these are dynamic matrix models, with equations rather than discrete numbers occupying the cells, statistical methods used to test their validity and sensitivity may be unfamiliar.

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Model Construction

A first step to any transition matrix model is the appropriate choice of age, size, or developmental stages. A dual system was chosen, first separating individuals into groups by developmental stage, then into smaller size classes within those stages.

Development was separated into four broad stages. The **cocoon** is the embryonic stage of the earthworm enclosed in a mucopolysaccharide capsule. **Immature** worms are those that have no external sexual characters. **Aclitellate** individuals have obvious *tubercula pubertatis* and genital papillae, but no well-developed clitellum; these are prereproductive or nonreproductive adults. Presence of a glandular clitellum that is often a lighter color than the rest of the worm denotes the reproductive, or **clitellate** condition. Only this last stage is considered when calculating fecundity. Size classes within stages were chosen to mirror size-specific growth rates observed during the field and laboratory experiments.

Model construction was divided into three major sections, summarized here and treated in detail in the next chapter:

(1) Determination of transition probabilities for each size class/developmental stage combination using pairs of equations that define the mean size/stage change and the spread of values about the mean, and an equation that determined the probability of survivorship. It was assumed that size or stage change within a population emulated a normal distribution, so the spread was taken to be the standard deviation. The mean and standard deviation in each case were estimated via bootstrapping (incubator runs) or multiple regression of actual data (field microcosms). Size class transition probabilities were apportioned into three possibilities using the calculated size and spread: the current size class, and the size classes immediately

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(2) Calculation of fecundity equations (cocoons produced per clitellate), fertility (percentage of viable cocoons), survivorship, and developmental rate for cocoons.

(3) Combination of matrices that modelled growth within developmental stages, stage change, and survivorship, then addition of fecundity estimates for clitellates to produce a single master matrix containing the transition probabilities for that particular set of environmental conditions. Postmultiplying by a population vector would then produce a projected population structure, just as one would use a "static" transition matrix.

Sources and Use of Data Collected

Data used in constructing and testing the models were collected from three sources. One was carried out in incubators with controlled environmental conditions, a second was a "natural experiment" in which captive populations were exposed to near-natural conditions that were closely monitored, and the third was a periodic census of natural populations and monitoring of natural environmental variables.

Incubator Rearing under Controlled Conditions

Replicate subpopulations were reared in incubators under constant conditions at several levels of both temperature and soil moisture. A few individuals, widely spaced in size, constituted each subpopulation, allowing individual masses and developmental stages to be tracked. See Chapter 3 for details of the methods used in processing and analysis.

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Field Microcosm Rearing under Near-natural Conditions

Replicate populations reared in microcosms under semi-natural field conditions with closely monitored temperature and moisture regimes. Since these microcosms were substantially larger than the incubator microcosms and were intended to be maintained for a longer time with more worms per population, individuals in these microcosms were permanently marked using tattoos to facilitate tracking of individuals. Pertinent techniques are outlined in Chapters 3 and 4.

Periodic Censuses of Natural Populations

Biweekly censuses (May through October) spanning a 10-year period were taken of natural populations in the field, with associated environmental data. These data were collected as part of the ELF ecological monitoring project discussed earlier.

Building and Validating the Models, and Testing for ELF Effects

Data from the incubator and field microcosm experiments were employed to develop the models. Separate models were constructed from the two sources, and tested against each other to determine whether they were sufficiently similar. After similarity between models was established, data from the two sources were combined, and a composite model for each species was built.

A similar strategy for validating the models using pre-ELF data was not possible due to the nature of the field data. It was a point-sampling population

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census rather than an extended record of individuals. As a result, a different method was employed, that of using a single date's population vector to project a vector four weeks later, then comparing the modelled with the actual vectors throughout the season.

Testing for potential effects of ELF electromagnetic fields on the *A. tuberculata* population was accomplished in the same manner as the validation process, by comparing projected population vectors against actual vectors determined by periodic censuses. These comparisons were analyzed by month, year, and entire ELF operational period, 1989 through 1993. The model structure allowed isolation of key life cycle stages to determine their importance in the overall success of the population.

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Chapter 3

METHODS

Site Descriptions

ELF Field Sites

The sites used in the ELF ecological monitoring project are described fully in Snider and Snider (1987). Two sites, a TEST site (T.44N, R.29W, sec.25) approximately 80 m from the north-south overhead element of the antenna, and a CONTROL site (T.44N, R.30W, sec.11) 11.5 km from the same element, were chosen for their similarities in soil type, forest cover, and elevation. Both were located in northern deciduous forests with approximately 80% sugar maple, 10% basswood, and 10% other deciduous trees composing the canopy and subcanopy. Spicebush (*Lindera benzoin* L.) and leatherwood (*Dirca palustris* L.) were common shrubs, and various grasses and spring flora sparsely covered the forest floor. The altitude of both sites was approximately 420 m. The A horizon in both sites tended strongly toward mull and was developed on sandy glacial till with occasional cobbles and small boulders. Table 3 shows the physical makeup of the TEST and CONTROL soils compared with the prepared soil (described later in this chapter) used in both field and laboratory microcosm studies.

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Table 3. Physical parameters of soil from Test and Control sites, and prepared soil used in microcosm studies.

Parameter	TEST Site A Horizon	TEST Site B Horizon	CONTROL Site A Horizon	CONTROL Site B Horizon	Microcosm
% Organic	9.6	2.7	9.3	2.0	5.7
% Sand	59.7	59.8	58.6	58.7	65.3
% Silt	23.3	22.6	24.9	23.2	19.2
% Clay	17.0	17.6	16.4	18.9	15.5
Texture	sandy loam	sandy loam	sandy loam	sandy loam	sandy loam
Horizon depth	8 - 15 cm	> 75 cm	5 - 15 cm	> 55 cm	---
pH	5.9	5.9	5.8	5.8	6.2

Sources for TEST and CONTROL site data: Snider and Snider (1987).

A weather station in Iron Mountain, approximately 30 km south of the Control site, provided mean annual weather data for the 30 years preceding the study. Mean annual precipitation is 768 mm, more or less evenly distributed throughout the year. Snowfall and snow cover generally occur from late October through early May. The mean annual air temperature is 5.4°C, with a mean high of 26°C in July and a mean low of -15°C in January. Average daily temperatures range from -9°C in January to 19°C in July.

Each site contained 20 sampling quadrats, 10 m square, with 1 m aisles between them. Besides the sampling quadrats, one quadrat near the center of each site contained the equipment for monitoring soil temperature at several depths, air temperature, and humidity. Maps of the sites are shown in Snider and Snider (1987).

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Field Microcosm Site

An area near the northwest corner of the ELF CONTROL site was selected for placement of field microcosms. Although completely shaded by canopy trees, it was clear of brush, herbaceous ground cover, and large boulders, making it reasonably homogeneous throughout.

Field Population Sampling Methods

Earthworm Censuses

Earthworms were collected at two-week intervals using a stratified random sampling design consisting of ten 25 × 25 cm samples per date (12 in 1985 and 1986). The samples consisted of five subsamples: the litter layer (O-horizon), the humus layer (A-horizon), and three successive 10 cm samples of subsoil (B-horizon). Samples were removed to the field lab for processing, and the holes were backfilled with similar soil from outside the site borders. Samples were processed and earthworms and cocoons retrieved using the protocol outlined by Walther and Snider (1984). Earthworms were killed with alcohol and preserved in 10% formalin. Upon identification and determination of developmental stage, worms and cocoons were weighed to the nearest 0.1 mg using a Mettler AE-200 electronic balance. Since formalin dissolves out some lighter fats and oils, regressions were derived (R.M. Snider, pers. comm.) and used to convert preserved mass into live mass before worms were assigned a size class:

$$\textit{A. tuberculata}: \quad FW = -0.7186 + 1.0214 \times PW$$
$$\textit{L. rubellus}: \quad FW = 1.5609 + 1.024 \times PW$$

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where FW = fresh (live) weight and PW = preserved weight in mg. No regression was calculated for *D. octaedra*, and preserved mass was presumed to be equal to live mass.

Environmental Data Collection for Field Populations

Soil temperatures were monitored at 2-hr intervals from early May through late October throughout the study using Omnidata #222 Datapods. During the 1991-92 and 1992-93 winter periods, the datapods recorded soil temperature daily at midnight. Soil moisture was determined gravimetrically from samples taken on each sampling day. Temperatures throughout each four-week period were averaged to obtain a mean temperature for that period. Moisture levels at the beginning, middle and end of each four-week period were averaged to obtain an estimate of mean soil moisture over the period. Since winter soil moistures were not taken and the soil surface was frozen and under snowpack during these periods, soil moisture during the winter was presumed to be the mean of the last fall and the first spring soil moistures for modelling purposes.

Collection of Earthworms for Rearing Experiments

Dendrobaena octaedra were collected near the ELF CONTROL site by hand-sorting moist litter in leaf-filled depressions. An area in the Copper Country State Forest (T.41N, R.29W, sec.22), off Merriman Road and approximately 15 km NW of Iron Mountain, was used as a collection site for *A. tuberculata* and *L.*

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rubellus. Collecting these species near the ELF TEST site was not prudent, since they might have been affected by the proximity of the ELF antenna.

Aporrectodea tuberculata and *L. rubellus* were collected using "worm traps." In an early collecting trip, it was noted that earthworms were found in high numbers in the soil directly below deer droppings, and in soil that had been disturbed by previous collections. Traps were constructed by digging pits approximately 40 cm square and 30 cm deep in natural depressions, keeping soil from the various horizons separate. Roots were sorted out, and the soil was replaced in original horizon order. Before replacing the leaf litter, about 3 cm of well-rotted horse manure was spread over the filled hole, and was left undisturbed for two to six weeks between collections. Earthworms were collected by sorting through the disturbed soil horizon by horizon. The traps could be reused several times by reapplying manure.

Soil and Litter Preparation for Incubator and Field Microcosm Rearings

Soil for both incubator and field rearing experiments was collected near the ELF CONTROL site. Soil and leaves for microcosms were collected two to three weeks before each sampling date, and soil and leaves for incubator rearings were all collected in early May 1993. In all other respects, the methods of soil preparation for these two portions of the study were identical.

Preliminary trials suggested that the structure of dried and sieved topsoil by itself was highly altered leaving little pore space for aeration and percolation, resulting in high earthworm mortality. Subsequent trials showed that mixing a

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quantity of sandy subsoil equal to 25% by volume improved water infiltration and aeration sufficiently to reduce mortality and more closely simulate natural soil water relations.

Soil was collected by first scraping off the leaf litter and coarse organic material from the soil surface, after which squares of A horizon were removed. A quantity of sandy subsoil was also taken and kept separate. On the first sunny day after collection, the topsoil squares were broken up and spread thinly on plastic sheets in the sun. Any earthworms and cocoons found in the process were removed. Roots were sorted out and placed in a corner of the sheet to dry with the topsoil. The subsoil was spread out similarly. Both fractions were left to sun-dry for two to three days to kill and desiccate any earthworms or cocoons remaining. When completely dry, the topsoil and subsoil were sieved through a hardware cloth screen (1.25 cm mesh) to remove rocks and small roots. Topsoil and subsoil were then passed through a 3 mm mesh sieve, using the dried root mass to rub them through. As a result, a quantity of dried fine root material found its way into the prepared soil, adding structure.

Topsoil and subsoil were mixed in the final sieving step: three measures of topsoil and one measure of subsoil were shaken through a window screen sieve with approximately 1 mm mesh to separate the smaller fraction, which was caught in a tray below and saved. The larger fraction, usually 15 to 20% of the total volume, was dried overnight in a 105°C oven to desiccate any remaining cocoons. After desiccated cocoons were removed, this oven-dried fraction was mixed thoroughly with the finer fraction.

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The leaves used in both experimental settings were removed from the forest floor by raking, taking care to remove only clean, nearly intact leaves and leave those that were well decomposed or partially buried in the soil below. Leaves were suspended in nets of 1.27 cm plastic mesh and allowed to air dry. After at least one week of drying, leaves destined for use in incubator rearings were stored in loosely sealed plastic bags. The bucket leaves were treated in the following manner: 15.0 ± 0.05 g of leaves were placed into each of fifty plastic bags with 10 ml water and a numbered plastic identification tag, and sealed. The leaves were moistened by turning the bags several times over the next 24 to 48 hours to redistribute the water.

Physical Characteristics of Prepared Soil

Several procedures were used to characterize the physical properties of the prepared soil used in the field and incubator microcosms so comparisons could be made between this and other studies. Composition analysis consisted of determining the proportion of organic matter, sand silt, and clay. Water-holding characteristics were examined by determining its field capacity; specific gravity, important in the relation between gravimetric and volumetric soil moisture, was also determined.

Samples were taken of three lots of prepared soil to determine its composition. An average of the lots (Table 4) showed that the soil contained 5.80% organic matter, determined by combustion at 600°C. The inorganic fraction

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Table 4. Percent organics and size distribution of inorganic fraction by mass in three lots of experimental soil mixture.

Lot #	% Organic Matter	Inorganic Fraction % Sand	% Silt	% Clay
1	5.82	64.0	20.3	15.7
2	5.76	66.2	19.0	14.8
3	5.82	65.7	18.3	16.0
Mean	5.80	65.3	19.2	15.5

contained 65.3% sand, 19.2% silt, and 15.5% clay, determined using a hydrometer method outlined by Bouyoucos (1927).

Field capacity of the prepared soil was measured via the following procedure: The soil was hand mixed with about 20% water by mass, allowed to sit overnight, then mixed again before placing it in a plastic tube 5 cm in diameter by 40 cm long, with filter paper fastened to the bottom. The tube was filled with soil, then dropped three times from a height of 10 cm onto a hard surface to compact it similarly to the treatment of soil in the field microcosms. Water was added slowly to the top of the tube until all the soil was thoroughly saturated and water was dripping from the bottom. The top of the tube was loosely covered with a plastic bag to reduce evaporative drying, and water was allowed to drain from the soil by gravity for approximately 48 hours. Three 40 g samples of soil were taken from the center of each tube, weighed, dried at 105°C for 24 hours, cooled in a desiccator, and re-weighed to measure water loss. A one-way ANOVA with the three tubes as treatments and the samples within each tube as replicates showed no

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significant difference within or between the tubes at the α=0.05 level. Mean field capacity was 28.98% (SD=0.89, n=9) water by mass. Figure 3 illustrates the apparatus used.

Specific gravity of the soil was determined by weighing ten random samples of air-dry soil level full in 100-ml crucibles, tapped on the counter several times to ensure packing. After removing the soil, the same crucibles were weighed level full with water, the ratio of soil mass to water mass being the specific gravity. The mean of the ten samples was 1.089 with a standard deviation of 0.027.

Earthworm Tattooing Procedure

A method was developed that allowed essentially permanent marking of earthworms so that growth and development could be observed on an individual basis in the field microcosms. The technique consists of three parts:

- A procedure to anesthetize worms that does not adversely affect them;
- The actual tattooing process, using a technique that does not damage the worm and pigments that are nontoxic and stay in place; and
- A method to easily observe tattoos without overly stressing or damaging the animal.

Anesthesia

Several anesthetic agents commonly used on invertebrates, such as LiCl solution, chloral hydrate, and carbonated water, were tested. All were ineffective at low concentrations or detrimental, often lethal, to the worms at higher concentrations. Carbonated water was the most effective, but mortality was still

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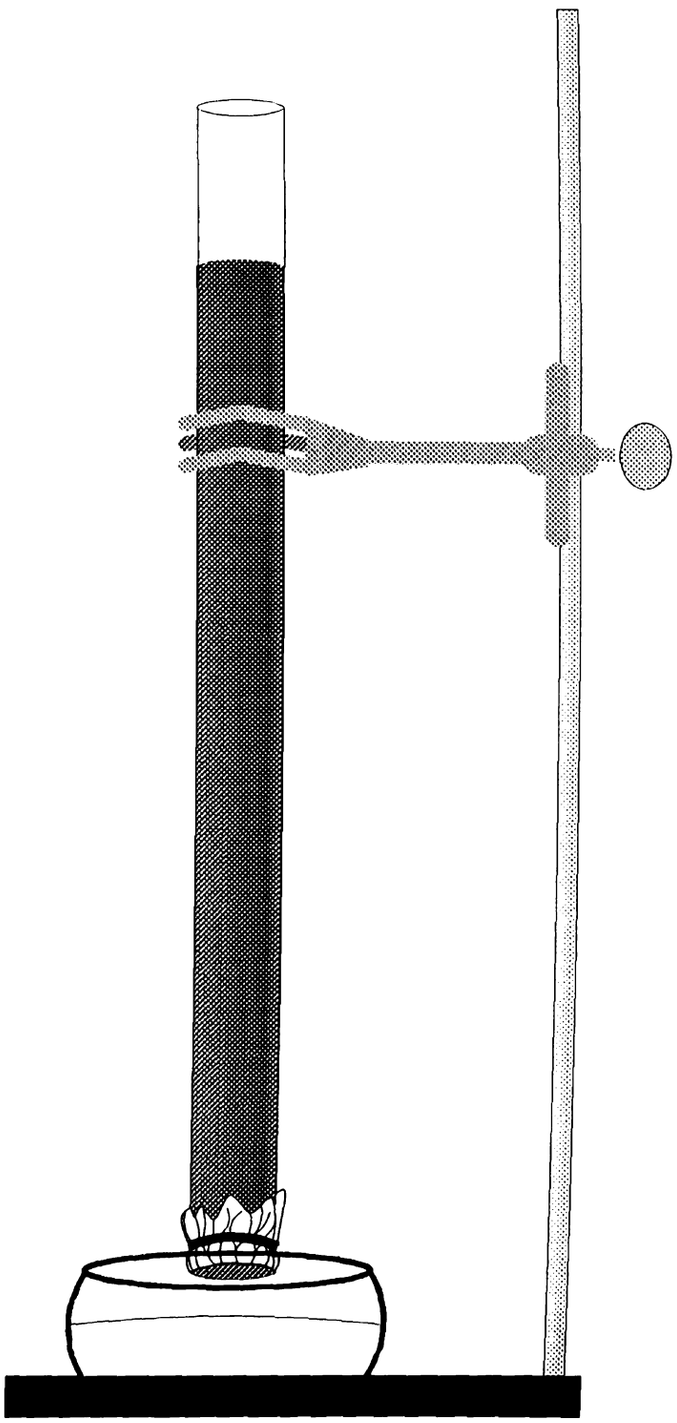

Figure 3. Diagram of the tube apparatus used to determine field capacity of the prepared soil used in the incubator and field microcosm experiments. See text for description.

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unacceptably high. Working on a hypothesis that pH was the detrimental factor, a solution of $NaHCO_3$ (baking soda) was tested and found both safe and effective.

Worms whose guts had been voided by holding them on moist paper toweling for 24 hrs were placed in a Petri dish partly filled with water and a small pile of baking soda until the worm was unresponsive to prodding of its prostomium. It was then immediately blotted dry and readied for marking. If the anesthetic required more than three minutes to take effect, additional baking soda was taken from the pile and mixed into solution. Twenty to 30 worms could be anesthetized before the water required changing due to mucus buildup. Earthworms treated in this manner were immobilized for approximately five minutes, allowing them to be tattooed if one worked quickly. After the tattooing procedure, earthworms were placed in clean water until they revived. They were then transferred to plastic containers with moist paper toweling to recuperate overnight before being returned to moist soil.

Tattooing Procedure

A variety of dyes and pigments were tested for efficacy, including food coloring, India and other drawing inks, and commercially available tattoo pigments. The tattoo pigments were found to work most satisfactorily; dyes and stains faded in a matter of days to weeks, and drawing ink pigments proved lethal in many cases. Tattooing was performed using a *Minutien Nadel* bent approximately 30° at the tip and mounted in a wooden dowel using a short piece of aluminum tubing, crimped with pliers to hold the pin (Figure 4). This arrangement also allowed the

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Figure 4. Diagram of tattooing tool. A -- *Minutien Nadel* with bent tip; B -- aluminum tube, crimped to hold needle in place (can be opened to allow tip replacement); C -- wooden handle. Total length of tool is approximately 12 cm.

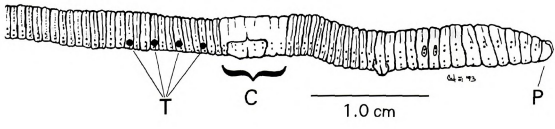

Figure 5. Anterior 2/3 of sexually mature (clitellate) *A. tuberculata*, showing placement of tattoos. T -- tattoos; C -- clitellum; P -- prostomium. Earthworm illustration by Catherine Nerbonne.

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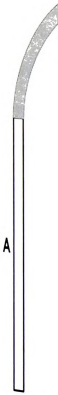
needle to be replaced if necessary. The integument was pierced several times through a drop of pigment placed on the worm's integument, burying minute amounts of pigment between the integument and outer muscle layer. Care was taken not to penetrate the coelom, as pigment in the coelom was found to kill the worm. Although necropsies were not performed to determine the cause of death, affected segments filled with fluid and increased greatly in size, while segments posterior to the affected segments wasted and became necrotic within 48 hours of tattooing. This suggested that a buildup of fluid probably pinched off the circulatory system, and possibly the gut as well, at the point of injury. Fluid buildup may have been due to blockage of nephrostomes or dorsal pores by pigment granules.

Four tattooed dots, three segments apart, were placed behind the clitellum along the dorsolateral row of setae (Figure 5). By using four sequential dots of four different colors (white, red, blue, and green), 256 unique marking patterns could be recognized.

Viewing of Tattoos

To observe marked earthworms, a mouth-operated aspirator apparatus (Figure 6) adapted from Thielemann (1986) was used to suction an earthworm from a water-filled dish into a glass tube of a diameter appropriate to immobilize the subject. The tube allowed thorough examination of the worm for its markings and developmental stage under a dissecting scope without damage. While the rubber hose above the examination tube was pinched, the worm could be held in the



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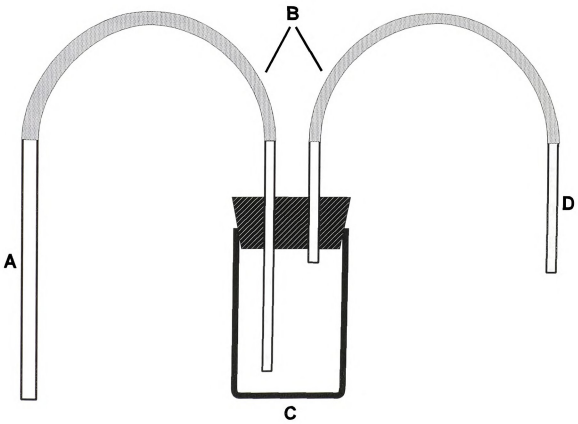

Figure 6. Aspirator apparatus used for viewing earthworms (adapted from Thielemann 1986). A -- Glass tube for examining earthworms; B -- rubber tubing; C -- jar with rubber stopper; D -- mouthpiece.

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tube by hydrostatic suction; when the hose was released, the extra water in the hose washed the worm out without injury.

Field Microcosm Rearings

Microcosm Construction

Microcosms for rearing earthworms under semi-natural temperature and moisture regimes were constructed from 5-quart polyethylene ice cream pails (Figure 7). Four quadrants were cut from the bottom of each bucket, leaving intact cross-strips 1 cm wide to support the weight of the soil it would contain. A circle of NITEX® netting (80 mesh) was fastened inside the bottom, using a soldering gun to tack it in place and latex caulk to seal the edges. Circles were cut out of the lids and replaced with netting that would breathe and admit rainwater while preventing escape of earthworms. The bottom 3 cm of an additional set of buckets was cut off, and the wire handles were removed. These buckets served as sleeves placed permanently in the ground to receive the microcosms, simplifying their periodic removal and replacement.

A small hole was pierced at one edge of the netting on each lid to allow passage of the moisture probe cable, and was reinforced with stiff plastic squares so the cables could move freely without escape of worms. Since both the probe and the connector plug on the other end of the cable were larger than the hole, the probe became part of the lid assembly.

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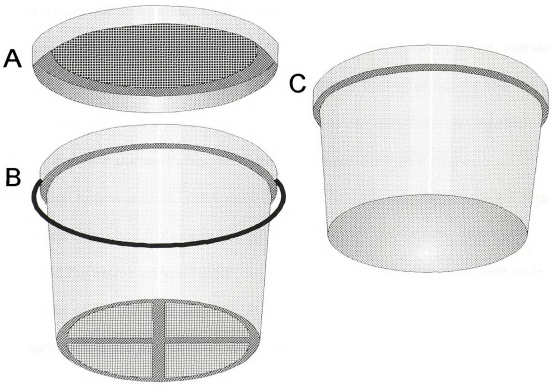

Figure 7. Diagram of bucket microcosms used in the field portion of the study. A -- Screened lid, shown here without the TDR moisture probe; B -- bucket with screened bottom; C -- bucket with bottom removed, used as a sleeve for easy placement and removal from the ground.

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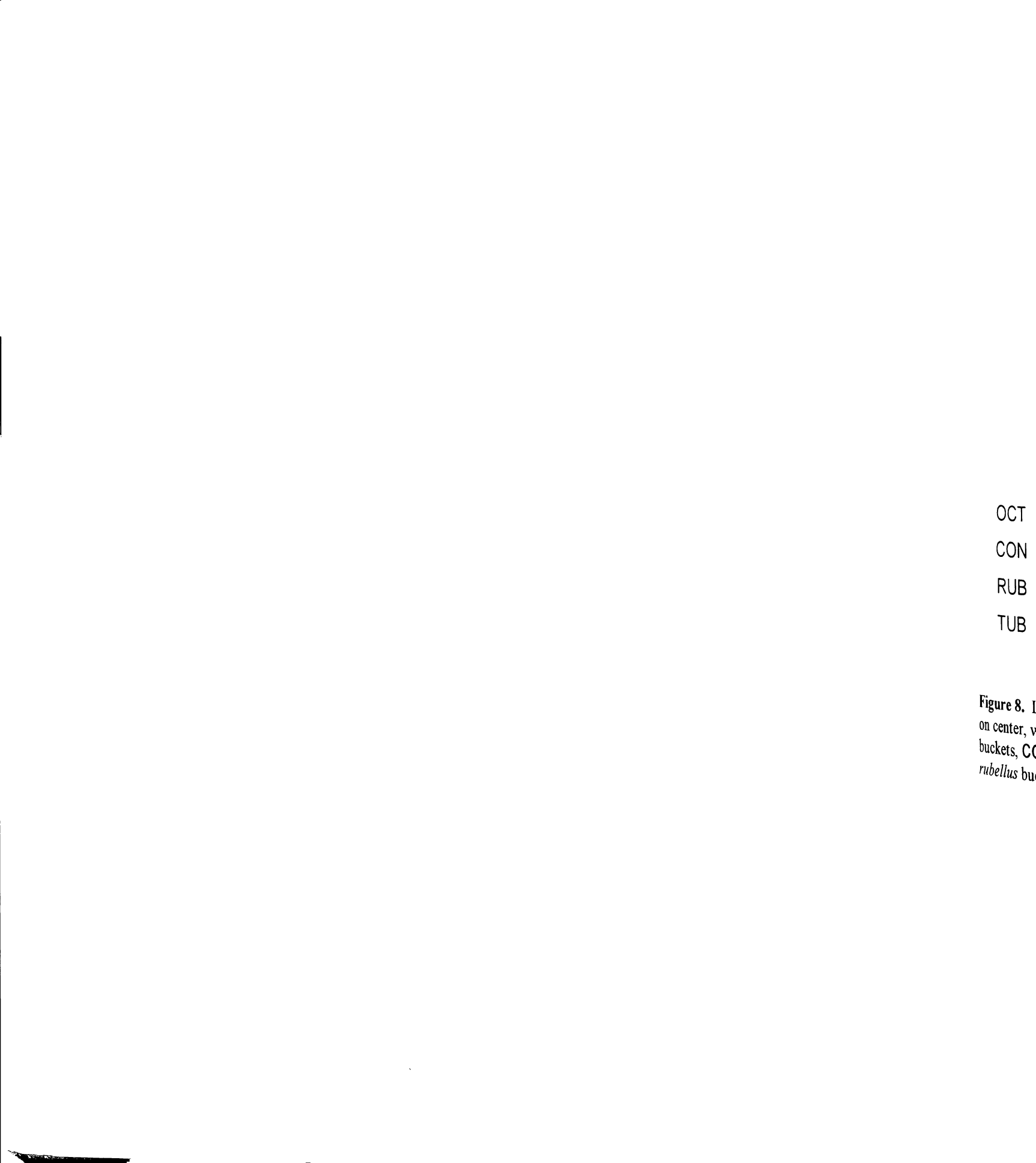
Field Placement of Microcosms

Microcosms containing prepared soil, leaves, and earthworms were placed in four parallel rows of ten holes each, 0.5 m apart. Microcosms were placed alternately 0.5 and 1.0 m apart along each row, leaving wider paths through the array to simplify their tending and retrieval. Holes were deep enough so that the soil surface inside and outside each microcosm was at the same height. Three rows contained replicate populations of each of the three worm species studied, and the fourth was a set of buckets with no worms, used as a control group for soil chemistry and physical property studies which were not completed during this project. Figure 8 shows the layout of the microcosms within this grid.

Each hole was lined with a sleeve, and loose sandy subsoil was placed in the bottom and smoothed flat to provide adequate hydraulic contact between the screen and the native subsoil below. A garden stake was driven next to each hole, and the end of the moisture probe cable was rubber-banded to it to decrease probe movement within the microcosm. A 100 ml plastic sample jar was inverted over the top of the stake and the connection plug to provide some protection from the weather.

A separate set of 12 microcosms, four for each species, was placed near the main set of field microcosms for field-rearing cocoons. All cocoons gathered from one species' microcosms each month were placed in a separate cocoon microcosm. These were examined monthly, and the number of cocoons in each developmental stage were counted. Hatchlings of each species were distributed back into their respective earthworm microcosms as described elsewhere in the text.



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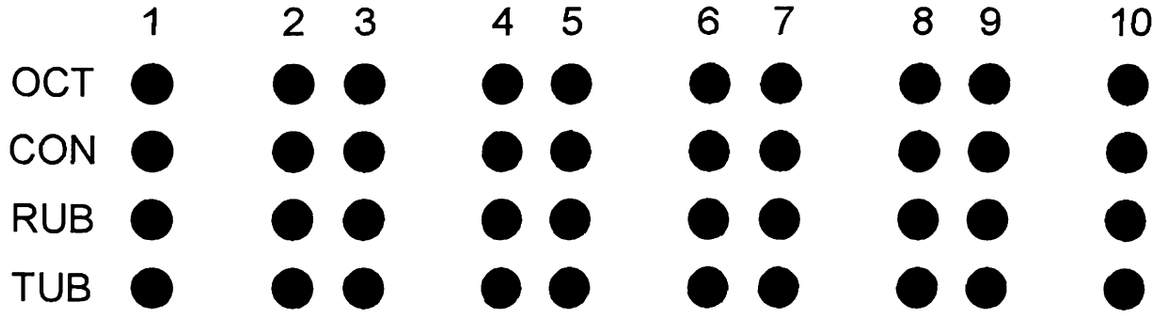

Figure 8. Layout of the bucket microcosm site. Buckets in each group are 0.5 m apart on center, with 1.0 m aisles between groups. Codes for treatments: **OCT** -- *D. octaedra* buckets, **CON** -- control buckets with no worms (not part of this project), **RUB** -- *L. rubellus* buckets, **TUB** -- *A. tuberculata* buckets.

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Temperature and Moisture Monitoring

Ambient soil temperature was monitored at 2-hour intervals throughout the study, using the data logger for the ELF Control site, about 35 m distant from the bucket array. During the second year of microcosm experiments, extra data loggers became available to test whether soil temperatures inside and outside the buckets were equal. Three field microcosms, one of each species, were chosen at random for temperature probes. Two additional probes were placed in the A horizon 5 cm deep at both ends of the bucket array to monitor ambient soil. Never was there more than ± 0.5 °C difference between individual buckets, nor was there more than ± 0.5 °C difference between bucket and ambient soil temperature, either immediately outside the microcosm array or at the ELF monitoring site 35 m away, during the three months these temperatures were monitored. This difference was equal to the precision of the temperature probes and data loggers used.

Soil moisture in the microcosms was measured using time-domain reflectometry (TDR). TDR has been used as a nondestructive method of measuring volumetric soil water content for about 15 years (Topp et al. 1980), but is just beginning to gain general acceptance because of the experience necessary to adequately interpret the waveforms generated by the apparatus (Catriona et al. 1991). Field measurements have usually been made by producing a paper tape recording of the oscilloscope waveform on the TDR meter. Interpretation of the waveforms invariably led to problems with human error. The improvement utilized in this study employs a laptop computer linked directly to the meter in place of the printer (Figure 9). The waveform is fed into the computer, where the trace is

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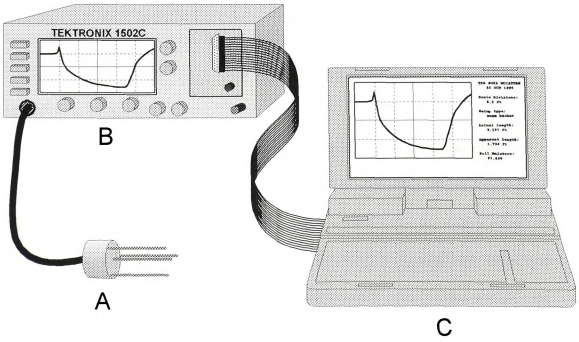

Figure 9. Time domain reflectometry (TDR) apparatus used in this study. A -- coaxial soil moisture probe; B -- Tektronix 1502C TDR meter; C -- laptop computer connected to TDR meter via a serial cable.

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smoothed and mathematically analyzed, providing consistent interpretation. The program stores the result in a *.WK1-formatted spreadsheet file (© Lotus Development Corp.). Both the TDR meter (mounted on a pack frame) and the computer are battery-powered, so that a nearly instantaneous measurement of soil moisture can be obtained using portable apparatus. The TDR meter can test 75 to 100 waveforms on a single battery recharge, and the laptop computer can run approximately two hours on one battery.

Microcosm sampling

Microcosms with earthworms were first placed in the field in early November 1991. The first regular sampling date was in early May 1992, and sampling was repeated every fourth week until late October, for a total of seven sampling dates the first season. The second season began in mid-May 1993, and continued until early October, for a total of six monthly samples the second year.

One day before bucket filling, prepared soil was rehydrated to approximately 20% gravimetric moisture, mixed thoroughly and allowed to equilibrate overnight. Just before filling, the soil was again thoroughly mixed. The buckets were loaded with 2 l of moist soil and dropped three times from a height of about 10 cm to compact the soil. A layer of moistened leaves was placed on the soil after earthworm reintroduction.

On each sampling date, the microcosms were removed to a field laboratory, the leaves were hand-sorted, and the soil first hand-sorted then water-sieved to

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retrieve all worms and cocoons, using techniques identical to Walther and Snider (1984). After all earthworms were identified by their tattoos, examined and weighed (gut-full mass), they were returned to their microcosms, which had been reloaded with moistened soil and leaves, and the buckets taken back to the field site. Large worms were replaced if they had died or were injured in the retrieval process. Newly hatched worms from cocoon rearing microcosms were added to the populations of one-third of the buckets, either buckets 1 through 3, 4 through 7, or 8 through 10 depending on the month. By rotating the times when hatchlings were added to each set of buckets, distinct size cohorts could be maintained until they were large enough to be removed and marked individually. Multiple ("replicate") cohorts allowed calculation of the variance between them. Cohorts were treated as sets of individuals of identical size in the model generation phase. Earthworms were out of soil less than one hour, and the buckets were usually removed from the field in early morning and returned the evening of the same day to reduce disturbance effects.

Incubator Rearings

Incubator Experimental Design

Levels of temperature and gravimetric soil moisture were arranged in a rotatable central composite design (Gill 1978), with levels at each design point listed in Table 5. Four additional points were placed at the center of the design (22.5% moisture, 10°C) to simulate an orthogonal design and allow goodness-of-fit tests (Myers 1971). The ranges of each variable were chosen to parallel the

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Table 5. Pairs of temperature and moisture levels used in the incubator rearing experiments.

Temperature (°C)	Moisture (% gravimetric)
3	22.5
5	17.2
5	17.2
10	15
10 *	22.5 *
10	30
15	17.2
15	17.2
17	22.5

Each level = four replicates except *, which had five sets of four replicates.

commonly observed ranges of these two parameters, based on environmental data collected as part of the ELF project.

Each design point was represented by four 1-quart polyethylene containers for each of the three earthworm species. They were loaded half full of prepared soil of the proper moisture level, and ten to twelve moistened sugar maple leaves. Each container was stocked with 6-8 (*A. tuberculata* and *L. rubellus*) or 8-10 (*D. octaedra*) individuals of different sizes and developmental stages. Additional containers with spare earthworms were kept at each level to replace those that died during the experiment. By monitoring a few individuals with widely spaced masses within each container, individual worms could be tracked through the entire experiment with little chance of confusion.

After a two-week acclimation period, containers were sampled every two weeks for ten weeks. On each sampling date, the gut-full mass of each worm was

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measured to the nearest 0.1 mg with a Mettler AE-200 electronic balance and its developmental stage determined. After hand-sorting to remove worms with as little damage as possible, the soil was water-sieved to retrieve cocoons. The containers were washed and reloaded, the live worms placed back in the same containers, and dead worms replaced by earthworms of similar mass and developmental stage. Cocoons were placed in Petri dishes filled with moist soil and monitored every second week for development, and up to two or three times weekly as cocoons neared hatching.

Analysis was performed on mass and stage changes over three pairs of biweekly sampling periods: periods 1-3, 2-4, and 3-5, corresponding to the 4-week periods used in the field microcosm rearing experiment. The actual masses were converted to discrete size classes, minimizing autocorrelation effects (J. Gill, pers. comm.).

Occasionally, all worms in a container would be found dead at the end of a two-week interval. Cause of death could not be determined, because earthworms decompose very rapidly and would have to be found shortly after death. These cases were restricted to replicates at the two highest temperature levels, and may have been a result of buildup of metabolic wastes, resulting in poisoning. Due to high mortality and the sensitivity of response surface designs to unbalanced data sets, analysis was performed on bootstrapped means derived by resampling with replacement of the values obtained at each design point.

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Response Surface Methodology and Bootstrapping Techniques Employed

Response surface methodologies (RSM) were developed to examine effects of multiple factors in situations where fully factorial designs were impractical. The application of response surface methodologies in ecology is quite limited, partly because ecologists are unfamiliar with the technique, and partly because of restrictions placed on the experimental design that make it inappropriate to the problem (Clancy and King 1993). The necessity of predetermined levels of experimental variables, makes it impossible to use RSM in many field situations where these levels cannot be precisely controlled. RSM is useful when the purpose of the experiment is to find the levels of two or more factors that produce an optimum in the response variable (Gill 1978:271). It consists of either augmentation of a general factorial design or a simple geometric pattern of design points representing specific combinations of the treatment variables. Secondarily, RSM produces a linear or quadratic regression that may be used to predict the behavior of the response variable in the region surrounding the optimum.

An important class of response surface designs is the central composite design, or CCD. Although not limited to second-order response surfaces, CCDs were developed with second-order polynomials in mind. The basic CCD begins with a factorial design in an orthogonal array, adding a design point (often multiple points) at the center of the array, and also points placed along all of the axes of rotation of the original factorial design. The design points are usually coded to denote the direction and distance from the center point in Cartesian coordinates.

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The center of the CCD might not be close to the optimum being sought, so it is often constructed so the precision of the estimated optimum is only affected by the distance from the center point, not its direction. Such a design is termed rotatable. One of the simplest of these is illustrated in Figure 10, the design used for the incubator rearings. Multiple points are placed in the center, producing a field bounded by the outer ring of points in which the precision of the estimate is nearly uniform, and is unaffected by distance from the design center. It then approximates an orthogonal design, allowing goodness-of-fit tests (Myers 1971, Gill 1978).

The advantage of this design is that it accomplishes roughly the same thing as a fully factorial 5 × 5 design with 13 points instead of the 25 necessary for a full second-order factorial, realizing a great saving in time and effort. The disadvantage of RSM is that, due to the reduction in number of points from a fully factorial design, a balanced design is essential. High mortality in all three earthworm species at the two highest temperatures severely unbalanced the design when examining growth rates and developmental stage change with respect to temperature and soil moisture. To correct for this, bootstrapping (Stine 1990) was employed, in which the available data were randomly sampled with replacement to obtain a balanced data set with which to run analyses. By resampling multiple times and determining a new mean of a fixed-size set each time, a variance of estimated means could be generated about the true population mean. This population mean was then used as the response variable at the appropriate design point in the RSM, and a second-order multiple regression was calculated to model

Figure 10.
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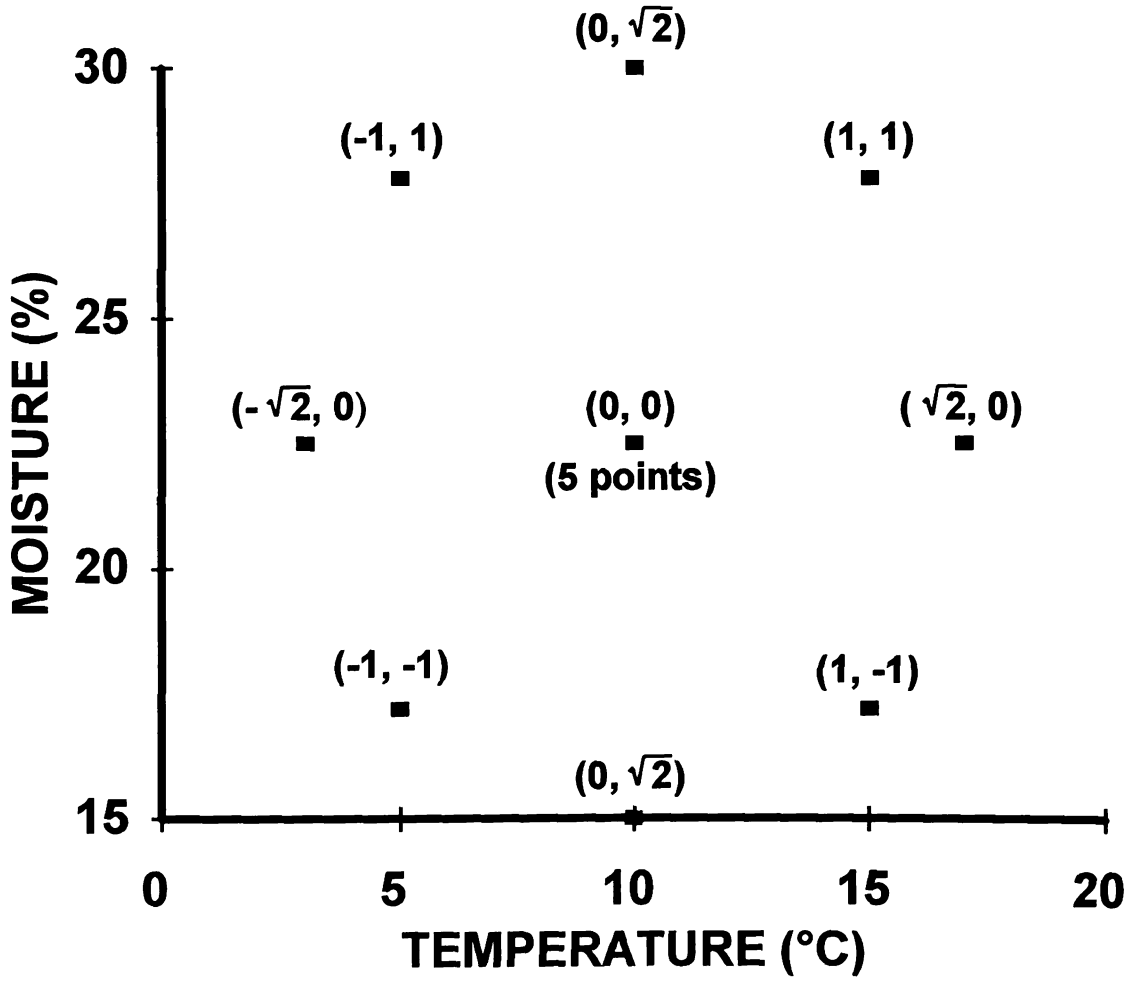

Figure 10. Design of incubator rearing experiments. Numbers in parentheses are the factor level codings used in the rotatable central composite design. Moisture is gravimetric moisture.

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the behavior of each size class or developmental stage in one of the incubator population models.

A program written in Turbo Pascal accomplished the resampling efficiently. It calculated multiple regression, storing the coefficients and their significances based on the resampled data set in a spreadsheet file for later analysis. The program also allowed stepwise elimination of variables, following a few basic rules:

- No first-order variables were removed before first eliminating any higher order or interaction terms including that variable. For instance, the first step involved all six variables: temperature (T), moisture (M), T^2, M^2, T×M, and initial size class (S). In this case, T and M would not be considered for exclusion, because they were included in higher-order terms, but T^2, M^2, T×M, and S could be eliminated on the first step.

- Terms were eliminated only if they were found to be nonsignificant at the α=0.05 level in at least 200 of the 1000 bootstrapped data sets, resulting in a de facto power of at least 0.8 for each variable.

- The least significant term was considered for elimination first; if the first criterion was not met by this term, the choice moved to the next least significant term if it satisfied the previous criterion.

- The process was repeated until the R^2 of the equation began to decrease significantly, or the critical value for R^2 was not met at the $\alpha = 0.05$ level. Table R in Rohlf and Sokal (1995:125) was used as the source for critical values, although critical values for five and six variables had to be extrapolated from the table.

An excellent review of resampling methods for ecological applications has been published by Crowley (1992). The concept for the bootstrapping program used here came indirectly from ideas presented in Crowley's work.

Bootstrapped significance values are sensitive to deviations in sample number from that actually observed (or expected) during data collection (Stine 1990); therefore, a different number of individuals per design point were used for

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Table 6. Incubator experiment demographic breakdowns for all earthworm species and stages used to calculate multiple regressions.

Species	Stage / Size Class	Total Worms Observed	N used in model
D. octaedra	all immatures	354	40
	immature classes 3, 4	236	20
	all aclitellates	196	20
	all clitellates	216	25
L. rubellus	all immatures	629	70
	immature classes 4, 5	185	20
	all aclitellates	85	10
	all clitellates	125	15
A. tuberculata	all immatures	632	70
	immature classes 5, 6	261	30
	all aclitellates	247	25
	all clitellates	141	15

each species and developmental stage to approximate the N expected at each of these levels. Table 6 lists the Ns used for each of these. The N used is approximately the total divided by nine (the number of experimental levels observed) and rounded to the nearest five individuals. The smallest immature size classes had no possibility of stage change, so smaller numbers approximating the expected number of large immatures were used to calculate the immature-to-aclitellate stage change regression. Results for the equations were also checked against predefined upper and lower bounds, which are listed in the tables in Appendix A with the coefficients for each equation.

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Model Development

The first step in developing any matrix model is deciding how many age, size, or stage classes to use; too few classes, and the model becomes insensitive to subtle differences between developmental stages or sizes; too many classes decrease the precision and make the model unwieldy and prone to multiplication of error. Size classes need not all be the same width, if their width reflects the instantaneous growth rate of that size class during a specified time period. The width of each size class should be chosen so that the organism, when subjected to ideal conditions, will not grow entirely through a class during a single period, i.e., from size class 3 to size class 5. Similarly, if the life cycle is split into developmental stages, it should not be able to skip stages, for instance from immature to clitellate, without spending at least one time period as an aclitellate.

After examining eight to ten individuals of each species that could be tracked from small immature through reproducing adult, growth in all three species could be modelled using a von Bertalanffy growth curve (Poole 1974):

$$m_t = M_{\max} \times [1 - (b \times e^{k \times (t - t_0)})]^3$$

where m_t = the predicted mass at time t, M_{max} = the maximum mass attainable, b and k are species-specific growth coefficients, and t-t_0 = the time elapsed since hatching. This produces an asymmetrical S-shaped curve whose inflexion point is under half the maximum mass. Using these calculated growth curves, the total growth range of each species was divided into six to eight discrete size classes based on mass, which cut across all developmental stages. Table 7 shows the

Table 7. Max

Dendrobae		
Size code	N[2]	m
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1	4	
2	20	
3	57	
4	135	
5	137	
6	66	

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Table 7. Maximum mass in each size class for the three earthworm species studied.

Dendrobaena octaedra				*Lumbricus rubellus*				*Aporrectodea tuberculata*			
Size code	N[2]	Max. mass (g)	Devel. stages[1]	Size code	N[2]	Max. mass (g)	Devel. stages[1]	Size code	N[2]	Max. mass (g)	Devel. stages[1]
0	---	---	coc	0	---	---	coc	0	---	---	coc
1	4	0.01	I	1	3	0.05	I	1	8	0.0313	I
2	20	0.025	I	2	2	0.1	I	2	13	0.0625	I
3	57	0.06	I,A	3	8	0.2	I	3	31	0.125	I
4	135	0.1	I,A,C	4	49	0.5	I,A,C	4	35	0.25	I
5	137	0.14	A,C	5	50	0.75	A,C	5	41	0.5	I,A
6	66	>0.14	C	6	94	>0.75	C	6	38	0.8	I,A,C
								7	80	1.1	A,C
								8	121	> 1.1	C
matrix order = 11				matrix order = 10				matrix order = 13			

[1] Developmental stages: I -- immature, A -- aclitellate or postclitellate, C -- clitellate, coc -- cocoon.

[2] N = individuals in each size class, irrespective of developmental stage, used to generate the VBGF.

maximum mass in each size class for the three species studied. Size classes at each end of a given developmental stage were combined (for instance, a few *A. tuberculata* aclitellates were actually size class 4) until each size class comprised at least 5% of the total number of individuals within that developmental stage.

Stage designations were included in the coding scheme by adding 10 to the size code for aclitellates and 20 to the size code for clitellates; thus a mid-sized aclitellate *D. octaedra* would be coded as a 14, and the largest clitellates would have a code of 26.

Cocoon development was tracked using a scoring system:

0 = cocoons showing no sign of development
1 = those with a recognizable embryo
2 = embryos exhibiting a functioning vascular system and pharyngeal hearts
3 = mature embryos with pigmentation on at least the first ten segments
4 = hatchlings

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Cocoon developmental rates were modelled with these scores using a degree-day approach to estimate length of time to development. Moisture was not a factor for cocoons since cocoon culture trials showed that they continued to develop as long as enough free capillary water was present for effective gas exchange.

Determination of Fate Probabilities for Inclusion in Matrices

During each time period, a given worm has the possibility of:

- living or dying (measured as survivorship);
- increasing, decreasing or staying in the same size (growth / retrogression); and
- entering the next developmental stage, regressing, or staying at the same stage (developmental stage change).

The first of these is straightforward, and can be represented as a probability of survivorship during the period. The latter two, however, require more effort to divide them into the three possible fates (growth, retrogression, or remaining in the same class or stage), and assign probabilities to those fates.

An assumption was made that in a large population these fates follow a normal distribution around some mean size or stage change, which can be calculated using levels of environmental variables as coefficients. To test this assumption, normality of growth differences between adjacent monthly samples (mass at time 2 minus mass at time 1) was tested using the Lilliefors modification to the Kolmogorov-Smirnov goodness-of-fit test (Sokal and Rohlf 1995). A combination of both field and incubator microcosm samples were used, with one exception: the winter field periods (dates 1-2 and 7-8) were excluded because they

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Table 8. Lilliefors probabilities for Kolmogorov-Smirnov goodness-of-fit tests on monthly size increments for three earthworm species.

Size Class	*D. octaedra* N	*D. octaedra* Probability	*L. rubellus* N	*L. rubellus* Probability	*A. tuberculata* N	*A. tuberculata* Probability
1	39	0.0221	120	0.0809	31	0.3807
2	97	0.4324	160	0.3982	92	0.1136
3	296	0.3015	186	0.1035	253	0.6259
4	342	0.1434	288	0.1202	103	0.9702
5	306	0.1575	193	0.3501	118	0.0654
6	227	0.0151	168	0.7606	115	0.0024
7	---	---	---	---	126	0.4930
8	---	---	---	---	127	0.9720

represented growth over approximate six-month periods. Table 8 shows probabilities of significant departure from normality. The dataset for each species was grouped by initial size class, because earthworms of different sizes grow at different rates. Although some size classes departed from normality (those with less than 0.05 probability), size increments were generally found to roughly conform to a normal distribution, and the assumption was accepted. A similar goodness-of-fit test could not be performed on developmental stage change; mass is a continuous variable, whereas stage change is not: it has only three possible values in this growth model.

Both the mean and standard deviation must be derived from the data to describe the size increment distribution before it can be divided among the three possible fates. The standard deviation can be used to generate a cumulative normal function with an offset equal to the mean change, and the resulting curve can be divided into three regions representing the three fates (Figure 11). In this example,

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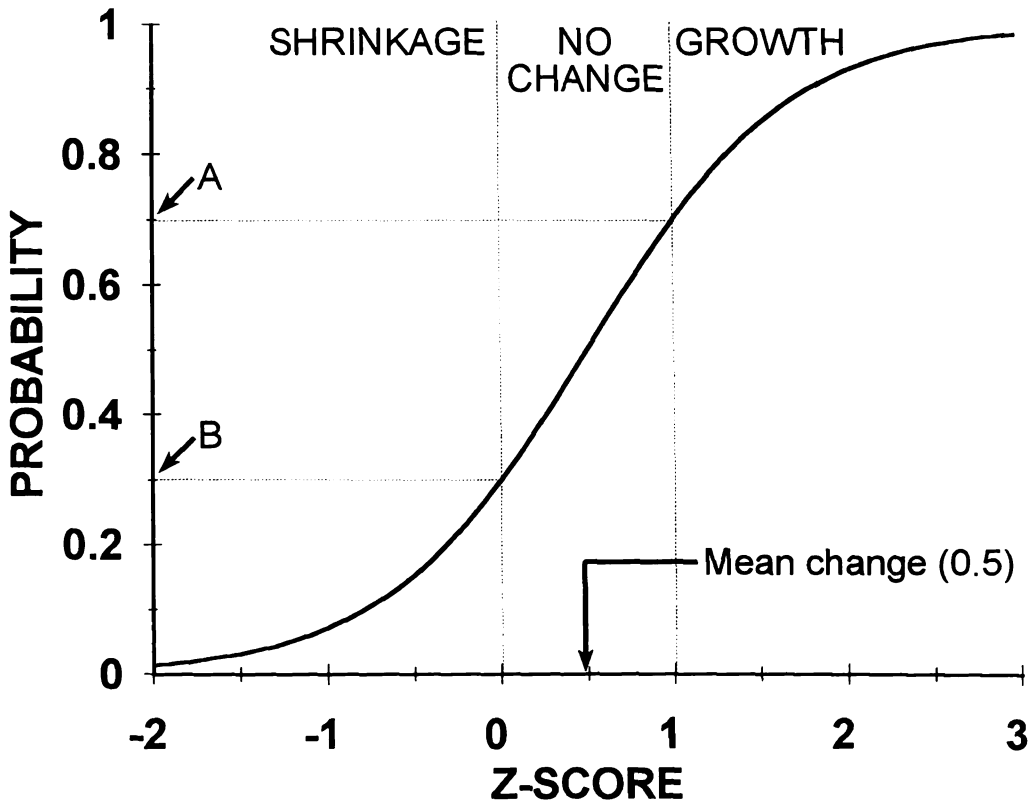

Figure 11. Hypothetical cumulative normal curve adjusted right to a mean change of 0.5. Labelled are the Z-scores which represent growth, no change in size, and shrinkage. A and B denote the probabilities associated with shrinkage and [no change + shrinkage], respectively.

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the shrinkage (B) and growth (1.0-A) probabilities are both about 0.3, and the probability of no change in size (A-B) is approximately 0.4.

To derive the cumulative normal function, a standard normal curve was generated to six standard deviations on either side of 0.0, and the increments were summed every 0.01 SD to obtain a cumulative normal curve. Since this function is based on powers of *e* and is symmetrical about its inflexion point, a logistic function was used to model it:

$$p = \frac{1}{1 + e^{(-1.701 \times Z)}}$$

where p = the probability that the measurement is equal to or less than a given *z*-score Z. This function has an $R^2 = 0.9999$, and an $F_{(2, 1198)} = 10{,}328{,}626$.

A second-order multiple regression in two variables, plus size, was calculated for size change and spread, stage change and spread, and survivorship for each developmental stage. The form of the full equation was

$$y = a + b \cdot T + c \cdot M + d \cdot T^2 + e \cdot M^2 + f \cdot T \cdot M + g \cdot S$$

where y = the response, T = soil temperature, M = soil moisture, and S = the size/stage class. Once the probabilities were calculated, they could be loaded into the matrix in their respective cells. The final matrix is actually the combination of three separate matrices: one describing size change, another stage change, and a third survivorship. The size and stage change were multiplied element-by-element to produce a combined matrix; this matrix was postmultiplied with the survivorship matrix, a matrix with the size- and stage-specific survivorships placed along the

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diagonal. Finally, the size-specific fecundities were placed along the top row after having been multiplied by the calculated cocoon fertility. Figure 12 is an illustration of an 11 × 11 *D. octaedra* matrix. The top row of numbers represents the size-stage codings at the beginning of a period, and the left column of numbers represents the possible fates of each class, denoted by letters within the matrix. The block letters ***A***, ***B***, ***D***, and ***F*** respectively indicate the position of cocoons, immatures, aclitellates and clitellates. The Roman letters ***C*** and ***E*** represent stage changes between immature and aclitellate, and aclitellate and clitellate respectively. The ***G***s along the top row represent size-specific fecundities. These are the only numbers in the matrix which may be > 1.0; with them removed, individual columns must sum up to ≤ 1.0. Blank cells are always zero; cells with letters in them are nonnegative. Cells on the long diagonal represent no size or stage change; those below denote growth or positive development, and those above shrinkage or negative development.

Model Testing and Validation

Validation was performed by comparing monthly ELF project population structures to those predicted by the models. Population vectors were constructed from pre-ELF (1984-1988) populations by pooling all population data for a species within individual sampling dates. These data were used as starting points for projection, and the projected vectors were compared by ANOVA with observed population vectors taken from the same site four weeks later. Ten monthly sets

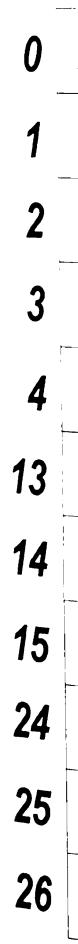

Figure 12.

	0	1	2	3	4	13	14	15	24	25	26
0	A								G	G	G
1	A	B	B								
2		B	B	B							
3			B	B	B	C	C				
4				B	B	C	C				
13				C	C	D	D				
14				C	C	D	D	D	E	E	
15							D	D	E	E	
24							E	E	F	F	
25							E	E	F	F	F
26										F	F

Figure 12. Representation of the *D. octaedra* matrix. Details in text.

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(dates 1-3, 2-4, 3-5, . . . , 10-12) were obtained for each year throughout the ELF pre-operational phase except 1987, when earthworms were sampled only monthly for the final two months. Although the dates overlapped, there was no problem with serial correlation because sampling was not performed using the same individuals sequentially; each vector was a temporally distinct subsample of the total population at the site. The only overlap involved temporal patterns of temperature and moisture.

Data Collection and Analysis, Model Building, and Other Computer Programs Used

Routine statistical analysis was performed with SYSTAT for Windows (© Systat, Inc. 1990). Database, spreadsheet and graphing functions were performed with Quattro Pro 6.0 (© Novell, Inc. 1994). Other graphics in this manuscript were produced with Presentations 3.0 (© Novell, Inc. 1994). Many programs for data collection and model building were written in Turbo Pascal 6.0 (© Borland International 1992). These included TDR and multiple regression bootstrapping programs, and programs used to build, run and test the population models.

Several routines and program units released to the public domain were used in the Turbo Pascal programs. One was a unit that simplified reading and writing Lotus *.*WK1* spreadsheet files, written By Dan Glanz. This unit made it possible to use output from custom Turbo Pascal programs directly in statistics and spreadsheet applications. It is found in nearly all the programs written for this project. Numerical techniques for multiple regression and matrix manipulation

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were taken from Press et al. (1986). A numerical method for quadratic smoothing (Savitzky and Golay 1964) was used in the TDR program to smooth the TDR trace for greater accuracy.

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Chapter 4

VALIDATION OF SPECIALIZED TECHNIQUES

Time Domain Reflectometry vs. Gravimetric Moisture Methods

The gravimetric soil moisture method, which involves weighing soil before and after drying, is one of the most commonly used methods, and was used for the incubator and field portions of this project. The problems with this method are (1) it is destructive, and cannot be used for monitoring changes in experimental units best left undisturbed; (2) time and space are required for drying the samples; and (3) results and length of drying time fluctuate with humidity, especially when air-drying. TDR, on the other hand, is nondestructive, can be used to monitor the same volume of soil periodically, is nearly instantaneous and free from variation due to differential drying. Its weaknesses are (1) considerable proficiency is needed to interpret the waveform traces, unless they are mathematically analyzed; (2) the difference in expense between the necessary apparatus; and (3) it measures the volumetric water content rather than water content by mass. If these methods are to be used together or compared, a conversion formula must be used.

TDR and gravimetric methods were compared in the field microcosms used for monitoring earthworm growth. During the first five collection dates in 1992, TDR volumetric moistures were taken in each bucket immediately before removal

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and transport to the field lab. Approximately 100 ml of soil taken from each microcosm was weighed to the nearest 0.01 g using a Mettler AE35 balance and oven-dried at 105°C for 24 hr. Samples were cooled to room temperature in a desiccator and reweighed to determine water loss, resulting in 200 comparisons over a wide range of moistures. The conversion formula from volumetric to gravimetric water content was

$$G = 18.95 - 0.2148 \times V + 0.01844 \times V^2$$

where G = gravimetric and V = volumetric moisture, respectively. The R^2 for the equation was 0.823, its standard error was 2.55 for 200 samples, and the ANOVA F-ratio was 463.6 ($p = 0.00000$). This equation was used to convert the periodically-monitored moisture data in the buckets to the gravimetric moisture units used in the remainder of the study. Figure 13 shows a graph of the 200 individual points and the regression line.

Testing the Tattooing Technique

Only the larger worms (above approximately 80 mg) of *L. rubellus* and *A. tuberculata* were tattooed. Smaller individuals were too easily damaged by the procedure, and were analyzed as cohorts of similar-sized individuals until they became large enough to tattoo.

Aporrectodea tuberculata accepted tattoos the most readily of the two species, both in terms of longevity of the marks and of survival immediately after tattooing. One hundred eighty-one individuals of this species were marked over the course of the project; 131 (72%) survived the tattooing procedure and were

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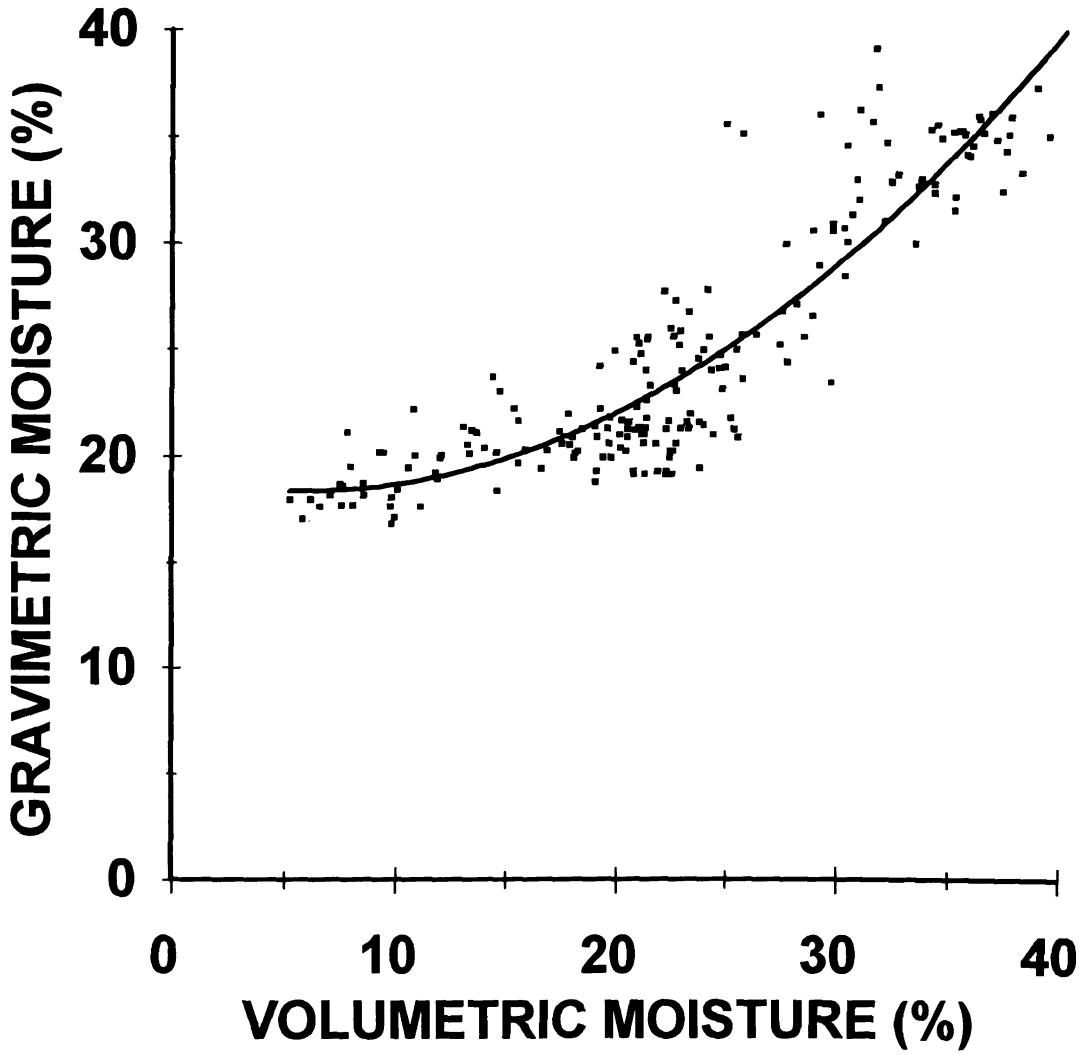

Figure 13. Regression of gravimetric on volumetric soil moisture in field microcosms filled with prepared soil.

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placed in field microcosms. Of the survivors, 112 (85%) lived one month or longer. All individuals dying during the first month initially weighed < 0.6 g. A small but significant linear increase (n =19, R^2=0.319, $F_{(1,17)}$ =9.45, p=0.007) was observed in survival with increasing initial mass (Figure 14):

$$Survival = 0.799 + 0.232 \times M,$$

where M=individual worm mass.

Of the 112 earthworms tracked at least one month, 82 were removed at various times during the study because two or more of the four dots were lost. The mean length of time that at least three dots remained visible (the "duration time") for the removed worms was 279 days (Figure 15). At the end of the study, 20 worms remained alive with readable tattoos; seven of these were among the first group to be marked, having retained their marks for 698 days. The mean duration time of these 20 individuals was 527 days, significantly longer (t = 7.54, df=100, p = 0.022) than worms that were removed; all of them had been in microcosms longer than the mean duration time of the group that had lost its tattoos. Mean masses between the two groups was not significantly different at the $\alpha = 0.05$ level, and no other factor that may have been the cause of this difference has been found.

Tattoos on *L. rubellus*, whose integument is iridescent and contains reddish-brown pigments, were not as easy to see. The marking duration was shorter in this species than in *A. tuberculata* because faded marks were masked by the worm's own pigments. One hundred ninety-three *L. rubellus* were tattooed; of these, 142 (74%) survived long enough to be placed in microcosms; 107 (75%) of the survivors remained in the microcosms at least one month. A strong tendency

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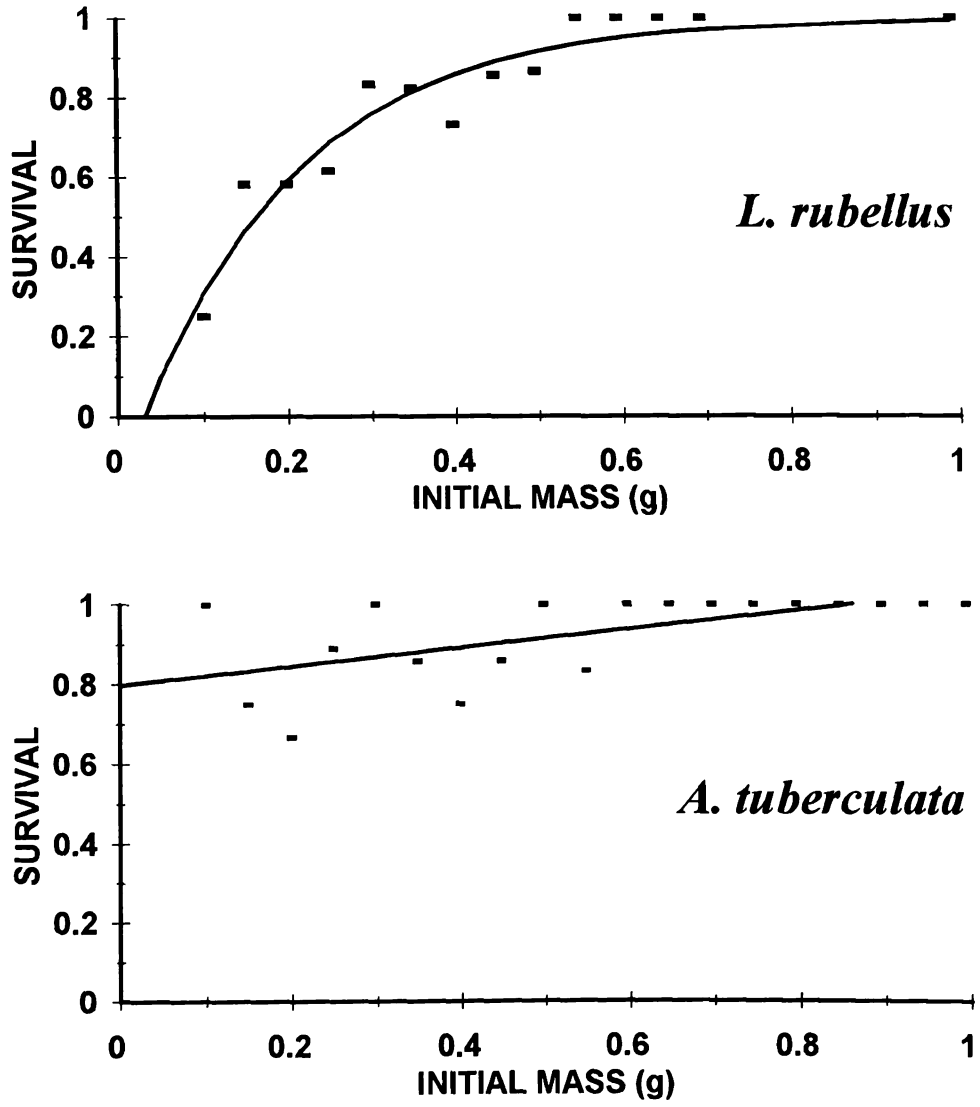
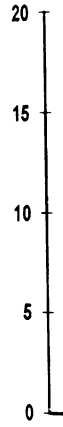
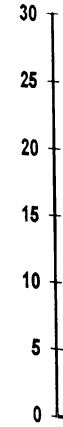


Figure 14. Survival rate vs. initial mass of tattooed *L. rubellus* and *A. tuberculata* following their first month after introduction to the field microcosms. Points are actual survival rate; lines are regression lines. See text for the equations.





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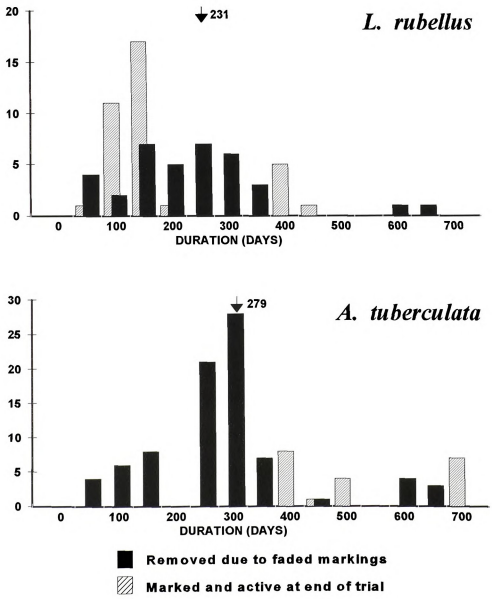

Figure 15. Marking duration distribution of worms of the two species studied. Removed worms were those removed due to loss of markings during the experiment, and were used to calculate the mean marking duration time (numbers next to arrows at top of graphs). The marked and active worms retained their marks throughout the experiment.

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toward decreased survival as a function of mass was noted in this species (n =15, R^2 =0.914, $F_{(2,12)}$ =1015.0, p=0) (Figure 14). The relationship was modelled with a negative exponential:

$$Survival = 1.0 - [1.168 \times e^{(-5.241 \times M)}],$$

where M = individual earthworm mass. No mortality of tattooed individuals was observed in *L. rubellus* individuals more than 0.5 g.

Of the 107 individuals tracked at least one month, 36 were removed during the study due to disappearance of two or more tattoos. These had a mean duration time, as defined above, of 231 days (Figure 15). Thirty-six individuals remained active at the end of the field study, with a mean duration time of 176 days. Unlike *A. tuberculata*, no significant difference between duration times of the removed group and those remaining alive was found at the p = 0.05 level.

Tattooing was an effective technique for marking and tracking individual earthworms, and might also be used with other soft-bodied invertebrates. Approximately 85% of aclitellate and clitellate worms survived the marking procedure, depending on size and species, and marks remained visible for a year or more, also depending on species. One drawback, however, was that certain species, such as *D. octaedra*, and small immatures were too fragile to be marked without unacceptably high mortality rates. Survival of earthworms smaller than 80 mg was well below 50% for *L. rubellus*; survival for *D. octaedra* of any size was low. Survival rates for *A. tuberculata*, however, were relatively high, even for small immatures.

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Chapter 5

DEVELOPMENT AND VALIDATION OF EXPERIMENTALLY DERIVED POPULATION MODELS

General Growth Pattern

Individuals of all three species fit a von Bertalanffy growth function (VBGF) (Poole 1974). Like the logistic, it increases monotonically but has upper and lower bounds. It is unlike the logistic curve in that it need not be symmetrical about its inflexion point. This model balances anabolism (tissue synthesis and development) and catabolism (tissue breakdown), reflecting the tendency for animals to put most of their energy into growth early in life, switching gradually to using their energy for maintenance and reproduction later. The form of this equation is

$$m_t = M_{\max} \times [1 - b \times e^{-k \times (t - t_0)}]^3$$

where m_t, the mass at a given time is a function of the maximum mass M_{max} and the length of time the animal has been growing, t-t_0. The entire equation is cubed because the original model derived by von Bertalanffy described growth in one dimension -- length -- rather than three dimensions -- mass, which is the object in this study. Table 9 lists equation parameters for a composite of all members of each species tracked for at least three months (four consecutive mass measurements within one season).

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Table 9. Parameters of the von Bertalanffy growth function for three earthworm species from experimental rearings in field microcosms.

Species	M_{max}	b	k	N points [1]	N worms [2]	R^2
D. octaedra	0.1192	2.4705	0.4067	426	61	0.5174
L. rubellus	1.0988	1.8655	0.2793	106	18	0.8142
A. tuberculata	1.2695	1.3702	0.1844	305	40	0.8309

[1] Number of points used in regression.
[2] Number of individual earthworms used to build the composite.

Population composites were constructed by first selecting the individuals with (1) the longest continuous record that (2) began with masses that were no greater than 10% of the maximum mass recorded for that species. VBGFs were calculated for each worm fitting these criteria, and the dates were adjusted so that all curves passed through the mean cocoon mass as determined from the pre-ELF data for that species. A preliminary VBGF was calculated for the composite of these long-lived individuals, and the remainder of individuals that had a continuous 3-month (four consecutive mass measurements) record were added in turn, placing the first recorded mass on the preliminary composite curve by time adjustment, starting with the longest-lived worms; if records began below 10% of the maximum mass, they were time-adjusted in a manner similar to the initial set. Individuals known to have been damaged during retrieval or examination were eliminated from the analysis. Figures 16, 17, and 18 show curves for (A) a representative long-lived individual and (B) the population composite for *D. octaedra*, *L. rubellus*, and *A. tuberculata*, respectively. Since the VBGF fits the growth patterns of all three species, it was used to divide each developmental stage into size classes.

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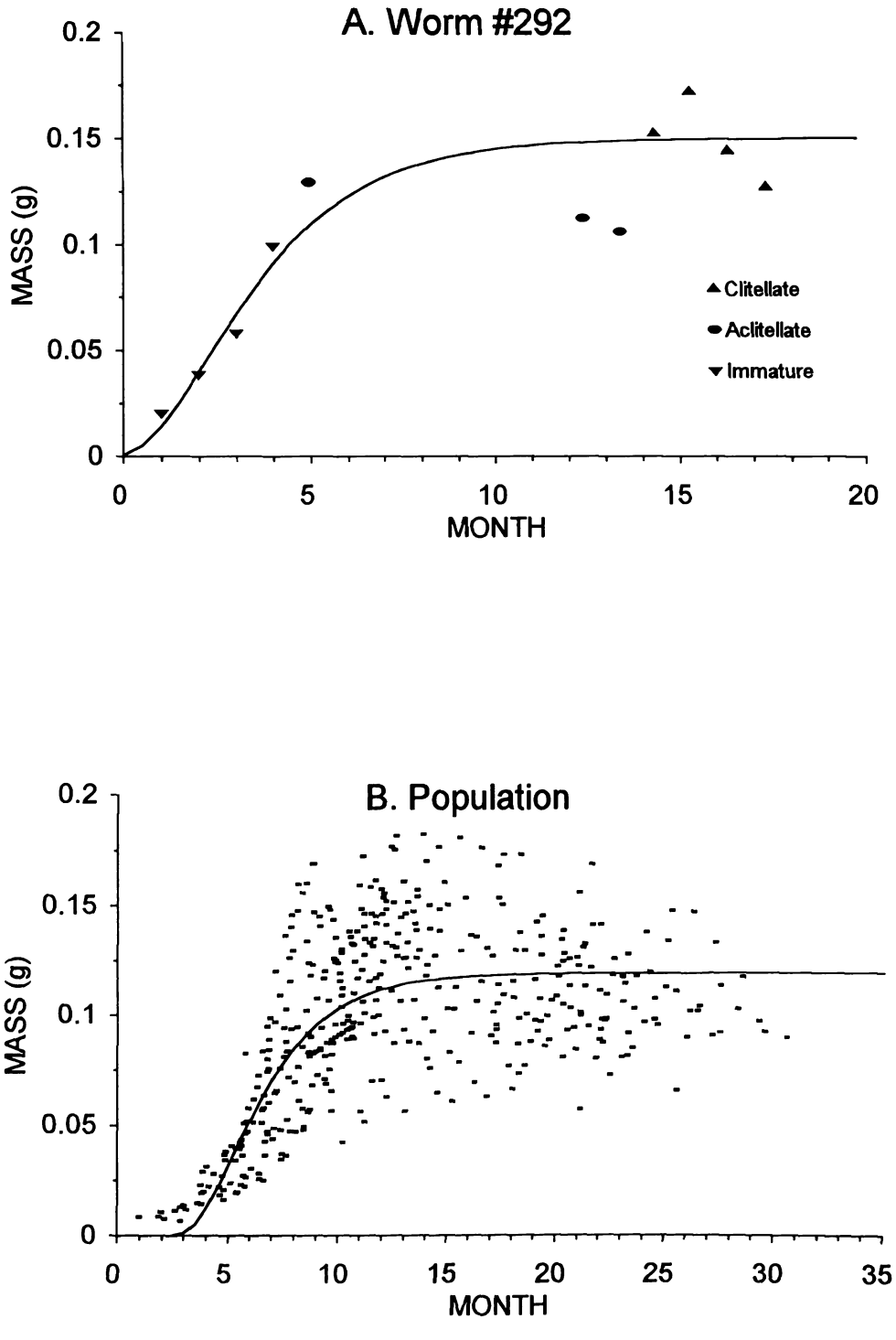

Figure 16. Von Bertalanffy growth curves for (A) a representative individual, and (B) the field microcosm population of *D. octaedra*. Construction details in text; VBGF parameters for (B) are found in Table 9.

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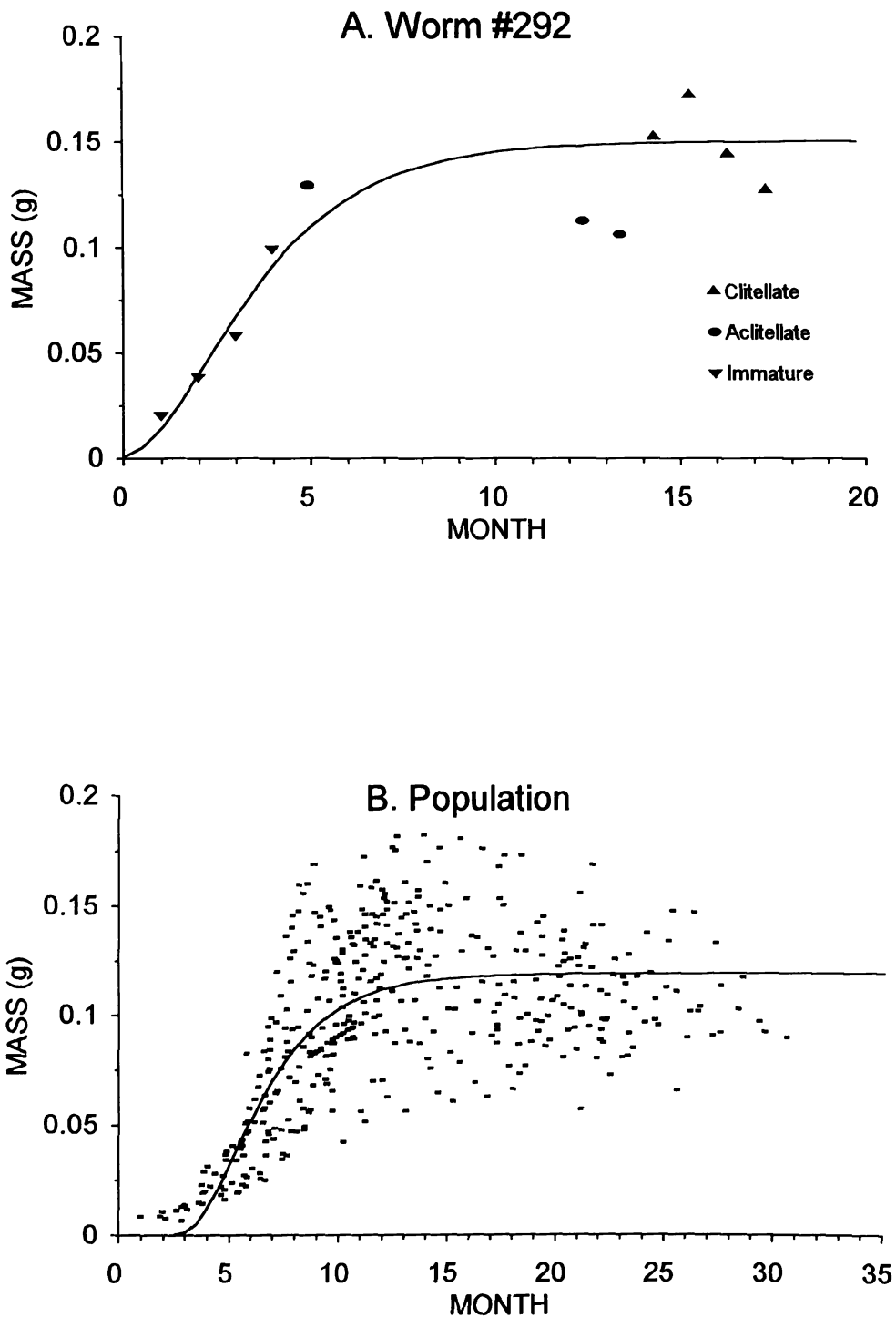

Figure 16. Von Bertalanffy growth curves for (A) a representative individual, and (B) the field microcosm population of *D. octaedra*. Construction details in text; VBGF parameters for (B) are found in Table 9.

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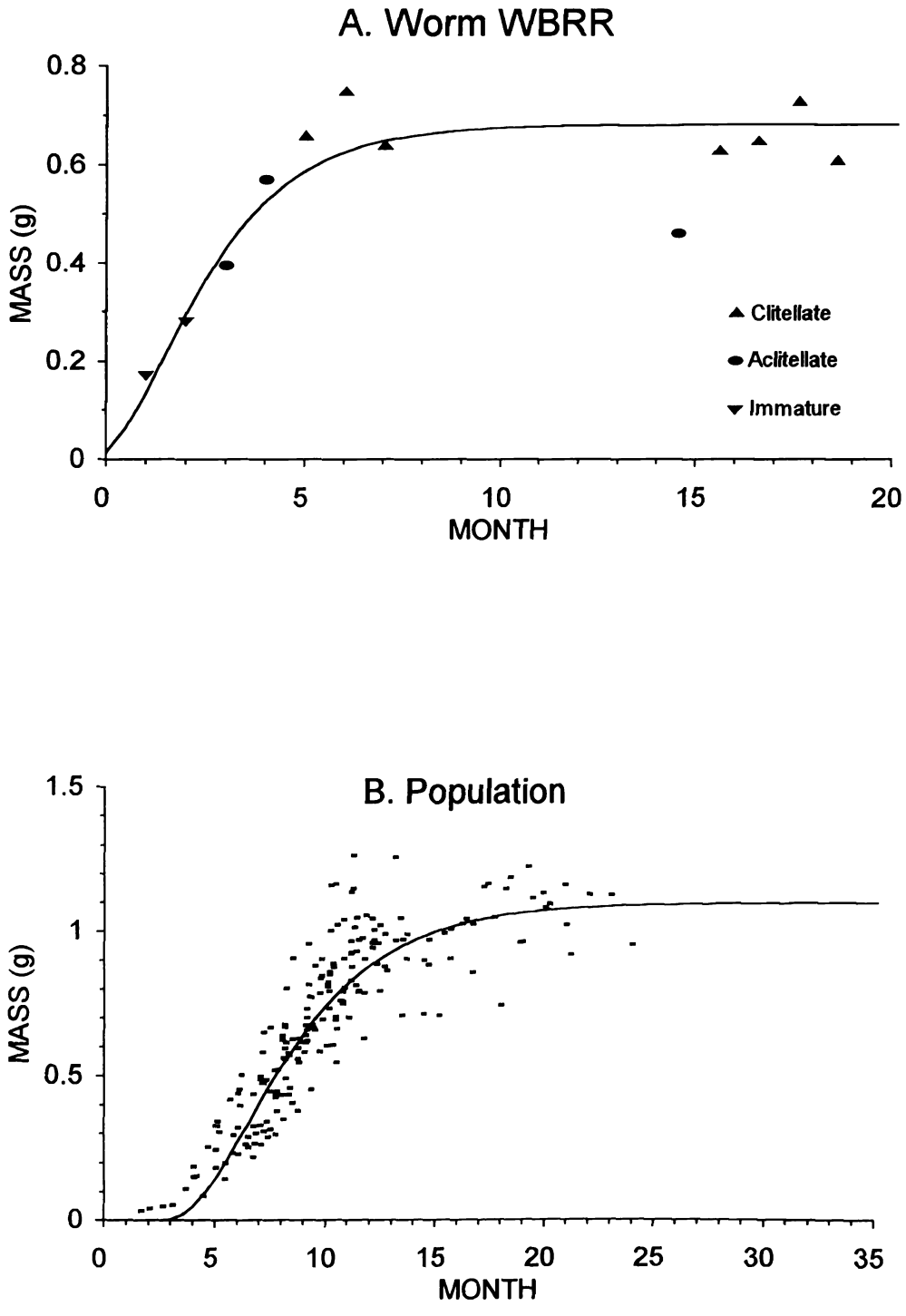

Figure 17. Von Bertalanffy growth curves for (A) a representative individual and (B) the field microcosm population of *L. rubellus*. Construction details in text; VBGF parameters for (b) are found in Table 9.

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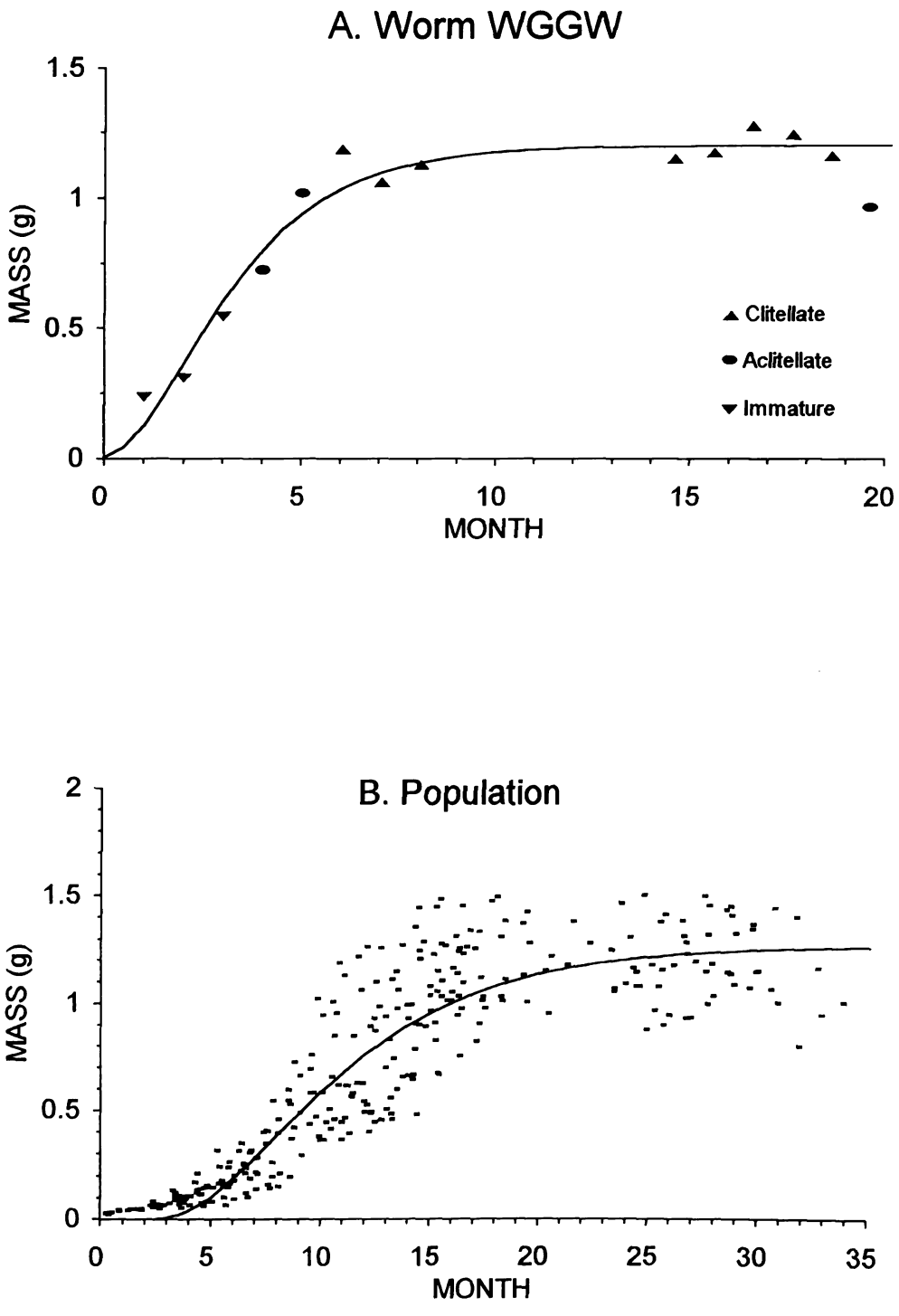

Figure 18. Von Bertalanffy growth curves for (A) a representative individual and (B) the field microcosm population of *A. tuberculata.* Construction details in text; VBGF parameters for (B) are found in Table 9.

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Comparison of Incubator and Field Microcosm Models

Since microcosm data on immature through clitellate worms covered temperatures from about 9°C to 17°C while the incubator data were more complete from 3°C to 10°C, a combined model incorporating both data sets was in order. To this end, it was necessary to ascertain whether the incubator and field microcosm models were statistically similar in their predictions. Tables 23 through 25 in Appendix A show the regression coefficients calculated for the incubator experiment from each of the three species, using the bootstrap regression technique outlined in Chapter 3. The regression coefficients for the field microcosm experiments are found in Tables 26 through 28 in Appendix A. Unlike the incubator trials, these were calculated directly from all the raw data collected from the microcosms without the use of bootstrapping techniques.

Incubator and field microcosm models were compared by using each model to project the next month's population vector from pre-ELF natural population data (n = 48 monthly sets), then performing an ANOVA on the results, using individual class densities as the dependent variable and developmental class (size and developmental stage) and model origin (incubator or microcosm) as factors. The ANOVA took the form

$$N = M + M \times C + e$$

where N = the class density or projected number of individuals in developmental class C of model M, and e = the error term. This statistical model was chosen because M should be sensitive to growth rate differences between models and the interaction $M \times C$ shows differences between predicted population structures of the

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two models. The single term *C* was not included because one would expect marked differences between different sizes and stages, and the associated error would artificially deflate the F-ratios and increase the type 2 error for the pertinent tests. As structured, a nonsignificant F-ratio for both tests indicates that the two models are statistically similar and their data can be combined. Table 10 gives the ANOVA results for all three species.

Since the tests for all three comparisons (species) had nonsignificant results and data were collected similarly for both sets (incubator and field microcosm), the incubator data files were appended to the microcosm files and new models were generated in the same manner as the microcosm models. The N for field microcosm, incubator, and combined models is listed in Table 11. Since cocoons and worms were analyzed separately using different techniques, the total number of cocoons examined in each phase of the study is listed, whereas the number of transition pairs (state at beginning of month and fate at end of month) is enumerated for worms.

Compared with other studies using transition matrices, the number of transition pairs per model cell is quite high. Bierzychudek (1982) used 104 and 149 individuals, respectively, to construct her two 7×7 matrices of *Arisaema triphyllum* L. demography; hers is one of only a few studies that even mentions the size of the data set. The high numbers, however, are offset by the fact that the present models are built using multiple regression equations, requiring large sample sizes to be good predictors. Terms for the combined models are given in Tables 29 through 31 in Appendix A.

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Table 10. ANOVA results from comparison of incubator and field microcosm models for all three earthworm species. n.s. = not significant at 0.05 level.

Source	SS	DF	MS	F	P	Signif-icance
D. octaedra						
MODEL	443.93	1	443.93	0.0516	0.8203	n.s.
MODEL × CLASS	1.8226×10^{4}	12	1.5189×10^{3}	0.1767	.9992	n.s.
ERROR	4.0673×10^{5}	1234	8.5982×10^{3}			
L. rubellus						
MODEL	255.31	1	255.31	0.7746	0.3790	n.s.
MODEL × CLASS	2022.6	12	168.55	0.5114	0.9085	n.s.
ERROR	4.0673×10^{5}	1234	329.60			
A. tuberculata						
MODEL	200.82	1	200.82	1.0505	0.3056	n.s.
MODEL × CLASS	2.7876×10^{4}	14	199.11	1.0416	0.4082	n.s.
ERROR	2.7222×10^{5}	1424	191.16			

Table 11. Number of cocoons and worm transitions used in model construction, by model type and developmental stage for the entire study. A more detailed summary by collection date and transition type may be found in Appendix C.

SPECIES/ MODEL	COCOONS	IMMATURES	ACLITELLATES	CLITELLATES	TOTAL WORMS
D. octaedra					
Incubator	490	377	209	215	801
Microcosm	1209	860	202	421	1483
Combined	1699	1237	411	636	2284
L. rubellus					
Incubator	129	605	85	125	815
Microcosm	484	546	130	181	857
Combined	613	1151	215	306	1672
A. tuberculata					
Incubator	66	632	247	141	1020
Microcosm	383	910	282	269	1461
Combined	1043	1542	529	410	2481

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Comparison of Composite Models with Pre-ELF Subset

A common method for validation of complex models involves regressing actual values on model predictions without a constant term (Poole 1974). By forcing the regression line through zero, one obtains both a slope, indicative of the relationship between the observed and predicted, and a standard error of the slope, without the confounding variables introduced by a constant term. A slope near 1.0 and a small standard error suggests that the model behaves in a manner similar to the observed data.

Regressions without constant terms of the total projected populations (worms and cocoons) on the total observed populations after one month for *D. octaedra*, *L. rubellus* and *A. tuberculata* are shown in Figure 19, 20, and 21 respectively. Observed populations and environmental data were taken from the ELF project pre-ELF data set (1984-1988), with an n = 48. This set covered several reasonably normal years (1984-1986), a warm, wet year (1987) and a year with an extended drought in midsummer (1988). The abnormally low points in the lower right portion of Figure 19 (*D. octaedra*) are from the summer of 1988. The total population regression for each species was:

D. octaedra: Observed = 1.0196 × Model, Std. error = 0.0539
L. rubellus: Observed = 1.0724 × Model, Std. error = 0.0545
A. tuberculata: Observed = 1.0220 × Model, Std. error = 0.0344

where Model = the total population predicted by the model and Observed = the total observed field population. In each case, the model prediction fell within the $\alpha = 0.05$ limits of significance.

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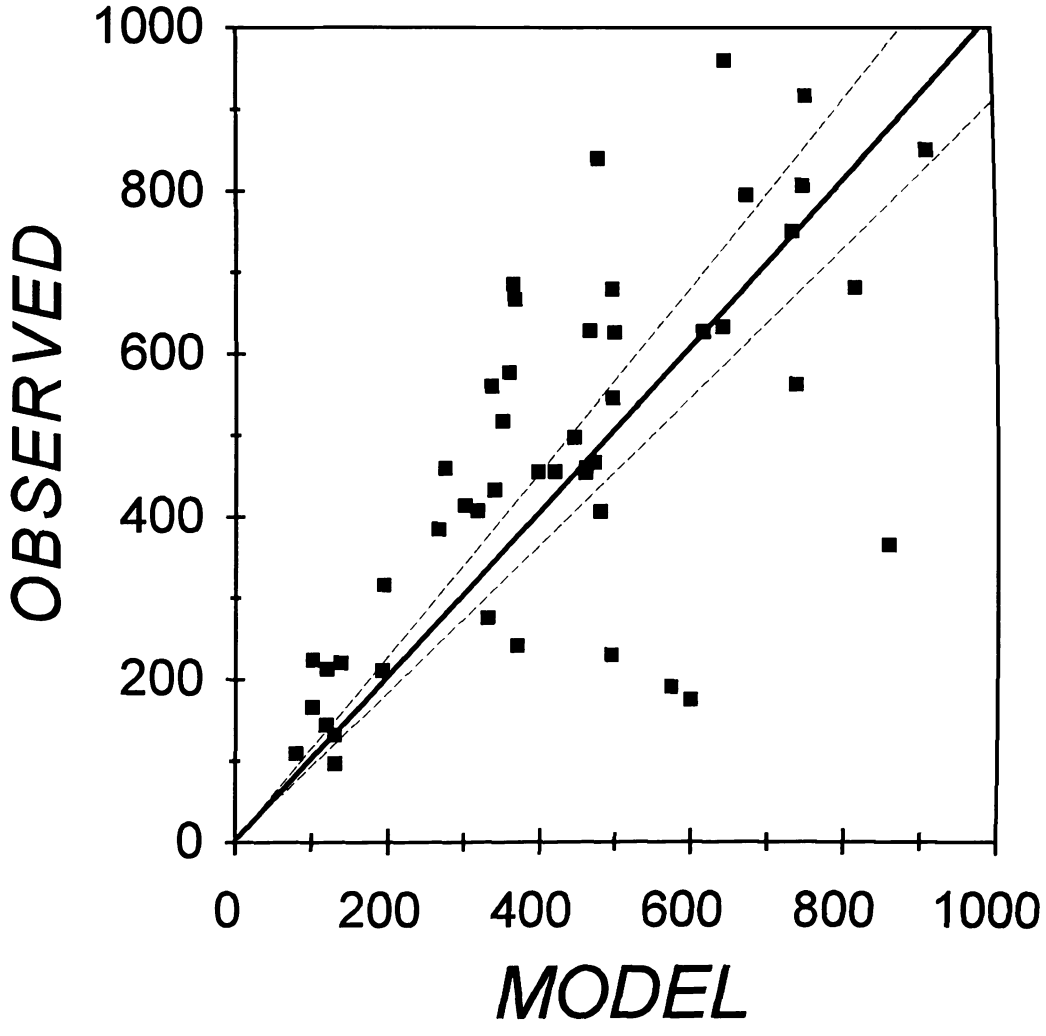

Figure 19. Comparison of total size of modelled populations (worms and cocoons) to actual observed populations of *D. octaedra* at the CONTROL site during the preoperational phase of the ELF project. The solid line is a least-squares regression line with slope = 1.0196 and $r^2 = 0.884$; intersection of this line with the upper right corner would indicate a 1:1 correspondence between modelled and observed populations. The dashed lines bound the 95% confidence interval about the slope of the regression line.

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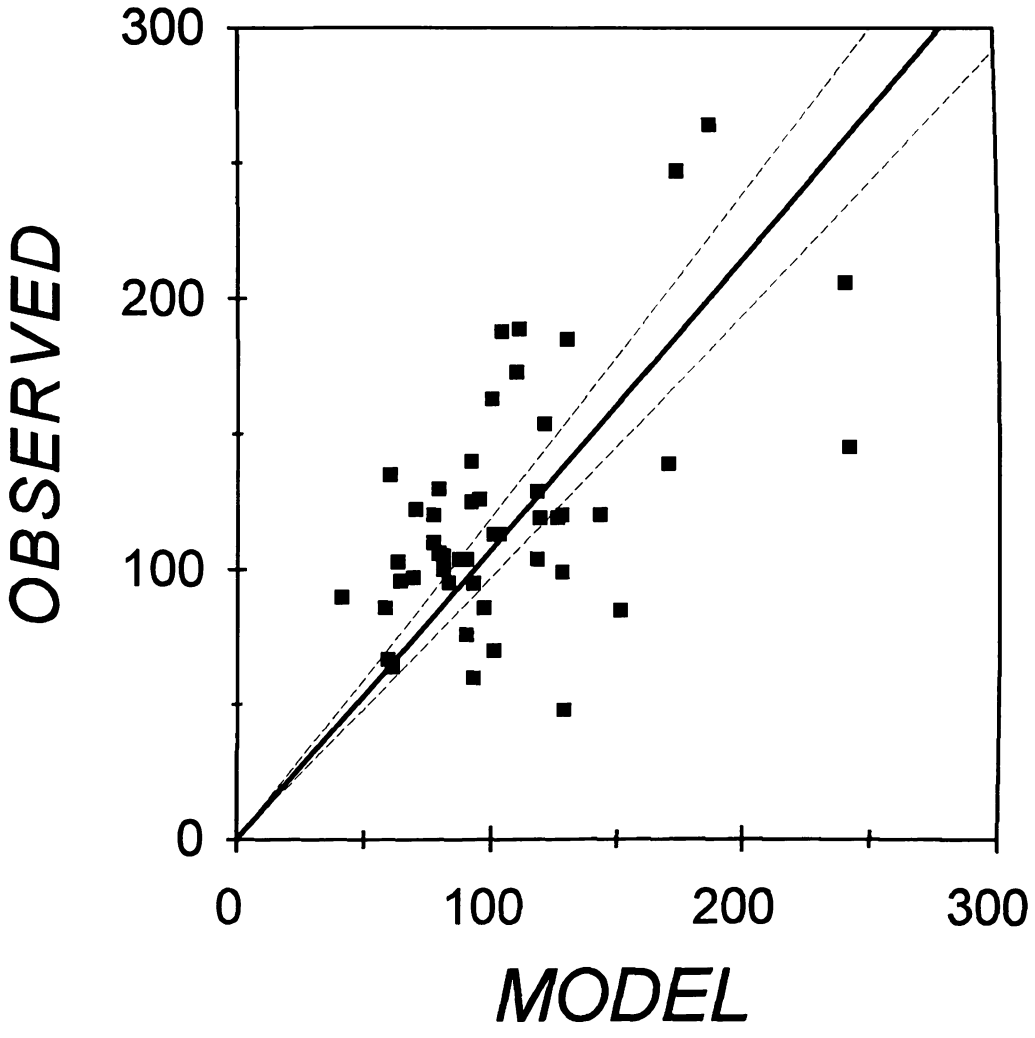

Figure 20. Comparison of total size of modelled populations to actual observed populations of *L. rubellus* at the TEST site during the preoperational phase of the ELF project. Slope = 1.0724 and $r^2 = 0.892$ for the regression line. See Figure 19 for line and significance details.

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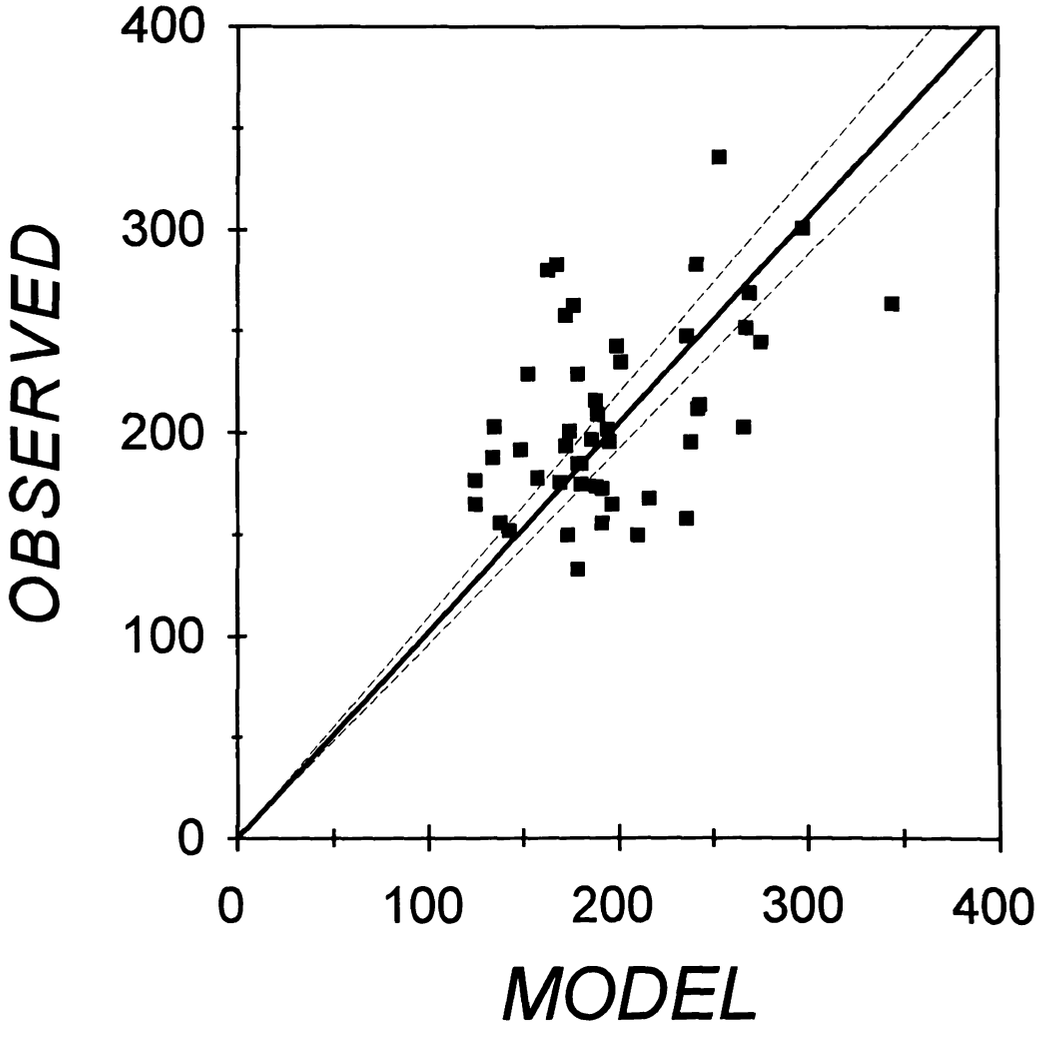

Figure 21. Comparison of total size of modelled populations to actual observed populations of *A. tuberculata* at the TEST site during the preoperational phase of the ELF project. Slope = 1.0221 and $r^2 = 0.490$ for the regression line. See Figure 19 for line and significance details.

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The *D. octaedra* Model

As first conceived, the model divided the population first into developmental stages, then assigned individuals to size classes within the stages. There was to be one set of equations for size change, stage change and survivorship for each stage. Examination of data showed that, especially in the immature stage, the size classes did not respond similarly to the environmental variables. Immature size classes were therefore divided into two subsets (size classes 1-2 and 3-4) to better reflect the nature of the environmental effects upon individuals of different sizes. The division was placed between classes 2 and 3 because classes 3 and 4 were also associated with change to the aclitellate stage, while classes 1 and 2 were not.

Table 12 shows the effects of temperature and moisture upon each group of worms. Temperature and initial size were important in growth of immatures, and soil moisture levels were moderately to weakly associated with their survivorship and stage change. Temperature and initial size also played critical roles in determining growth and stage change of aclitellates, with moisture being a minor influence in stage change only. Clitellate growth and survivorship were moderately to weakly influenced by temperature and moisture, but growth and stage change were strongly affected by initial size class. These last two effects combine to almost ensure that once a *D. octaedra* becomes clitellate it remains in reproductive mode, and the weak positive effect of temperature on survivorship indicates that most clitellate worms will probably not survive through a long winter. Strongly

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Table 12. Effects of environmental variables on *D. octaedra* individuals of various sizes and developmental stages. Effects are classified as strong (S), with a $p \leq 0.01$, moderate (M), $0.01 < p \leq 0.05$, or weak (W), $p > 0.05$ determined from multiple regression significance values. The direction of change, positive or negative, is indicated by a + or -.

		Temp	Temp^2	Moist	Moist^2	Size
Immature Classes 1-2	Growth	M+				W-
	Survivorship			M+		S+
	Stage Change	no stage change				
Immature Classes 3-4	Growth	S+	M-			M-
	Survivorship	regression nonsignificant; constant used				
	Stage Change	M+		W+	W-	S+
Aclitellates	Growth	S+	S-			S-
	Survivorship	regression nonsignificant; constant used				
	Stage Change	W-	W+	W-		S+
Clitellates	Growth	M+	M-	W-		S-
	Survivorship	W+				
	Stage Change					S+

Temp = soil temperature, **Moist** = soil moisture, **Size** = beginning size class.

positive temperature-dependent growth and stage change of aclitellates serve to replenish clitellate stocks early in the warm season.

Because changes in population structure and size depend on a regime of variable temperatures and soil moistures, it is impractical to determine population parameters without first knowing the environmental regime for a given site, and the intrinsic growth rate of the population at any practical combination of temperature and moisture. In matrix algebra, the growth increment, e^r, can be approximated by the dominant eigenvalue, λ_1, of the matrix (Caswell 1989). By determining the λ_1 at several levels of both soil temperature and moisture, one can construct a contour map of the λ_1 surface. It is then possible to plot a trajectory on the contour map

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corresponding to the temperature and moisture regime of the area in question to determine if a modelled population is viable at that site. If a substantial portion of the year as determined by the temperature-moisture trajectory is spent in an area of the map with $\lambda_1 > 1.0$, the population will remain stable or grow; if little time is spent in this area, it will decline.

This was accomplished for each of the earthworm species by determining the λ_1 in a 7×7 grid of temperature (every 5°C from 0°C to 30°C) and moisture (every 5% from 10% to 40%). Contours were plotted using SYSTAT with distance-weighted least-squares interpolation. Figure 22A shows the λ_1 response surface for *D. octaedra* graphically. Increasing temperature above 15°C at moderate moistures, or 20°C at low or very high moistures results in population growth (Fig. 22B), and growth rates rise rapidly to a maximum of >1.1 near 20°C and 30% moisture. This makes sense because *D. octaedra* consumes litter conditioned by microbes; an environment more conducive to microbial growth (warmer and wetter) in and on leaves would also provide more food for this species. Quiescent individuals were observed early in the spring on the surface of the A horizon under several layers of leaf litter. If this is their mode of winter diapause, they would be subject to wide swings in temperature and moisture during the winter, and more susceptible to a high mortality rate.

The *L. rubellus* Model

Unlike *D. octaedra*, *L. rubellus* immatures did not have to be divided into multiple groups. The number of transitions used to generate this model was

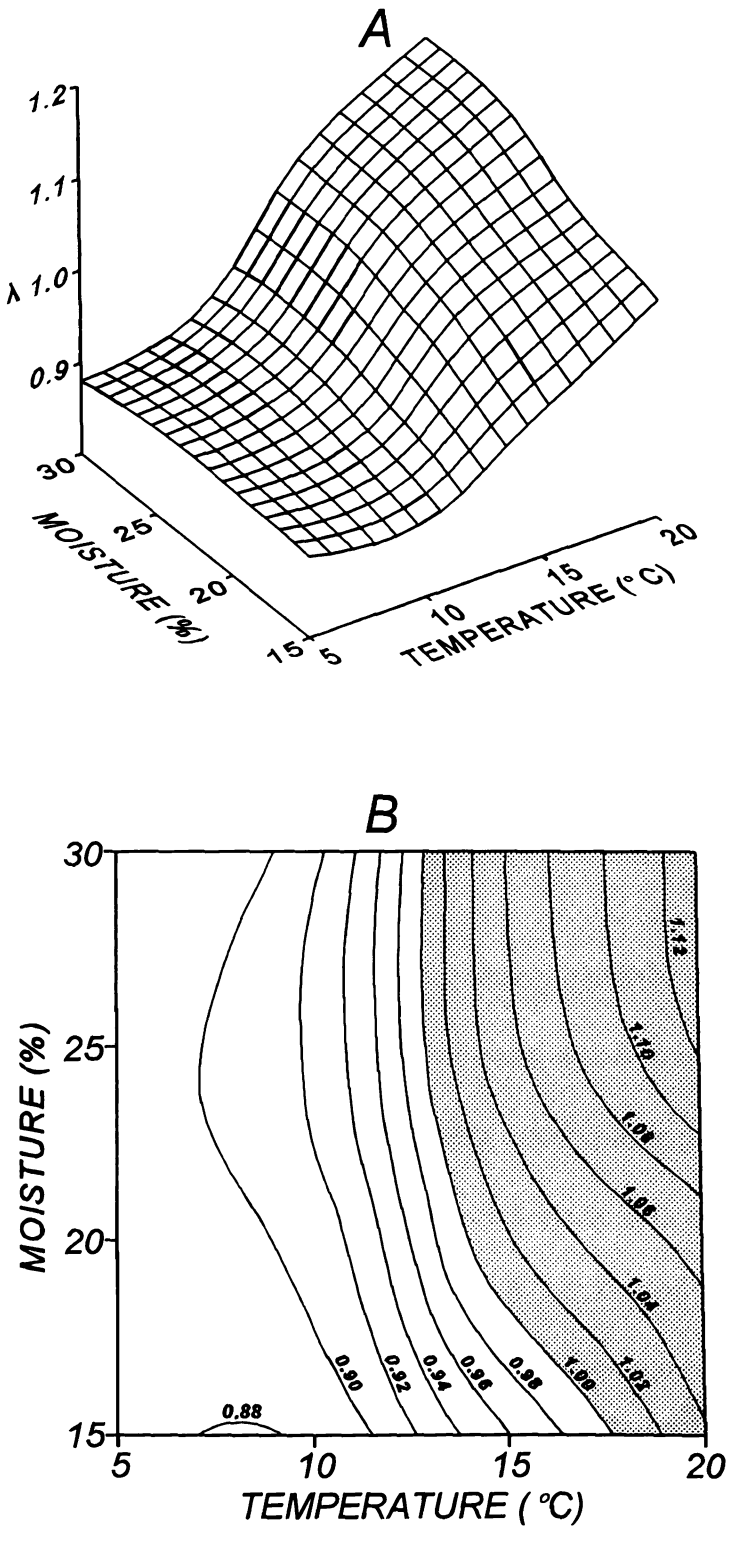

Figure 22. A: 3-dimensional response surface plot of the population growth rate for *D. octaedra* from modelled data. B: Contour plot of the same surface. The shaded portion indicates the temperature and moisture conditions under which population growth occurs.

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Table 13. Effects of environmental variables on *L. rubellus* individuals of various sizes and developmental stages. See Table 12 for symbol and caption explanations.

		Temp	Temp^2	Moist	Moist^2	Size
Immatures	Growth	S+	W-	W+		S-
	Survivorship	W-				S+
	Stage Change	W-	M-	W-		
Aclitellates	Growth	S+	S-			
	Survivorship					W+
	Stage Change	W+		M+	M-	S+
Clitellates	Growth					S-
	Survivorship					S+
	Stage Change	M+		M+	M-	

substantially less than either of the other two; the result is evident in weaker regression coefficients (Table 13) as compared with either *D. octaedra* or *A. tuberculata.*

Temperature figured prominently in determining growth, survivorship and stage change of *L. rubellus* immatures, while moisture was less important. Initial size was also important in growth and survivorship. Aclitellate growth was strongly affected by temperature factors, whereas moisture was more important in relationship between temperature and stage change in clitellates, this stage is determining stage change. Increase in size was weakly associated with higher survivorship, and strongly related to a higher probability of stage change in aclitellates. Because of the positive linear common in mid-to-late summer samples, and much less so in the early spring or late fall. Clitellate survivorship, as in the

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The response surface and contour plot (Figure 23) show that *L. rubellus* populations do well at combinations of moderate temperature and high moisture, but fare very poorly in low moisture-high temperature situations. Just as *D. octaedra* depends on conditioned leaf litter for food, so does *L. rubellus*, although it can also consume soil organic matter. The survival of the smallest size classes likely determines the fate of the entire population; if conditions are favorable when individuals are small, juvenile mortality is lower and the population will grow.

The *A. tuberculata* Model

Like *D. octaedra*, the immature size classes did not show similar responses to the environmental variables across the range of sizes (Figure 24). The model significantly underestimated the number of class 1 individuals actually collected in field censuses, and overestimated the class 6 population by a substantial margin. This may be expected, as the range in mass, from class 1 hatchling to largest class 6 immature, spans nearly two orders of magnitude.

The first attempt at dividing the stage was similar to the course taken in the *D. octaedra* model: separate the larger classes which have the capacity for stage change from the smaller classes which do not. After separation, classes 5 and 6 behaved well, but class 1 was still very different from classes 2 through 4; in the second phase, class 1 was isolated, and the modified model became substantially more accurate.

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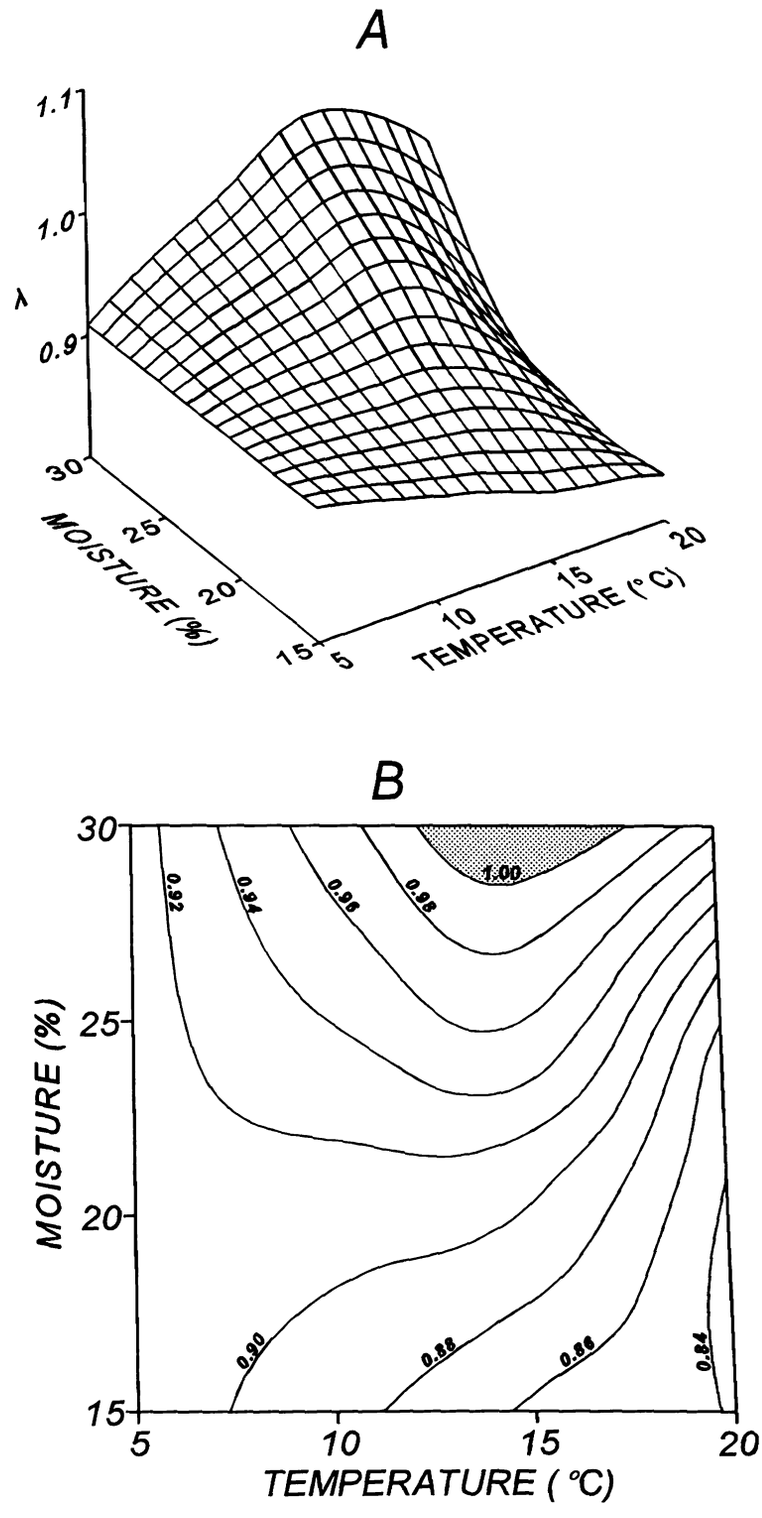

Figure 23. A: 3-dimensional response surface plot of the population growth rate for *L. rubellus* from modelled data. B: Contour plot of the same surface. The shaded portion indicates the temperature and moisture conditions under which population growth occurs.

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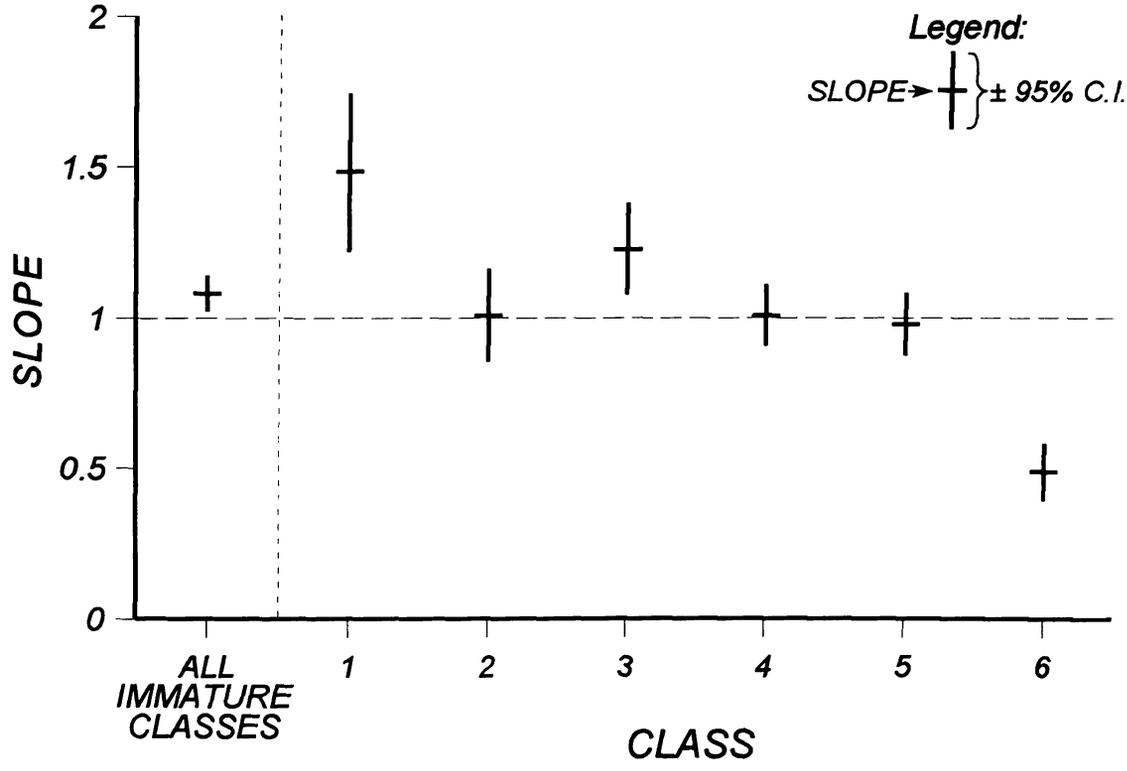

Figure 24. Slopes of observed vs. modelled *A. tuberculata* populations for each of the immature size classes individually, from data initially modelled with one set of equations for all immature size classes. Slope > 1.0 indicates that the model underestimated the true population; slope < 1.0 shows that the observed population was overestimated by the model. Pooled slope of all six classes is shown for comparison.

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Since the class 1 equations still underestimated the population and this model was to be used for further experimentation, the pre-ELF field population data were split into two subsets, 1984-85 and 1986-88, so that the first portion could be used to fine-tune the model by adjusting the equations and the second could serve as a validation subset. Only the *a*, or constant, term of the survivorship equation was adjusted because it was thought that the method used to remove earthworms from the buckets (water-sieving of a volume of soil) may have differentially injured the smallest worms more than larger individuals, subjecting them to artificially high mortality. After adjustment of this term to bring the class 1 model into agreement with actual numbers using the 1984-85 subset, the entire model was applied to the 1986-88 subset for validation. Regression statistics of observed numbers on modelled populations for each stage/class combination in the model are shown in Table 14.

Table 15 shows the level of significance of environmental variables in each of the equation sets. Temperature was the only significant factor in the growth and survivorship of the smallest immatures, and continued to be important throughout the immature stage. Moisture became important in the intermediate immature size classes; interestingly, it had a negative influence on mid-sized immature survivorship. Size was also important in survivorship: an increase in size increased survivorship.

Aclitellate growth increased, but survivorship decreased with moisture. Temperature was important in survivorship, but the only significant factor in stage

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Table 14. Slopes and confidence intervals of regressions of observed on modelled populations of *A. tuberculata* after adjustment. The 1984-85 subset was used to adjust the experimentally-derived model; the 1986-88 subset was used to validate the adjustments.

Stage	1984-1985 subset (n=20) Slope	95% C.I.	1986-1988 subset (n=28) Slope	95% C.I.
Cocoons	0.9991	0.8232 - 1.1749	1.0104	0.8282 - 1.1926
Class 1	1.1172	0.9122 - 1.3223	0.8540	0.7067 - 1.0014
Classes 2-4	1.0237	0.8756 - 1.1719	0.9524	0.8407 - 1.0641
Classes 5-6	0.9528	0.8009 - 1.1047	0.9269	0.7816 - 1.0721
Aclitellates	1.0857	0.8832 - 1.2882	1.0960	0.9231 - 1.2689
Clitellates	1.1167	0.9407 - 1.2927	0.9317	0.7285 - 1.1349
Total population	1.0285	0.9208 - 1.1362	1.0181	0.9225 - 1.1137

Table 15. Effects of environmental variables on *A. tuberculata* individuals of various sizes and developmental stages. See Table 12 for explanations.

		Temp	Temp^2	Moist	Moist^2	Size
Immature Class 1	Growth	M+	M-			
	Survivorship	W+	M-			
	Stage Change	no stage change				
Immature Classes 2-4	Growth	S+		W+	W-	
	Survivorship			S-		S+
	Stage Change	no stage change				
Immature Classes 5-6	Growth	M+	W-			S-
	Survivorship	Regression nonsignificant; constant used				
	Stage Change					S+
Aclitellates	Growth			M+		M-
	Survivorship	W+	S-	S-		S+
	Stage Change					S+
Clitellates	Growth	W+	S-	S+	S-	S-
	Survivorship	W-	W-	S+		
	Stage Change	W+	S-	S+	S-	

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change was size. On the other hand, the entire suite of variables seemed to be important for growth, survivorship and stage change of clitellate *A. tuberculata.*

The λ_1 response surface and contour map are presented in Figure 25. This map, in contrast with that of *D. octaedra*, shows that *A. tuberculata* populations tended to increase at relatively low soil temperatures and moderate moistures, and decline sharply as temperatures rise. The point of maximum population growth is not nearly so pronounced, either; the area of positive growth is a nearly flat, wide "plateau" rather than a steep "mountain" as is the case with the *D. octaedra* response surface. This is evidence of *D. octaedra's* ability to rapidly colonize under favorable conditions, and *A. tuberculata's* tendency to maintain a more or less stable population over more variable conditions.

Life Cycle Inferences and Comparisons Using Models

Once accurate population models are generated and tested, they may be used to infer and examine many aspects of the life cycle and life history of an organism, such as survivorship and longevity, and phenological questions about the timing of development and reproduction. This portion of the chapter will attempt to answer selected questions pertaining to life histories of the three species

Temperature-related cocoon development

Cocoon development times were modelled using a degree-day approach:

$$N = \frac{DD}{(T_M - T_\alpha)}$$

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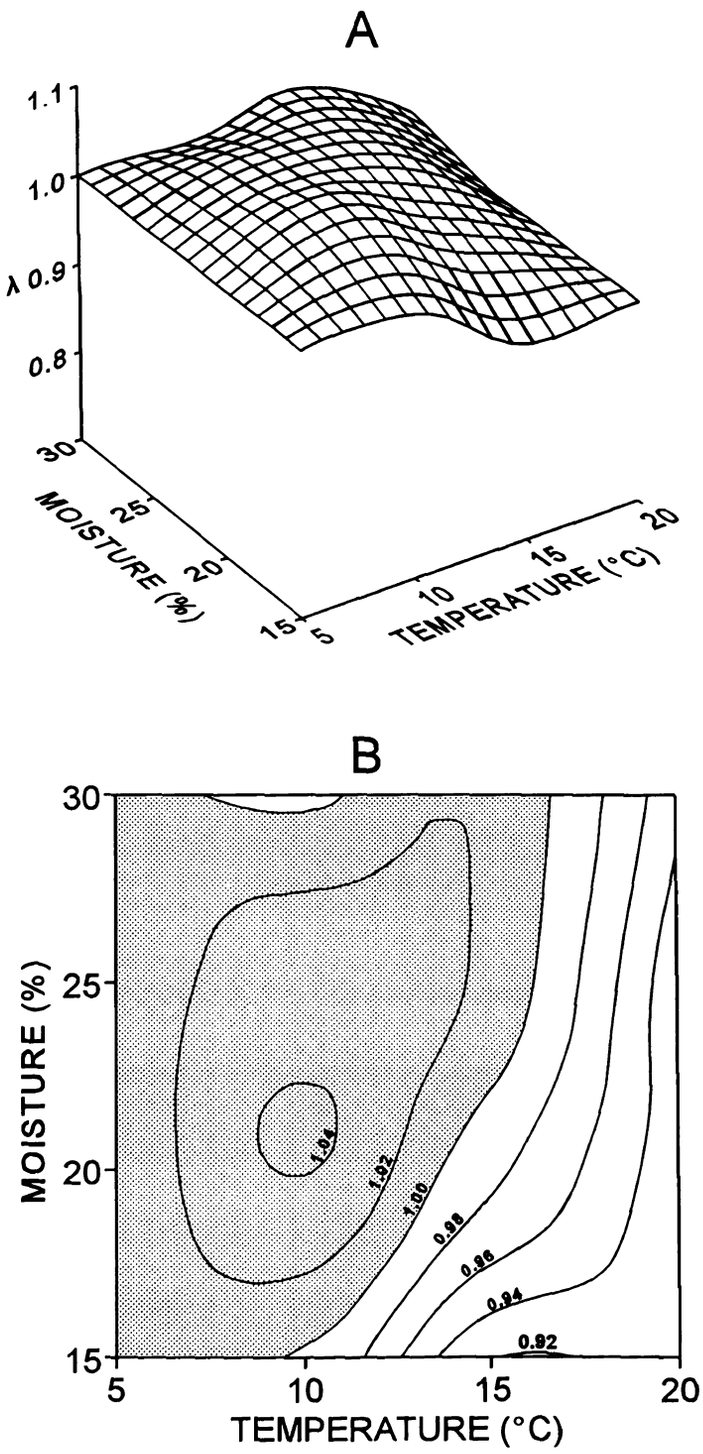

Figure 25. A: 3-dimensional response surface plot of the population growth rate for *A. tuberculata* from modelled data. B: Contour plot of the same surface. The shaded area indicates the temperature and moisture conditions under which population growth occurs.

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where N = calendar days needed to complete development, DD = the degree-day constant for the species (a unit of energy accumulation over time), T_m = mean temperature over the time measured, and T_α = the base temperature below which development ceases.

The cocoons of the three species developed at somewhat different rates (Figure 26), although 95% confidence bands about the regression line indicate no significant difference. *Dendrobaena octaedra* cocoons were found to continue development at < -1°C (Table 16), whereas cocoons of *L. rubellus* cease development below 0.14°C, and *A. tuberculata* cocoons will not develop below 0.20°C. Each point used in these regressions represents the mean daily developmental rate of a cocoon cohort between two sampling dates:

$$\frac{mean\ score\ 2 - mean\ score\ 1}{date\ 2 - date\ 1}$$

where *mean score x* is the mean of the cocoon developmental scores at time x, and the denominator is the number of days between two consecutive observation dates, related to the mean soil temperature between the two dates.

Cocoons were also deposited at different levels in the soil. Most *D. octaedra* cocoons were found on or very near the surface of the A-horizon, and some were found in the leaf litter. *Lumbricus rubellus* cocoons were found throughout the A-horizon and into the mineral soil. The cocoons of *A. tuberculata* were found deeper in the mineral soil than those of either of the other species. Holmstrup et al. (1990) investigated the frost tolerance of cocoons of several lumbricid species, among them *D. octaedra* and *A. caliginosa* [*tuberculata*?].

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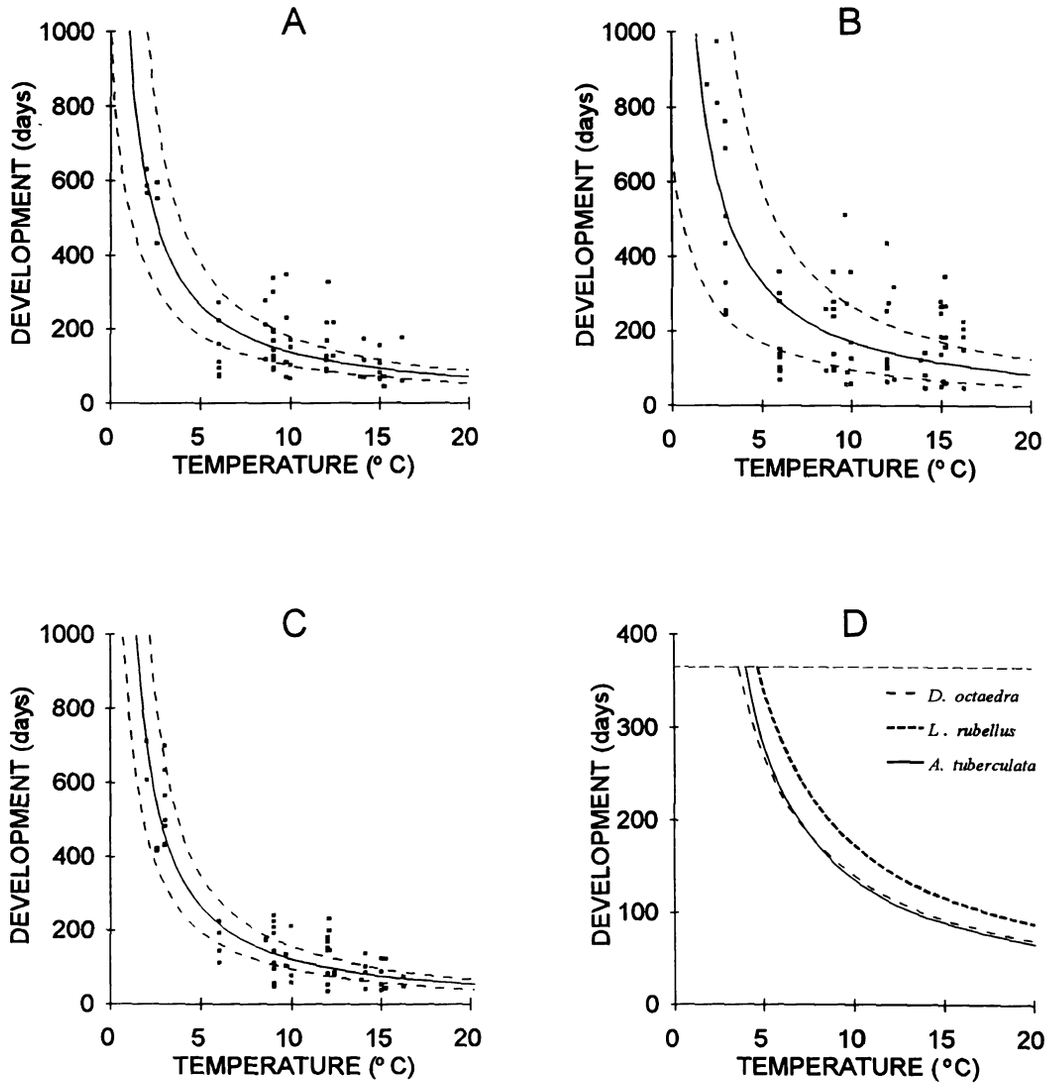

Figure 26. Combined field microcosm and incubator cocoon development times vs. temperature. A: *D. octaedra*; B: *L. rubellus*; C: *A. tuberculata.* Dashed curves in graphs A, B and C are 95% confidence intervals about the regression lines. D: comparison between the three regressions; dashed horizontal line is 365 days.

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Table 16. Parameters for cocoon development equations for three lumbricids, derived from combined incubator and field microcosm data

	T_α (°C)	Degree-days	N points	Regression R^2	95% Conf. Interval (lower to upper) T_α	Deg. Days
D. octaedra	-1.11	1854	30	0.838	-1.48 to -0.74	1874 to 1836
L. rubellus	0.14	2417	35	0.701	-0.84 to 1.11	2762 to 2148
A. tuberculata	0.20	1520	30	0.814	-0.13 to 0.53	1607 to 1443

Dendrobaena octaedra cocoons tolerated soil temperatures to -10°C, although at reduced hatchability; *Aporrectodea* cocoons did not survive at temperatures below -5°C. Since the cocoons of the first species are deposited on or near the surface of the soil, they must be able to withstand colder and possibly more variable temperatures than those of species that deposit their cocoons in lower strata where temperature effects are ameliorated. The series of minimum developmental temperatures (T_α in Table 16) corresponds with the mean depth of cocoon deposition, and to some extent the degree-day accumulation necessary for development from zygote to hatched worm (Table 16), suggesting that all of these factors (cocoon deposition depth, frost tolerance, developmental rate and minimum development temperature) vary in concert in the evolution of life history traits in these species.

Both incubator and field microcosm studies indicated that survivorship in the cocoon stage was very high, close to 1.0. Three cocoons, one *L. rubellus* and two *A. tuberculata*, were parasitized by an unidentified nematoceran fly. All other

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Table 17. Regressions of proportion of fertile cocoons on temperature shortly after cocoon deposition in field microcosms, incubators, and combined microcosms and incubators for three lumbricid species.

Species and Source	Constant	Slope	N points	R^2	Std. Error	ANOVA p
D. octaedra						
microcosms	0.776	0.0116	9	0.556	0.0485	0.021
incubators	0.125	0.0533	5	0.860	0.1001	0.014
combined	0.453	0.0325	14	0.402	0.1702	0.008
L. rubellus						
microcosms	0.811	0.0086	8	0.321	0.0586	0.143
incubators	0.389	0.0364	5	0.794	0.0853	0.027
combined	0.587	0.0241	13	0.440	0.1143	0.008
A. tuberculata						
microcosms	0.912	0.0224	11	0.035	0.0517	0.581
incubators	0.648	0.0106	5	0.607	0.0374	0.075
combined	0.766	0.0104	16	0.152	0.0934	0.076

cocoons that showed early evidence of development eventually hatched. Fertility rates, however, were less than 1.0, and varied with temperature (in this study, any cocoon that never visibly showed development was considered infertile; no distinction was made between truly infertile cocoons and those that aborted early in development). Table 17 shows fertility regression parameters for all phases of the study. Infertile cocoons carried through with the rest of the cohort to which they belonged appeared to be live, newly-deposited cocoons even after several months. The fertility of field microcosm-raised *D. octaedra* and *L. rubellus* cocoons increased linearly with temperature at the time of deposition (Figure 27). Mean daily temperatures during the time of year when cocoons were deposited ranged

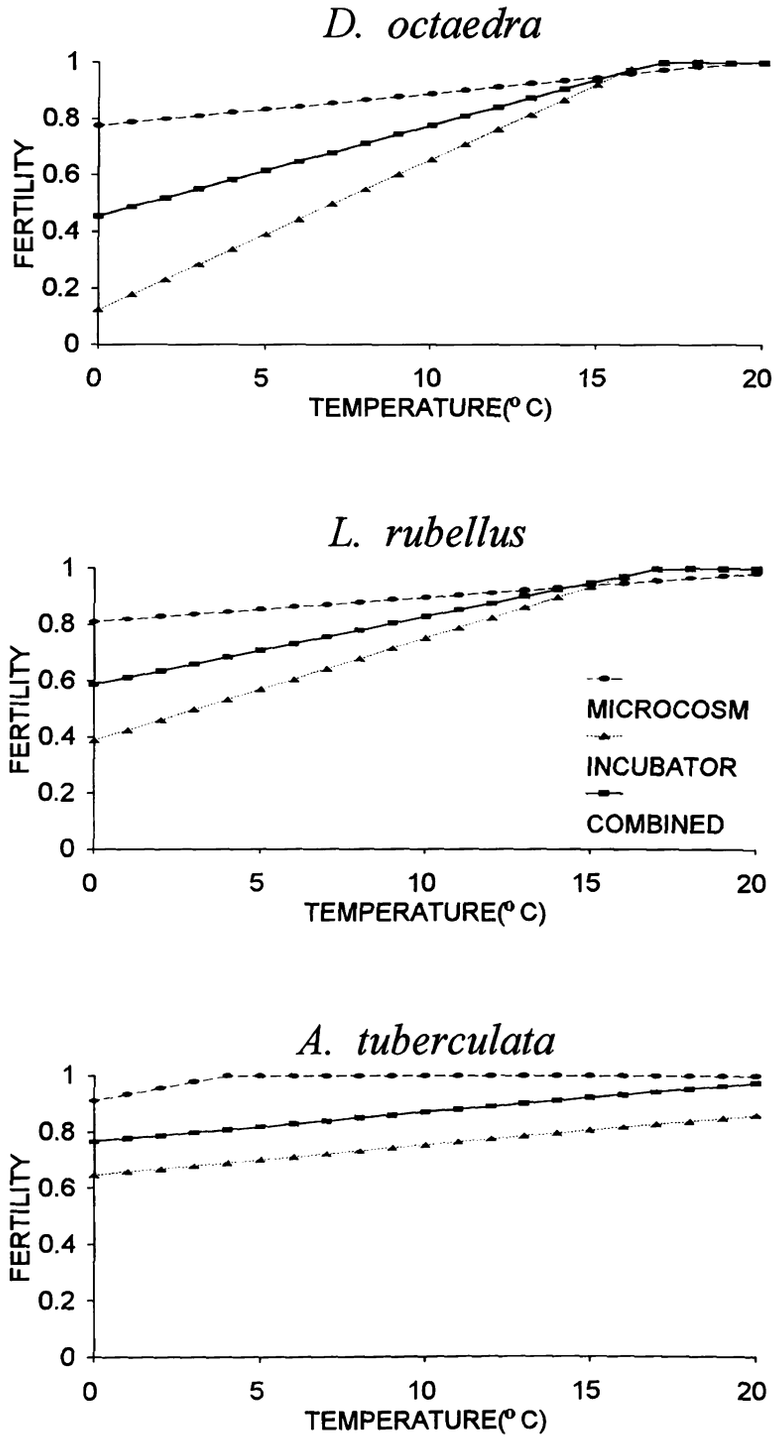

Figure 27. Fertility rates of the cocoons of three lumbricids with respect to temperature at time of deposition in field microcosms, incubator rearings, and combined microcosm and incubator studies.

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from about 10 to 20°C for both species. In this temperature range, *D. octaedra* cocoon fertility was between 75 and 100%, and *L. rubellus* cocoon fertility was between 83 and 100%.

Aporrectodea tuberculata cocoon fertility was not significantly affected by temperature (Table 17); therefore, the mean (0.8814, or 88.14% fertility) was used in the model. Because about 12% of cocoons did not develop, and they can remain in soil for several months and appear to be fresh, some of the cocoons identified as "new" (no apparent development) in this study and the ELF project data may not have been new at all, but actually infertile or aborted cocoons that had been in the soil for some time.

Phenology of Earthworms after Hatching

All analyses of survivorship and phenology in this section are based on the mathematical models generated during this project. A "typical" year of thirteen 28-day months was used, starting with May 1 as the first day of month 1 (Table 18). Levels of soil temperature and moisture for months 1 through 6, and 7 and 13 in part, were generated from the mean temperatures and moistures for each period obtained by data loggers (temperature) and from A horizon soil samples (moisture) at the ELF Control site from 1984 through 1993. Winter temperatures (months 8 through 12, and 7 and 13 in part) were taken from daily temperatures measured via data logger during the winters of 1991-92 and 1992-93. Winter moistures were derived from TDR readings measured through the snow on November 10, 1991 and April 20, 1992. Winter moisture levels were assumed to be constant (the mean of

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Table 18. Temperature and A horizon soil moisture means for each of thirteen 28-day months in a typical year, employed for phenological analysis using earthworm models.

Month	Start Date	Mean Temperature	Mean Moisture
1	May 1	9.5	33
2	May 29	12.5	30
3	June 26	15.0	24
4	July 24	16.0	25
5	August 21	15.0	25
6	September 18	11.0	30
7	October 16	8.0	25
8	November 13	5.0	25
9	December 11	1.0	25
10	January 8	0.0	25
11	February 5	0.0	25
12	March 5	1.0	30
13	April 2	3.0	33

the above two readings) under snowpack for modelling purposes, since no data were available other than the begin-end points stated. Table 19 lists temperatures and moistures for the months of a typical year.

Effects of hatching time on survival and development of worms

Cohort analyses of populations of earthworms hatching and appearing as class 1 immatures at different times were examined using the derived population models. A population vector consisting solely of 10,000 class 1 individuals was used to seed the three models, starting at each of Months 1 through 6 of the typical year defined above. Each month's resulting vectors were passed to the next month in series until Month 1 at the beginning of the third year, resulting in a period of 26

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months (two full years) for the cohort starting in Month 1, and a period of 21 months for the cohort started at Month 6. The population vector was recorded at this time for comparison to the other cohorts of the same species, and placed back in the model until all had died to estimate maximum lifespan and cocoon production. Table 19 lists the results of this set of model runs for all three species.

Dendrobaena octaedra cohort analysis shows that performance of the cohort drops significantly in terms of total population remaining at end of year 2 and total cohort cocoon production if cocoons hatch after the beginning of Month 3, with the highest numbers if cocoons hatch at Month 2. This timing coincides with pre-ELF data from the CONTROL site, where old cocoons, ready to hatch, were only found in quantity during the first and second sampling dates in early and mid May, and many small immatures were collected from mid May through mid June. The high number of small immatures hatching during spring and early summer can not only take advantage of the ample food resources of newly conditioned leaves from the previous autumn's litterfall to grow rapidly, but may possibly decrease the risk of predation by sheer numbers. Cohort analysis also showed that maximum lifespan of a class 1 immature appearing after Month 4 was decreased by more than 1 full year over those appearing earlier in the year. Under these environmental conditions, it may be very advantageous for cocoons to hatch early in the year, allowing time for small worms to grow and gain energy for development and reproduction.

Lumbricus rubellus populations at the end of year two decrease with later cohort start times, but not as dramatically as those of *D. octaedra*. Cocoon

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Table 19. Comparison of cohorts of 10,000 class 1 individuals started at different times (Month 1 = May, Month 6 = late September to mid October) for three lumbricid species at the end of Year 2.

		Population structure at end of Year 2						
Start month	End month	Im-mature	Aclitel-late	Clitel-late	Total Worms	Cocoon sum to date	Total cocoons for cohort	Maximum lifespan (months)
Dendrobaena octaedra								
1	26	0	0	19	19	1705	1907	40
2	25	0	0	25	25	1665	1918	40
3	24	0	0	21	21	1240	1445	38
4	23	0	0	14	14	759	890	37
5	22	0	0	3	3	135	143	25
6	21	0	3	2	5	23	26	24
Lumbricus rubellus								
1	26	6	2	7	15	729	844	42
2	25	8	2	4	14	501	571	37
3	24	9	2	4	15	240	346	42
4	23	10	1	3	14	48	106	32
5	22	9	1	2	12	18	29	25
6	21	8	1	1	10	2	4	24
Aporrectodea tuberculata								
1	26	143	25	6	174	816	1157	88
2	25	126	22	5	153	667	994	87
3	24	28	4	1	33	84	136	71
4	23	20	2	0	22	26	40	70
5	22	30	4	1	35	44	96	69
6	21	37	5	1	43	57	109	68

End month = the number of months from start to end of Year 2.

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production, however, does decrease significantly, from a maximum for the Month 1 cohort to 67% of the maximum for the Month 2 and 40% for the Month 3 cohorts, to less than 1% of the maximum production in Month 6. Cocoons were found in fairly high but variable numbers throughout the first three months of ELF sampling, and decreased thereafter, also supporting model output. Cohort analysis showed that this species, like *D. octaedra*, exhibited a decreased lifespan -- 1 to 1.5 years of its approximate 3-year maximum -- if the young appear in Months 4 through 6.

Aporrectodea tuberculata shows a pattern similar to the other two species in that the population remaining at the end of year 2, cocoon production, and maximum lifespan are all highest in cohorts starting during the first two months. Total populations at end of year 2 and cocoon production drop precipitously at this point, to roughly 20% and 10%, respectively, of the values for earlier cohorts. Lifespan also decreases, from roughly 7 years to a little over five years. Pre-ELF data from TEST indicate that old cocoons are found throughout the sampling period, but their frequency decreases somewhat after mid-July. Class 1 immature densities are quite variable from year to year, but differences between date-specific lifespan as indicated by the models varies significantly between the three species studied. *Dendrobaena octaedra* loses 90% of its initial population to juvenile mortality by month 4 of its 40-month lifespan, with noticeable mortality of all stages, particularly clitellates, during the late winter months (10-13). *Lumbricus rubellus* loses individuals more slowly to juvenile mortality, with 10% surviving through month 6 of its 41-month lifespan. It does, however, experience greater

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mean densities are not significant, with the exception of the mid- and late October dates, which show a small decrease in small worms. The supply of old cocoons and the presence of hatchlings seems to indicate that this species hatches throughout the warm season, rather than concentrating most of the hatch in the period most conducive for population increase. The longer lifespan and iteroparous reproductive pattern of this species (discussed in the next section) may decrease the selective pressure for concentrating the hatch into a shorter period, as seems to be the case for *D. octaedra* and *L. rubellus*.

Phenological and life history comparisons between species

Because all three species studied showed maximum lifespan and cocoon production for cohorts begun early in the warm season, comparisons between the modelled populations were made using cohorts of 10,000 class 1 immatures started at the beginning of Month 1 (May 1) of a typical year (Table 18). Complete records of population developmental stage structure on a monthly basis are listed in Appendix B.

Graph A of Figures 28, 29 and 30 shows survivorship curves for *D. octaedra*, *L. rubellus* and *A. tuberculata* cohorts respectively. Graph B of Figures 28, 29 and 30 shows the phenology of aclitellates, clitellates and cocoons in each of the species. All three of the survivorship curves resemble a Type II curve (Deevey 1947) superficially, the more or less constant negative slope of the semilog graph indicating a constant mortality rate throughout much of the lifespan. The differences between them lie primarily in either end of the curve. Maximum

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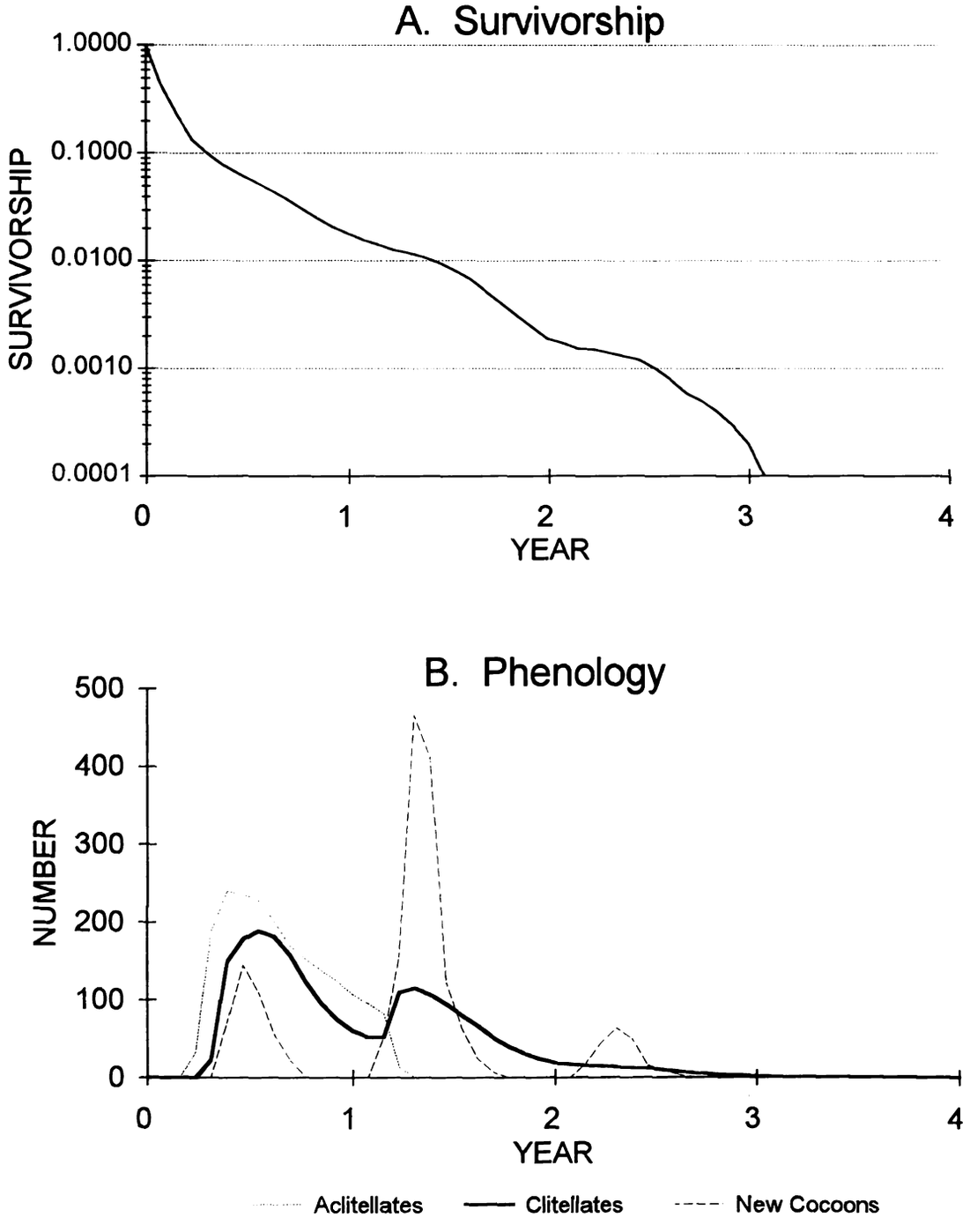

Figure 28. (A) Total cohort survivorship and (B) phenology of selected *D. octaedra* stages, based on a modelled cohort of individuals started May 1.

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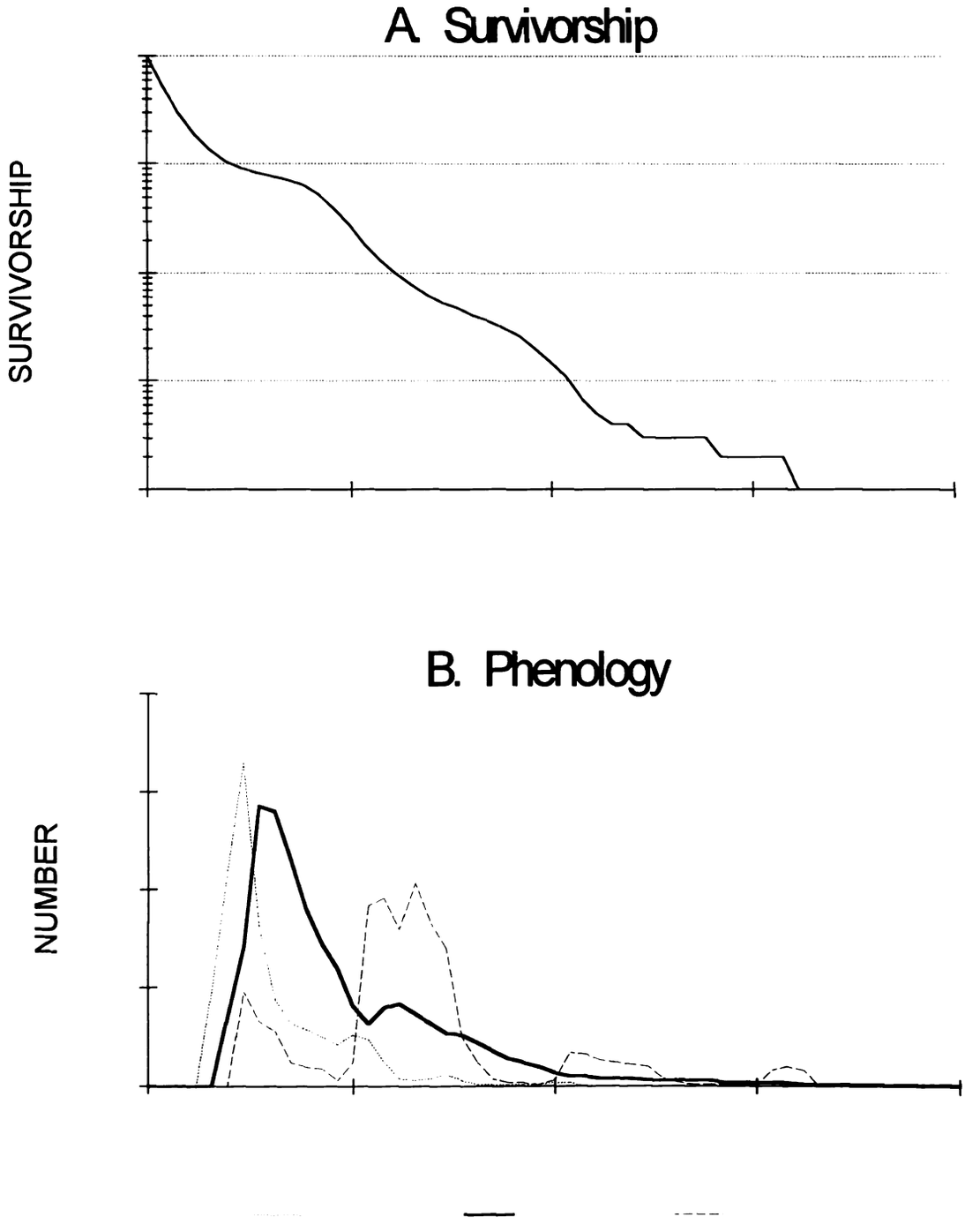

Figure 29. (A) Total cohort survivorship and (B) phenology of selected *L. rubellus* stages, based on a modelled cohort of 10,000 individuals started May 1.

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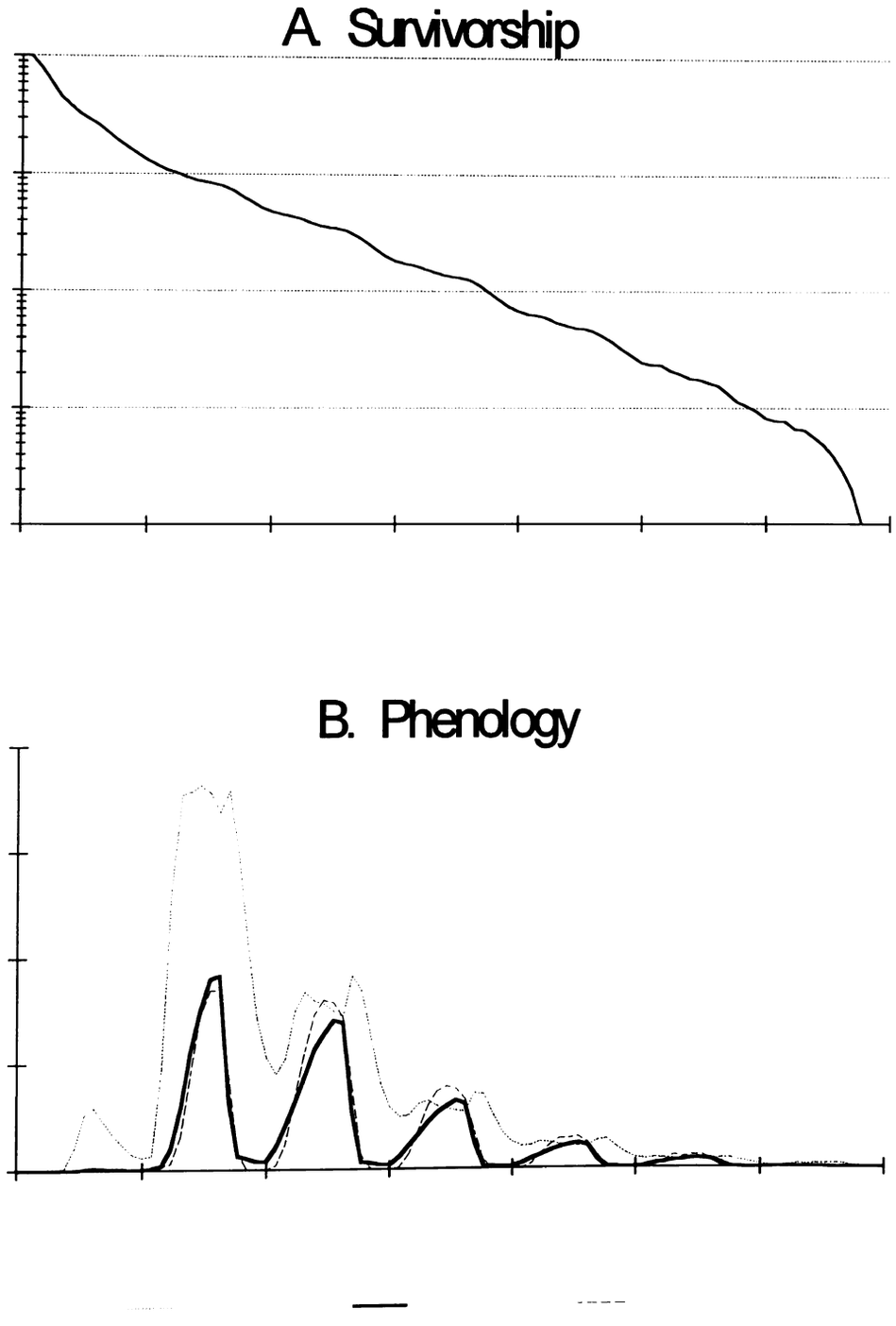

Figure 30. (A) Total cohort survivorship and (B) phenology of selected *A. tuberculata* stages, based on a modelled cohort of 10,000 individuals started May 1.

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mortality during the winter months, particularly among aclitellate and clitellate worms (Figure 29B and Appendix C).

Aporrectodea tuberculata had a much longer lifespan, a maximum of 88 months. Juveniles tended to survive a longer proportion of the lifespan as well, with 10% of the individuals surviving 17 months or longer, more than twice as long as either of the other species. This is evident in the part of each of the curves between the top two "decade" lines. The slope of this portion of the *A. tuberculata* graph is nearly the same as that of the next two decades, indicating a nearly constant mortality through most of its lifespan. The other two species demonstrated markedly steeper slopes in the first decade, indicating heavy juvenile mortality.

On the opposite end of the survivorship curve, *A. tuberculata* (Figure 30A) showed a significant negative change in slope between years 6 and 7, indicating that about 0.1% of all individuals approached some maximum physiological age, reminiscent of Deevey's (1947) Type I survivorship graph. The other two species showed a nearly constant mortality rate until the end of the lifespan.

The timing of reproduction was also different among the three species. In both *D. octaedra* and *L. rubellus*, a significant number of clitellates began to produce cocoons during the first year, with the peak falling in month 7, at the end of the warm season. In *D. octaedra*, about 70% of clitellates died during the winter, and were supplemented by overwintering aclitellates for a second major clitellate peak in month 5 of the second year (Figure 28B). The first peak was comprised of clitellates with a mean size/stage class of 24.71; the second peak

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Table 20. Modelled maximum cocoons deposited per clitellate in any given month of each year for three modelled lumbricid populations.

	D. octaedra		*L. rubellus*		*A. tuberculata*	
Year	Maximum Cocoons	Month of Occurrence	Maximum Cocoons	Month of Occurrence	Maximum Cocoons	Month of Occurrence
1	144	6	48	6	---	---
2	466	4	104	4	85	7,8
3	63	4	17	1	80	6
4			10	2	39	6
5					15	7
6					6	6,7
7					---	---

--- = Presence of clitellates, but no cocoon production.

mean class size was 24.95, indicating that the first-year reproducers may not have gained enough energy for an intensive reproductive effort. The first peak also occurred later in the year, when fecundity was depressed due to falling temperatures. Another indication was the maximum number of cocoons deposited per clitellate in any given month each year (Table 20). Although there are only about two-thirds as many clitellates the second year, the combination of larger clitellates and more favorable conditions produce more than twice as many cocoons as the first year, approximately 68% of the total cocoon production (Appendix B). About 11% of the total cocoon production by this cohort is deposited in the third year, because clitellate densities rapidly decline. Peaks attributable to separate generations are indistinguishable in the natural population censused during the ELF project, but the greatest number of clitellates collected during an average year are found during the late summer and early fall, just as the model predicts. Figure 28B

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shows that about 75% of the clitellates from the first year do not survive the winter into the second year. Very few *D. octaedra* clitellates revert to the aclitellate state to overwinter (Table 21); a clitellate is about 14 times more likely to die than to revert to the aclitellate condition. Figure 28B also clearly shows a decrease in aclitellates coinciding with an increase in clitellate numbers during the first two years, indicating that aclitellates become clitellates, but there is no reversal of this trend later each year; aclitellate numbers remain stable or decrease as clitellates decrease.

Given cocoon development times, *D. octaedra* cocoons deposited at the end of the first year will likely hatch about Month 3 of the second year when conditions are not as favorable for juvenile survival, whereas cocoons produced during Month 5 of the second year will have a chance to develop significantly before onset of winter, hatching in Month 1 of the following year.

Like *D. octaedra, L . rubellus* also exhibits a second clitellate peak in year 2, around Month 3 (Figure 29B), although the peak is not nearly so pronounced as in *D. octaedra.* The mean size class of clitellates at the year 1 peak is 24.85; in year 2 it is 25.17. Again, the earlier timing of reproduction coupled with larger clitellates that produce more cocoons over a longer period, allows only one-third as many clitellates to produce nearly four times as many total cocoons during the second year, compared to the first. Only about 14% of the total cocoons produced by this cohort are deposited in subsequent years, due to rapidly declining clitellate numbers; however, large clitellate size may partially compensate and allow a few worms to produce a high number of cocoons (Table 19). As is the case with *D.*

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Table 21. Summary of proportions of each earthworm developmental stage experiencing stage change or mortality during a sampling period, for three lumbricid species. Proportions are calculated using both incubator and microcosm datasets irrespective of temperature and moisture.

ORIGINAL STATE	FATES				TOTAL
	IMM	ACL	CLI	DEAD	
D. octaedra					
IMM	0.5835	0.0769	0	0.3396	1.0000
ACL	0.0047	0.7307	0.1635	0.1011	1.0000
CLI	0	0.0095	0.8578	0.1327	1.0000
L. rubellus					
IMM	0.6138	0.0754	0.0008	0.3100	1.0000
ACL	0.0511	0.5069	0.3255	0.1165	1.0000
CLI	0	0.0649	0.7075	0.2276	1.0000
A. tuberculata					
IMM	0.7201	0.0485	0	0.2314	1.0000
ACL	0.0508	0.6278	0.2068	0.1146	1.0000
CLI	0	0.1936	0.6962	0.1102	1.0000

IMM = immature; **ACL** = aclitellate; **CLI** = clitellate.

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octaedra, many of the cocoons from the first year will hatch later in the second season when juvenile mortality is high, conferring a selective advantage to delayed reproduction under this temperature and moisture regime.

As is the case with *D. octaedra*, *L. rubellus* also tends to remain clitellate until death, but not as markedly; *L. rubellus* is only about 3.5 times more likely to die than to revert to aclitellate. Chris Klok (pers. comm.) has also observed that clitellates of this species are more likely to move downward in the soil profile during cold or dry conditions while retaining the clitellum.

Both of the above species exhibit basically a two-year life cycle, although substantial differences exist between their survivorships and phenologies, particularly in the areas of juvenile mortality and cocoon production. Both have the capacity to live longer than two years and produce a few cocoons for another breeding season, so generations overlap somewhat and cohorts spill into one another. *Aporrectodea tuberculata* is very different. This species lives for a maximum of nearly seven years, and begins cocoon production in its second year. It then goes through a breeding cycle every year, the number of clitellates increasing throughout the summer and peaking in Months 7-8, after which clitellate numbers decrease rapidly to Month 13 (Figure 30B). Just as in the other two species, total cocoon production in the second reproductive year (year 3 in this species) increases by 26% over the first year, although there are only 79% as many clitellates. Since the clitellate peak occurs at the same time each year, the only explanation for the higher number of cocoons during the second reproductive year is the increase in mean size class, from 27.12 in year 2 to 27.58 in the third year,

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with larger individuals producing cocoons at a faster rate. Clitellate mean size increases every year except the last, reaching 27.75 in the penultimate year and remaining at that level.

Ninety percent of the total cocoons produced by this cohort are deposited in years 2 through 4: 31%, 39%, and 20%, respectively (Table 19). Most cocoons are deposited late in the warm season and during the early winter, and overwinter partly developed. Since development ceases at temperatures near 0°C, they depend on the comparatively low number of degree-days necessary for development (Table 16) to allow them to hatch early in the warm season. Although the modelled maximum lifespan of *A. tuberculata* is nearly seven years, the effective length of the life cycle is approximately four years, with three reproductive seasons and considerable overlap of successive cohorts. There is no reproduction during the last year (Table 20); this, coupled with the increasingly negative slope of the survivorship curve during this time (Figure 30A) indicates that seven years is probably the maximum physiological age of this species.

Unlike the preceding two species, *A. tuberculata* aclitellate numbers increase in winter, just as clitellate numbers are declining. This indicates that the species uses a different overwintering strategy -- it reverts to an aclitellate state, possibly to conserve energy during the cold season. Once they become clitellate, members of the other two species remain so; three-quarters of them only reproduce a single season. *Aporrectodea tuberculata*, however, is truly iteroparous, reproducing up to seasons. Because this species reproduces for several years, it also demonstrates a propensity for switching between aclitellate and clitellate

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stages; unlike the other two species, it is nearly twice as likely to revert from clitellate to aclitellate as it is to die. Proportions between staying clitellate and changing to aclitellate indicate that it remains clitellate for about 3.5 months.

Iteroparity in this species increases the probability that a population will remain stable, because an extended period of suboptimal conditions will not impact an iteroparous species as severely as essentially semelparous species like *D. octaedra* or *L. rubellus*. It would also lessen the effect of suboptimal hatching times because individuals hatching at these times are still likely to reproduce for several seasons. Iteroparity is further evidence of K-adaptation in *A. tuberculata*; this species is more effective at surviving periodically stressful conditions. Populations of the other two species are probably better able to colonize new habitat rapidly and proliferate under favorable conditions, but are likely to decline in numbers when conditions are unfavorable.

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Chapter 6

USING THE *A. tuberculata* MODEL TO TEST FOR ELF EFFECTS

The ELF project was designed to detect soil ecological effects of low-level extremely low frequency electromagnetic fields in soil (76 Hz nominal, field strength in soil of 53.9±6.6 $mV \cdot m^{-1}$) (Snider and Snider 1994) near the ELF TEST site, by comparing it with a similar CONTROL site in a before-after preoperational (1984-1988) and an operational (1989-1993) 2×2 design. Because *A. tuberculata* was abundant at the ELF TEST site, and the model developed for this species in the previous chapter was a good predictor of its population dynamics, it was used to test the hypothesis that there was no effect of the ELF EM field on earthworm populations. If the EM field induced in the TEST site soil were to affect the *A. tuberculata* population, a deviation of the actual field population from that predicted by the model after antenna activation would be expected.

The two-sample t-statistic (Sokal and Rohlf 1995) was employed to test for differences between field populations and model predictions during pre-ELF and operational periods. A test of the regression slopes of observed on projected populations before (n = 48) and after (n = 50) antenna activation showed no significant difference (t = 0.0133, 94 df) between total predicted population densities during the pre-ELF and operational periods. When each stage was

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Table 22. t-tests of model prediction vs. field observations between pre-ELF and operational periods, for the entire population and for each developmental stage separately.

	Pre-ELF		Operational		
Stage/Class	**Mean**	**Std. Error**	**Mean**	**Std. Error**	**t-value**
Cocoon	1.0056	0.0620	0.8821	0.1093	1.1206
Class 1	1.0277	0.0633	0.8817	0.0664	1.5915
Class 2-4	0.9746	0.0428	1.0316	0.0431	1.0056
Class 5-6	.9387	0.0502	0.9675	0.0543	0.3895
Aclitellate	1.0927	0.0633	1.0819	0.0637	0.1203
Clitellate	1.0109	0.0681	0.6477	0.0691	3.7436***
Total Population	1.0221	0.0344	1.0214	0.0400	0.0133

N = 98, df = 94 for all tests. ***: Significant at $\alpha = 0.001$.

examined individually, however, significant deviations from model predictions became evident. The statistics for these comparisons are summarized in Table 22.

During the ELF operational period, clitellates exhibited a highly significant decrease ($\alpha = 0.001$) compared with pre-ELF model predictions. The cocoons and smallest immatures also showed small, but not statistically significant, negative deviations from model predictions for the operational period. It should be noted that the cocoon values in Table 22 were calculated from the total number of cocoons, not just those newly deposited.

One might wonder whether this effect occurred in all years, or if it was concentrated in one or two years. Figure 31 shows the clitellate, total cocoon and fecundity slopes and their associated 95% confidence intervals for each year. Although there was a significant deviation below 1.0 in the 1986 clitellate slope,

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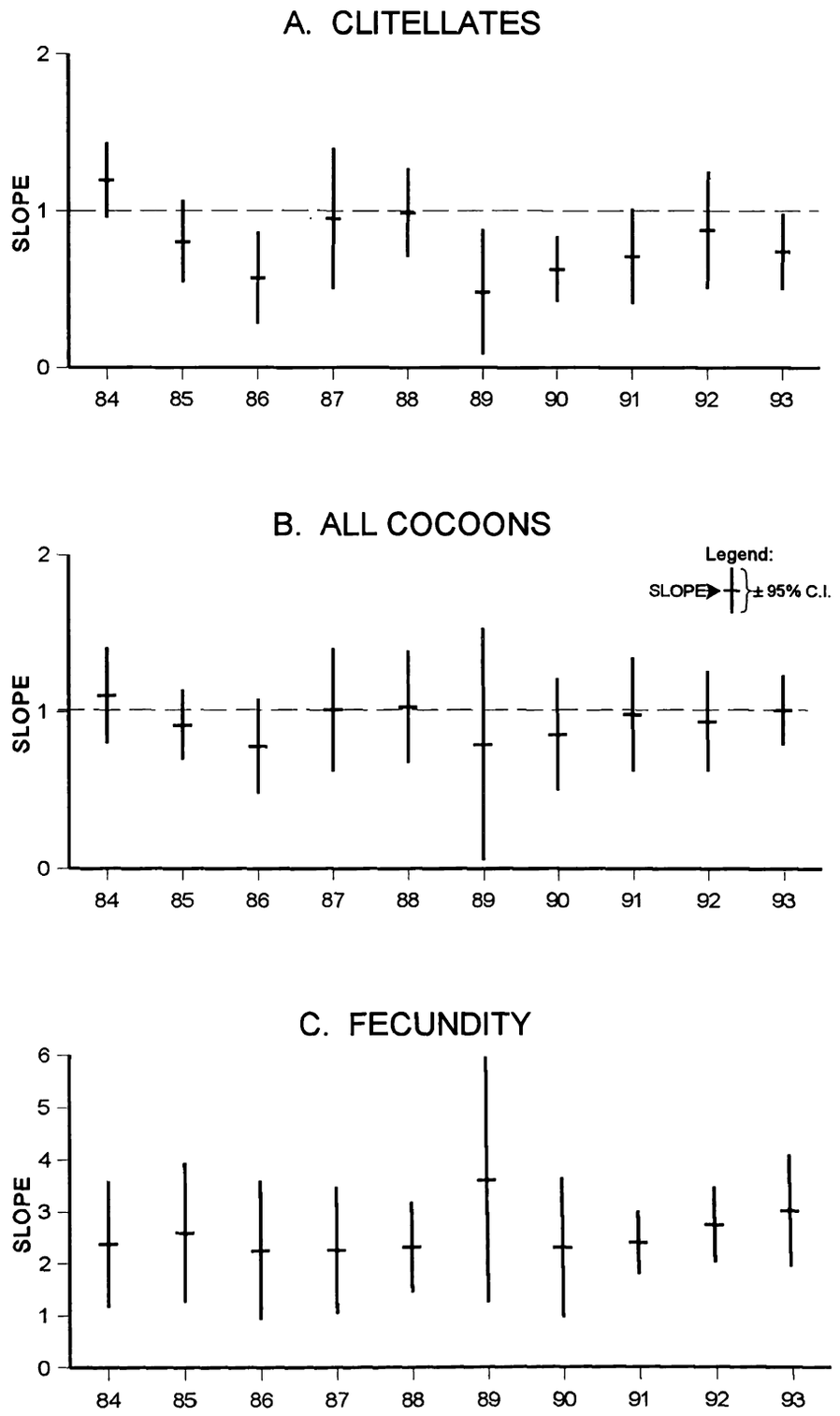

Figure 31. Observed vs. modelled population slopes and 95% confidence intervals by year for (A) clitellate numbers, (B) total cocoon numbers, and © clitellate fecundity. Dashed lines in (A) and (B) indicate a slope of 1.0, where observed and modelled agree exactly.

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the pre-ELF clitellate slopes were generally quite close to 1.0. Yearly operational period values, on the other hand, were all below 1.0, with two of them (1989 and 1993) significant at the $\alpha = 0.05$ level and one (1990) significant at $\alpha = 0.01$. One possible hypothesis is that the glandular clitellum makes them more susceptible to electric current because it is more conductive than the remainder of the integument. Another is that large worms are more susceptible to electric current than smaller ones because there can be greater difference in electric potential between the ends of the worm if it is longer, depending on how it is oriented with respect to the field.

Aporrectodea tuberculata is a long-lived species, with a possible life span of seven to eight years (Satchell 1967, referring to *A. caliginosa*). The model developed in Chapter 5 corroborates this estimate, and sets the maximum lifespan at about seven years. If they mature in two years, each worm may be able to reproduce for up to five years. This results in considerable overlap of generations, and population-level changes could be slow. It would be interesting and informative to return to the TEST site after several years to sample for a season or two to determine if the trend continues.

The total cocoon slopes (Figure 31B) did not vary significantly from 1.0 throughout the study; however, the 95% confidence interval about the 1989 slope jumped to roughly twice the average of previous years, due to two sampling dates of that year: one (date 3 in early June) where the actual number of cocoons collected in the field far exceeded model predictions, and the following month (date 5 in early July; monthly periods overlap by 2 weeks) when the reverse occurred. The high number of cocoons collected on Date 3 was due to a single sample in

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which several times the mean number of cocoons was found; a reasonable explanation of this phenomenon has not been found. After the initial operational year of 1989, confidence intervals returned to a more usual width.

Fecundity (Figure 31C) again showed no significant differences between predicted and actual values after antenna activation; however, there was a marked increase in both the slope and confidence interval in 1989, with a return to more usual values afterward. The jump was due to two consecutive dates (3 and 4) in which the fecundity was three to four times the normal level, again due to the large number of cocoons found in a single sample. This is generally the period when individuals which have overwintered as aclitellates become clitellate and begin to produce cocoons. An explanation should be made here about the high slopes in the fecundity plot. There are two possible reasons for this:

(1) Observed values are based on the number of "new" cocoons (those without a developed embryo) found in the field. Data from the field microcosm and incubator trials used to construct the models show that infertile cocoons or those with embryos that died early in development can remain in the soil and appear viable to external examination for several months. These same data show that approximately 12% of all cocoons deposited are infertile. This alone may inflate the number of observed new cocoons by 50% or more.

(2) The method of dividing cocoons into categories used in this study varied somewhat from that used in the ELF monitoring project. In the latter, cocoons were divided into "new", "intermediate", and "old", the new class being cocoons which did not display any development, as well as those which had a small embryo which was not yet wormlike. They were also observed after being preserved in formalin, which may have rendered the yolk more opaque, obscuring small embryos. This study divided cocoons into four classes: "new", "embryo", "hearts", and "old", where the first stage was undeveloped and the second contained a recognizable embryo, viewed while alive. This again could substantially inflate the number of observed cocoons assumed to be newly deposited.

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Although these tests do not prove conclusively that differences in population structure were attributable to an ELF EM field effect, they show that there may have been an effect due to a time-dependent factor not included in the model which coincided with activation of the ELF antenna. The number of clitellates was significantly lower, and the number of cocoons was only somewhat lower than what the model predicted; as a result, the fecundity of *A. tuberculata* was higher in the operational period than in the pre-ELF period, at least for the first year after antenna activation. It is interesting to note that the total population of *A. tuberculata* was not significantly different in the operational period, suggesting that, even though there were fewer clitellates (or adults remained clitellate a shorter time), they produced enough cocoons to make up the difference. Since clitellates make up only a small fraction of the total population, the loss of a few individuals did not significantly affect population levels as a whole during the period of study.

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Chapter 7

SUMMARY AND CONCLUSIONS

Aspects of the life cycle and life history of three lumbricid species (*Dendrobaena octaedra*, *Lumbricus rubellus*, and *Aporrectodea tuberculata*) were examined using data collected from three sources: (1) biweekly partial censuses of natural earthworm communities five years before (1984-1988) and five years following (1989-1993) activation of an extremely low frequency (ELF) radio antenna in the vicinity of the sampling sites, (2) replicate marked populations reared in field microcosms under near-natural conditions, and (3) earthworms reared in incubators controlled for constant temperature and moisture. Sites for natural population censuses were located in mixed deciduous forest in Michigan's Upper Peninsula. The TEST site was situated approximately 100 m from an aboveground element of the U.S. Navy's ELF antenna, and contained substantial populations of *L. rubellus* and *A. tuberculata*; the CONTROL site was approximately 11.5 km from the antenna, and contained a high population of *D. octaedra*. The field microcosm rearings were performed near the CONTROL site.

In order to obtain sequential records of individuals in the field microcosms, a tattooing technique was developed and shown to be an effective method of permanently marking earthworms. Modifications were also made to the time-

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domain reflectometry (TDR) method of nondestructive soil moisture measurement to allow continuous monitoring of soil moisture within the microcosms; this modified procedure was validated and compared to a more commonly used gravimetric method, and a second-order regression equation was developed to convert values from one to the other.

Dynamic matrix population models driven by soil moisture and temperature were constructed for each species using the microcosm and incubator data, and were validated and tested with census information from the five-year pre-ELF period. Once validated, the *A. tuberculata* model was used to examine differences between population behavior during the ELF operational period and model predictions. All three models were utilized to delineate the life cycle and various aspects of the life history of the three earthworm species in northern Michigan, based on mean temperature and moisture data over a "typical" year of thirteen 28-day months, starting on May 1.

Summary of Modelling Techniques and Approach

Cocoon development was modelled using the degree-day approach. Rate of develoment of cocoons was shown to be directly related to temperature, and derived degree-day equations for each species described developmental rate reasonably well. No significant difference between the three species was seen, primarily because of the degree of developmental variation within each species.

A substantial proportion of cocoons deposited were either infertile, or the embryos did not develop. Cocoon fertility rate was found to be significantly

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positively correlated with temperature in *D. octaedra* and *L. rubellus*, and positively, although not significantly, correlated with temperature in *A. tuberculata*.

Hatchlings of all three species have the highest survival rate if they hatch early in the warm season (May and June), when there is abundant food in the form of conditioned and decomposing leaf litter and soil moisture is high. Those hatching later in the season enter their first winter smaller, less able to burrow, and possibly in poorer condition to handle the cold stress. Because of this, life cycle and life history inferences, based on a "typical year" of thirteen 28-day periods, used Month 1 (May 1) as the starting point for hatchling cohorts.

After hatching, earthworm growth irrespective of temperature and moisture tended to follow the von Bertalanffy growth equation. Use of assimilated energy gradually switched from growth in young individuals to maintenance and reproduction in older, larger earthworms. This growth behavior was utilized to separate populations of each of the three species into size classes related to growth rate potential. Populations were also separated by developmental stage into cocoon, immature, aclitellate (nonreproductive adult) and clitellate (reproductive) stages.

The models derived for each species treated each size class and stage separately with respect to soil temperature and moisture. Comparisons of expected model predictions with observed censuses of natural populations showed close agreement between observed and expected.

Life Cycles and Life Histories of Individual Species

Dendrobaena octaedra (Savigny) is a small worm, rarely over 0.15 g at maturity. It is epigeic and straminicolous, and consumes leaf litter conditioned by microbes. Satchell's (1980) classification scheme would place *D. octaedra* in the "r-adapted" category, and the model produced in Chapter 5 confirms it. It is small, comparatively short-lived, produces many small cocoons (maximum monthly rate of 4.5 cocoons per clitellate in its second season), has high mortality early in life, and probably is only sexually mature for a single summer. Cocoon fertility shows a positive linear relationship with temperature; cocoons deposited at 5°C are fertile about 60% of the time, and cocoons deposited above 17°C are always fertile, according to the model. A generalized life cycle for this species in upper Michigan would be:

- Most cocoons are deposited in mid to late summer. They go through much of their development during summer and fall, completing it slowly over the winter. Most cocoons hatch during the month after snowmelt the following spring.
- Hatchlings grow very quickly but experience high mortality, 90% having died by the fourth month after hatching. Some reach the clitellate stage the first year. Of these, approximately 75% do not survive the winter. Those that do, begin producing cocoons shortly after becoming active once again. Those that overwinter as immatures or aclitellates rapidly grow and become clitellate, leaving very few one-year-old nonclitellate individuals by early July of the second year.
- Only about 15% of the worms in their second year survive to reproduce in the third, and these die over winter. The model and its supportive data give no indication that clitellates revert to a nonclitellate state when stressed by cold.

L. rubellus Hoffmeister digs shallow, horizontal temporary burrows, is medium-sized (1 g or less as an adult), produces a moderate to high number of cocoons (maximum monthly rate of 3.40 cocoons per clitellate at the beginning of

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its third year), is straminicolous as an immature and moves more into the soil as it increases in size, consuming a combination of raw humus and leaf litter it has conditioned on the surface by burying it with castings (R.W. Parmelee, pers. comm.). This species is in roughly the same place as *D. octaedra* in the r-K continuum, growing to maturity just as rapidly but producing fewer cocoons per clitellate, except at the very end of its life when it seems to spend all of its energy reproducing. Cocoon fertility rates in this species also show a positive linear relationship with temperature; cocoons deposited at 5°C are fertile about 70% of the time; those deposited above 17°C are always fertile. A generalized life cycle for Upper Michigan follows:

- Cocoons are deposited throughout the warm months. Those that are deposited early and hatch late in the season have a limited chance of survival, as winter mortality of small worms is high. Those that overwinter as cocoons and hatch the next spring have a better chance of success, but mortality of spring hatchlings is still approximately 90% over a period of six months.

- Hatchlings grow rapidly; 17% reach the clitellate state by the end of the first warm season. Of these, about 80% die during the winter, but by the middle of the warm season of the second year, 42% of all worms from this cohort are clitellate.

- Only about 15% of the clitellates alive at the beginning of their second year survive to the third, but all third-year members of the population are clitellate. Only a rare individual survives its third winter, but if it does, it produces cocoons until it dies. As in *D. octaedra*, the model shows that clitellates retain the clitellum; only occasionally do they revert to the aclitellate state.

Aporrectodea tuberculata (Eisen) tends more toward being K-adapted. It produces a few large cocoons per season (maximum monthly rate of 2.75 cocoons per clitellate in its fourth season), has significantly lower juvenile mortality than the r-adapted *D. octaedra* and *L. rubellus*, finally reaching 10% survival in the fourth

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month (August) of the second year. It is endogeic, comes to the surface only rarely, and constructs semipermanent horizontal burrows extending well into the mineral soil. Adults over 1 g are regularly found, and may be reproductively active for several seasons. Unlike the preceding two species, no significant relationship between temperature and cocoon fertility was found; mean fertility of deposited cocoons was about 88%. A generalized life cycle derived from the model follows:

- Cocoons are deposited mainly in the last half of the warm season and into November. They undergo rapid development when the soil is warm, but development is arrested for three to four months during the winter. After snowmelt, cocoons rapidly complete their development and hatch early in the warm season.

- The first year is spent in slow growth relative to the other two species. Very few (about 1%) become aclitellate the first year, and there are almost no clitellates. Juvenile mortality is low compared to the other two species, with 10% of all members of this cohort living until the middle of the second year.

- Reproduction commences about late July of the warm season during the second year, with approximately 12% of the total second-year population in reproductive condition at the peak in mid-September to mid-November. Adult mortality is low and relatively constant throughout the remainder of the life cycle. The third year sees 21% of the total population in reproductive condition, which rises to roughly 25% in the following years.

- During the warm season, the probability for clitellates to revert to the aclitellate state is about 40%, depending on temperature, moisture and size according to the model outlined in Appendix 1. At the same time during the warmest month, large aclitellates will become clitellate about 60% of the time. It can be concluded from the summer clitellate:aclitellate stage change probabilities that *A. tuberculata* undergoes cyclic reproduction, probably twice or three times each season, between which it becomes aclitellate to gain energy for the next cycle. During the winter, the probability for clitellate reversion to aclitellate increases to approximately 90% and the aclitellate-to-clitellate stage change probability decreases to about 10%, indicating most mature worms would be aclitellate . This species also loses reproductive capacity over the winter, probably because it is costly to retain the clitellum during this time. Maximum lifespan in a northern deciduous forest is about seven years, with about 0.1% of the population living to what appears to be a maximum physiological age.

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In conclusion, the first two species were similar in that they developed rapidly, produced many cocoons in a short time, and had a relatively short lifespan characterized by high mortality early in life. *Aporrectodea tuberculata*, on the other hand, developed more slowly, taking two years to reach maturity. Its reproductive period was extended over several years, and it tended to live to a maximum physiological age. Absolute juvenile mortality, as well as juvenile mortality in proportion to lifespan, was substantially lower in *A. tuberculata* than the other two species.

Effects of ELF Exposure on *A. tuberculata*

Significant changes in the life cycle and population structure of *A. tuberculata* due to exposure to ELF electromagnetic fields were shown to be restricted to clitellates. A lower proportion of clitellates to total adults was observed than was predicted by the model (significant at $p=0.05$ in three of the five ELF operational years, but remaining lower than predicted throughout), but these clitellates had a somewhat higher than predicted (nonsignificant at $p=0.05$) fecundity, balancing the net effects on the population. It must be concluded that, even though the operation of the ELF antenna does change the population structure, it does not significantly affect the reproductive capacity or the intrinsic growth rate of the population as a whole. It would be informative to return to the TEST site at some time in the future to sample for a couple years to test this possibility, censusing the earthworms to determine if population-level changes have occurred, or if the

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depression of clitellate numbers seen in the ELF operational period is an extended version of the depression of observed vs. expected clitellate numbers seen in 1986.

Directions of Future Research

Several areas can be studied more intensively to increase the accuracy of these models. The first would be studies to determine a minimum temperature threshold for hatching. It would then be feasible to subdivide the cocoon stage into new, developing, and fully-developed cocoons, using the last group as a repository for cocoons that complete development during the winter. More study on cocoon frost tolerance (sensu Holmstrup *et al.* 1991) would also allow this factor to be included in cocoon mortality calculations. Testing the frost tolerance of clitellates and their response to cooling temperatures in the laboratory would also yield useful information for incorporation into the model.

Another factor that would make the model more general is the addition of some measure of food availability and assimilation over each time period. Martin and Lavelle (1992) came to similar conclusions, incorporating burrowing behavior into their model, together with depth-specific soil organic content: worms forced into lower strata due to drought or heat did not grow as fast, because they experienced lower food quality in lower soil horizons. Determination of food quality was attempted as part of this study, but the proper chemical tests of the experimental soil and litter (total and soluble N and P, and total C) before and after each month were prohibitively expensive.

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The general form of the model was designed to be extensible to other earthworm species, given the proper data to construct it. The contour plots of response surfaces presented in Chapter 5 could be particularly useful, because a trajectory of mean monthly temperatures and moistures can be plotted on the graph. If a substantial part of the year is spent in the area where the intrinsic growth rate, r, is greater than 1.0, the population will remain stable or increase. In this way, the success or failure of an introduction or a natural population experiencing environmental stress can be predicted. Applied to a commercially raised species such as *Eisenia fetida*, application of the model would enable worm growers to maintain optimum conditions for population growth, allowing an estimate of the number that can be culled from the population while still maintaining viability.

Appendix A

MULTIPLE REGRESSION COEFFICIENTS FOR INCUBATOR, FIELD MICROCOSM, AND COMBINED MODELS

In the tables below, the "spread" rows contain the equation coefficients used to calculate standard deviations of the life history character immediately above. Input and output ranges refer to the coded sizes/stages.

Table 23. Multiple regression coefficients for *D. octaedra* incubator model.

	Input Range		Output Range								
COCOONS											
development	-	-	-	-	T[a] = -2.7000			Slope= 1746.0			
					a	Soil Temp	Soil Moisture	Temp²	Moisture²	Temp x Moisture	Initial Size
fecundity	-	-	-	-	1.8640	-0.2233	-0.1316			0.0221	
fertility	-	-	-	-	-0.3418	0.1973		-0.0084			
survivorship	-	-	-	-	1.0000						
IMMATURE WORMS											
growth	1	4	1	4	-0.3268	0.1296	0.0180	-0.0042			-0.2580
spread					1.2620	-0.0527	-0.0528		0.0006	0.0028	
stage	3	4	3	14	-2.1680	0.2223	0.1113	-0.0112	-0.0019		
spread					-5.3240	0.2360	0.3939	-0.0074	-0.0074	-0.0040	
survivorship	1	4	-	-	0.8672		-0.0854		0.0022		0.2003
ACLITELLATE WORMS											
growth	13	15	13	15	2.0160	0.2544		-0.0101			-0.2259
spread					-1.2260	0.0526	0.1466	-0.0036	-0.0036	0.0011	
stage	13	15	3	25	0.8823	-0.1192	-0.1494	0.0092	0.0031		0.0842
spread					0.3299	-0.1141	0.0151		-0.0014	0.0061	
survivorship	13	15	-	-	-1.9170	0.0853	0.1370		-0.0023	-0.0040	0.0682
CLITELLATE WORMS											
growth	24	26	24	26	8.4290	0.1552	-0.1419	-0.0075	0.0039		-0.3283
spread					-0.8824	0.0198	0.1208		-0.0026		
stage	24	26	14	26	-0.3264	0.0216	0.0109			-0.0009	0.0104
spread					2.2430	-0.0671	-0.1531		0.0025	0.0027	
survivorship	24	26	-	-	-0.7560	-0.0102	0.0806		-0.0017		0.0312

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Table 24. Multiple regression coefficients for *L. rubellus* incubator model.

COCOONS												
development	-	-	-	-	T[a] = 0.3900				Slope= 1967.0			
	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²	Moisture ²	Temp x Moisture	Initial Size
fecundity	-	-	-	-	-46.530	0.2204	0.1430				1.6990
fertility	-	-	-	-	0.3892	0.0364					
survivorship	-	-	-	-	1.0000						
IMMATURE WORMS											
growth	1	4	1	4	0.9731	0.0375	-0.1024		0.0023		0.0506
spread					-0.3480	0.0497	0.0299			-0.0018	
stage	4	4	4	14	-0.5904						0.1494
spread					-2.2740	0.1088	0.1408	-0.0048	-0.0021		
survivorship	1	4	-	-	0.5947	0.0406		-0.0028			0.0678
ACLITELLATE WORMS											
growth	14	15	14	15	-3.2000	0.2168	0.2720	-0.0108	-0.0059		-0.0375
spread					-1.6190		0.2031		-0.0050		
stage	14	15	4	25	-7.5050	0.0341	0.3674		-0.0079		0.2184
spread					-5.3110	-0.0794	0.5405	0.0042	-0.0120	0.0001	
survivorship	14	15	-	-	0.7977						0.0118
CLITELLATE WORMS											
growth	24	26	24	26	13.600		-0.0349		0.0072		-0.3829
spread					-0.1949		0.0111				0.0036
stage	24	26	14	26	-3.0180	0.0278	0.7081		-0.0158		-0.1939
spread					2.2590	-0.0404	-0.1722	0.0010	0.0039	-0.0003	
survivorship	24	26	-	-	-1.0730						0.0746

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Table 25. Multiple regression coefficients for *A. tuberculata* incubator model.

	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²	Moisture²	Temp x Moisture	Initial Size
COCOONS											
development	-	-	-	-	T[a] = 0.59			Slope= 1037			
fecundity	-	-	-	-	-2.73	-0.16	-0.065			0.0094	0.154
fertility	-	-	-	-	0.6483	0.0106					
survivorship	-	-	-	-	1						
IMMATURE WORMS											
growth	1	6	1	6	-1.216	0.0336	0.1077		-0.002		-0.09674
spread					1.818	0.0006	-0.134		0.0032		
stage	4	6	4	16	-1.993	0.0403	0.0348	-0.002	-7e-04		0.2858
spread					-2.589	0.0903	0.1923	-0.005	-0.004	0.0007	
survivorship	1	6			0.5741	0.0632		-0.004			0.03599
ACLITELLATE WORMS											
growth	15	17	15	17	3.244	0.0215	0.0304				-0.2597
spread					0.872	-0.029	-0.094		0.0027	0.0027	
stage	15	17	5	27	-0.85	-0.224	-0.055	0.0041		0.0074	0.1402
spread					-1.684	0.0273	0.141	-0.002	-0.003	0.0018	
survivorship	15	17			-0.143	0.0379	-0.004	-0.003			0.07066
CLITELLATE WORMS											
growth	26	28	26	28	5.221	0.1557	0.0331	-0.007			-0.2583
spread					4.06	-0.209	-0.259	0.0057	0.0051	0.0041	
stage	26	28	16	28	-4.222	0.0056	0.3292	-0.005	-0.008	0.0054	
spread					2.352	-0.015	-0.159	0.0033	0.0037	-0.003	
survivorship	26	28			1.35	0.0547	-0.048	-0.004	0.0011		

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Table 26. Multiple regression coefficients for *D. octaedra* field microcosm model.

	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²	Moisture²	Temp x Moisture	Initial Size
COCOONS											
development	-	-	-	-	T[a] = -1.3600			Slope= 1857.0			
fecundity	-	-	-	-	-56.960	0.4522	-0.1509				2.3530
fertility	-	-	-	-	0.7764	0.0116					
survivorship	-	-	-	-	0.9946						
IMMATURE WORMS											
growth	1	4	1	4	-4.3830	0.7997		-0.0305			-0.0995
spread					0.0496						0.0866
stage	3	4	3	14	-4.2490	0.0551	0.2100		-0.0047		0.4820
spread					-0.4168						0.1734
survivorship	1	4	-	-	-0.2767		0.0193				0.1534
ACLITELLATE WORMS											
growth	13	15	13	15	-8.8520	2.3170		-0.0910			-0.3341
spread					-1.1010	0.0609	0.0325				
stage	13	15	3	25	-5.8340	0.1102	0.1285		-0.0030		0.2454
spread					0.1898						
survivorship	13	15	-	-	0.8988						
CLITELLATE WORMS											
growth	24	26	24	26	7.2120	1.4480	-0.2238	-0.0558	0.0038		-0.5205
spread					0.3000						
stage	24	26	14	26	-0.3179						0.0122
spread					0.8878	-0.0054					-0.0314
survivorship	24	26	-	-	-0.0224	0.1424		-0.0052			

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Table 27. Multiple regression coefficients for *L. rubellus* field microcosm model.

	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²	Moisture²	Temp x Moisture	Initial Size
COCOONS											
development	-	-	-	-	T[a] = 0.1100			Slope= 1675.0			
fecundity	-	-	-	-	-30.920	-2.4210	-0.7853	0.0189	0.0010	0.0846	2.0640
fertility	-	-	-	-	0.9073						
survivorship	-	-	-	-	0.9876						
IMMATURE WORMS											
growth	1	4	1	4	-3.6900	0.5454	0.0306	-0.0201			-0.0754
spread					-0.2814	0.0265					0.0929
stage	4	4	4	14	-5.4130	0.7513	0.0196	-0.0292			0.1414
spread					3.9340	1.3430	-1.0940		0.0387		
survivorship	1	4	-	-	-2.9770	0.1470	0.1849		-0.0022	-0.0056	0.1421
ACLITELLATE WORMS											
growth	14	15	14	15	-8.9350	1.6890	-0.1175	-0.0388	0.0090		-0.0265
spread					-31.281	3.0490	-0.0210	-0.2981	-0.0457	0.1890	1.0650
stage	14	15	4	25	-9.5270	0.4232	0.1970			-0.0160	0.3279
spread					-20.131		0.9264	-0.0182			0.6122
survivorship	14	15	-	-	-2.4090	0.2993		-0.0112			0.0926
CLITELLATE WORMS											
growth	24	26	24	26	2.7990	0.4166		-0.0164			-0.2056
spread					7.2840		0.0594				-0.3220
stage	24	26	14	26	-1.1020	0.1643		-0.0061			
spread					0.3000						
survivorship	24	26	-	-	-4.9470	0.0177	0.2157		-0.0042		0.1113

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Table 28. Multiple regression coefficients for *A. tuberculata* field microcosm model.

COCOONS											
development	-	-	-	-	T[a] = 2.6030			Slope= 746.10			
	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²	Moisture²	Temp x Moisture	Initial Size
fecundity	-	-	-	-	-8.0880	1.5130		-0.0552			
fertility	-	-	-	-	1.0120	-0.0069					
survivorship	-	-	-	-	0.9863						
IMMATURE WORMS											
growth	1	6	1	6	0.8585		-0.0230				
spread					0.3844						
stage	4	6	4	16	4.2760		-0.2991		0.0052		
spread					4.2312		-0.2923		0.0050		
survivorship	1	6			-0.6084	0.1224	0.0441			-0.0051	0.1116
ACLITELLATE WORMS											
growth	15	17	15	17	-1.1970	0.6198	-0.1905	-0.0262	0.0042		
spread					0.3095						
stage	15	17	5	27	0.0572		-0.0123		0.0022		0.1157
spread					-1.1260		-0.0157				0.1086
survivorship	15	17			-0.3364	0.1879		-0.0083			0.0182
CLITELLATE WORMS											
growth	26	28	26	28	0.4256						
spread					0.4352						
stage	26	28	16	28	4.1530						-0.1459
spread					4.3060						-0.1515
survivorship	26	28			2.1370	-0.0799	-0.0454			0.0032	

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Table 29. Multiple regression coefficients for *D. octaedra* combined incubator and microcosm model.

COCOONS											
development	-	-	-	-	T[a] = -6.8800			Slope= 2394.9			
	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²	Moisture²	Temp x Moisture	Initial Size
fecundity	-	-	-	-	-38.481	-0.8422	0.6710	0.0267	-0.0192	0.0257	1.3870
fertility	-	-	-	-	0.4527	0.0325					
survivorship	-	-	-	-	0.9990						
IMMATURE WORMS classes 1-2											
growth	1	2	1	3	0.2832	0.0442					-0.1818
spread					2.3903	-0.1752	-0.0737			0.0058	
stage	-	-	-	-							
spread											
survivorship	1	2	-	-	-0.4456		0.0181				0.2741
IMMATURE WORMS classes 3-4											
growth	3	4	2	4	-0.4633	0.2231		-0.0078			-0.2120
spread					0.3857						
stage	3	4	3	14	-2.7603	0.0266	0.1320		-0.0029		0.3769
spread					-0.3588						0.1661
survivorship	3	4	-	-	0.7677						
ACLITELLATE WORMS											
growth	13	15	13	15	2.1609	0.4794		-0.0186			-0.3145
spread					0.4898						
stage	13	15	3	25	-2.9750	-0.0634	0.0160	0.0062			0.2520
spread					-1.1674						0.0958
survivorship	13	15	-	-	0.9047						
CLITELLATE WORMS											
growth	24	26	24	26	11.6610	0.2274	-0.0236	-0.0084			-0.5036
spread					0.3298						
stage	24	26	14	26	-0.4248						0.0165
spread					0.1.159 9						-0.0451
survivorship	24	26	-	-	0.7761	0.0102					

Table 30. Multiple regression coefficients for *L. rubellus* combined incubator and microcosm model.

COCOONS												
development	-	-	-	-	T[a] = -2.2100				Slope= 2271.6			
	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²		Moisture ²	Temp x Moisture	Initial Size
fecundity	-	-	-	-	-32.520	-0.5447	-0.1351				0.0298	1.4010
fertility	-	-	-	-	0.5866	0.0241						
survivorship	-	-	-	-	0.9983							
IMMATURE WORMS												
growth	1	4	1	4	-0.9114	0.1536	0.0164	-0.0048				-0.0853
spread					0.1396							0.0638
stage	4	4	4	14	1.3785	-0.0086	-0.0969	-0.0083			0.0090	
spread					0.1905							
survivorship	1	4	-	-	0.5171	-0.0137						0.1382
ACLITELLATE WORMS												
growth	14	15	14	15	-1.5020	0.3268		-0.0135				
spread					0.3135							
stage	14	15	4	25	-8.5967	0.0290	0.2556			-0.0051		0.4029
spread					-4.7103							0.3106
survivorship	14	15	-	-	-0.4902							0.0965
CLITELLATE WORMS												
growth	24	26	24	26	5.9323							-0.2339
spread					0.4275							
stage	24	26	14	26	-1.3557	0.0162	0.0966			-0.0020		
spread					1.7940	0.0646	-0.1710	-0.0042		0.0037		
survivorship	24	26	-	-	-2.3118							0.1241

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Table 31. Multiple regression coefficients for *A. tuberculata* combined incubator and microcosm model.

	Input Range		Output Range		a	Soil Temp	Soil Moisture	Temp²	Moisture²	Temp x Moisture	Initial Size
COCOONS											
development	-	-	-	-	T[a] = 0.5500			Slope= 938.64			
fecundity	-	-	-	-	-15.803	0.0841					0.5995
fertility	-	-	-	-	0.8814						
survivorship	-	-	-	-	0.9968						
IMMATURE WORMS class 1											
growth	1	1	1	2	-7.4285	1.4330		-0.0632			
spread					0.4751						
stage	-	-	-	-							
spread											
survivorship	1	6			0.3167	0.1968		-0.0109			
IMMATURE WORMS classes 2-4											
growth	2	4	1	5	-1.9768	0.0427	0.1553		-0.0032		
spread					0.4005						
stage	-	-	-	-							
spread											
survivorship	2	4			0.9650		-0.0189				0.1065
IMMATURE WORMS classes 5-6											
growth	5	6	4	6	2.3081	0.3667		-0.0146			-0.9297
spread					0.3927						
stage	5	6	5	16	-1.4909	0.0166					0.2748
spread					0.1238						
survivorship	5	6			0.9548						
ACLITELLATE WORMS											
growth	15	17	15	17	1.7030		0.0243				-0.1291
spread					-1.2255						0.0963
stage	15	17	5	27	-2.6167	0.0188					0.1602
spread					0.2432						
survivorship	15	17			-0.3991	0.0126	-0.0273	-0.0042		0.0025	0.0605
CLITELLATE WORMS											
growth	26	28	26	28	1.6522	0.1586	0.3289	-0.0144	-0.0079	0.0077	-0.2429
spread					-0.0997		0.0189				
stage	26	28	16	28	-2.9088	0.0067	0.2214	-0.0072	-0.0059	0.0072	
spread					2.9655						-0.1022
survivorship	26	28			1.5007	-0.025 4	-0.0256	-0.0012		0.0020	

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Appendix B

MODEL-GENERATED MONTHLY POPULATION STRUCTURES

Table 32. Monthly changes in modelled population structure of a cohort of class 1 *D. octaedra*, starting on May 1 (day 1, month 1) of a typical year.

Year	Month	Temperature (°C)	Moisture (%)	Cocoons	Immatures	Aclitellates	Clitellates	Population	Cocoons per clitellate
				0	10000	0	0	10000	---
1	1	10	33	0	4255	0	0	4255	---
1	2	13	30	0	2247	0	0	2247	---
1	3	15	24	0	1296	32	0	1328	---
1	4	16	25	0	773	189	23	985	0.00
1	5	15	25	70	393	239	150	782	0.47
1	6	11	30	144	237	236	178	651	0.81
1	7	8	25	109	129	228	189	546	0.58
1	8	5	25	55	80	201	181	462	0.30
1	9	1	25	22	55	170	158	383	0.14
1	10	0	25	1	34	153	124	311	0.01
1	11	0	25	0	18	138	96	252	0.00
1	12	1	30	0	11	124	75	210	0.00
1	13	3	33	0	13	107	60	180	0.00
2	1	10	33	0	10	96	52	158	0.00
2	2	13	30	53	7	82	53	142	1.00
2	3	15	24	155	3	14	110	127	1.41
2	4	16	25	466	2	1	115	118	4.05
2	5	15	25	412	1	0	107	108	3.85
2	6	11	30	123	0	0	95	95	1.29
2	7	8	25	63	0	0	81	81	0.78
2	8	5	25	24	0	0	67	67	0.36
2	9	1	25	8	0	0	52	52	0.15
2	10	0	25	0	0	0	40	40	0.00
2	11	0	25	0	0	0	31	31	0.00
2	12	1	30	0	0	0	24	24	0.00
2	13	3	33	0	0	0	19	19	0.00

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Table 32 (cont'd).

Year	Month	Temper-ature (°C)	Moisture (%)	Cocoons	Imma-tures	Aclitel-lates	Clitel-lates	Popu-lation	Cocoons per clitellate
3	1	10	33	0	0	0	17	17	0.00
3	2	13	30	17	0	0	15	15	1.13
3	3	15	24	44	0	0	15	15	2.93
3	4	16	25	63	0	0	14	14	4.50
3	5	15	25	50	0	0	13	13	3.85
3	6	11	30	15	0	0	12	12	1.25
3	7	8	25	9	0	0	10	10	0.90
3	8	5	25	3	0	0	8	8	0.38
3	9	1	25	1	0	0	6	6	0.17
3	10	0	25	0	0	0	5	5	0.00
3	11	0	25	0	0	0	4	4	0.00
3	12	1	30	0	0	0	3	3	0.00
3	13	3	33	0	0	0	2	2	0.00
4	1	10	33	0	0	0	1	1	0.00
4	2	13	30	0	0	0	1	1	0.00
4	3	15	24	0	0	0	1	1	0.00
4	4	16	25	0	0	0	1	1	0.00
4	5	15	25	0	0	0	1	1	0.00
4	6	11	30	0	0	0	1	1	0.00
4	7	8	25	0	0	0	1	1	0.00
4	8	5	25	0	0	0	1	1	0.00
4	9	1	25	0	0	0	1	1	0.00
4	10	0	25	0	0	0	1	1	0.00
4	11	0	25	0	0	0	1	1	0.00
4	12	1	30	0	0	0	1	1	0.00
4	13	3	33	0	0	0	1	1	0.00

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Table 33. Monthly changes in modelled population structure of a cohort of class 1 *L. rubellus*, starting on May 1 (day 1, month 1) of a typical year.

Year	Month	Temperature (°C)	Moisture (%)	Cocoons	Immatures	Aclitellates	Clitellates	Population	Cocoons per clitellate
				0	10000	0	0	10000	
1	1	9.5	33	0	5248	0	0	5248	---
1	2	12.5	30	0	3007	0	0	3007	---
1	3	15	24	0	1925	0	0	1925	---
1	4	16	25	0	1311	49	0	1360	---
1	5	15	25	0	920	110	36	1066	0.00
1	6	11	30	48	688	165	71	924	0.68
1	7	8	25	33	615	82	143	840	0.23
1	8	5	25	28	592	44	140	776	0.20
1	9	1	25	12	571	32	116	719	0.10
1	10	0	25	10	521	29	91	641	0.11
1	11	0	25	9	428	25	73	526	0.12
1	12	1	30	3	313	21	60	394	0.05
1	13	3	33	12	213	26	41	280	0.29
2	1	9.5	33	92	127	24	32	183	2.88
2	2	12.5	30	96	80	12	40	132	2.40
2	3	15	24	80	54	4	42	100	1.90
2	4	16	25	104	38	3	37	78	2.81
2	5	15	25	83	27	4	32	63	2.59
2	6	11	30	70	20	6	27	53	2.59
2	7	8	25	25	18	3	26	47	0.96
2	8	5	25	12	17	1	22	40	0.55
2	9	1	25	4	17	1	18	36	0.22
2	10	0	25	2	16	1	14	31	0.14
2	11	0	25	2	13	1	12	26	0.17
2	12	1	30	1	9	1	10	20	0.10
2	13	3	33	3	6	2	7	15	0.43
3	1	9.5	33	17	4	2	5	11	3.40
3	2	12.5	30	16	2	0	5	7	3.20
3	3	15	24	13	1	0	4	5	3.25
3	4	16	25	12	0	0	4	4	3.00
3	5	15	25	11	0	0	4	4	2.75
3	6	11	30	10	0	0	3	3	3.33
3	7	8	25	4	0	0	3	3	1.33
3	8	5	25	2	0	0	3	3	0.67
3	9	1	25	1	0	0	3	3	0.33
3	10	0	25	1	0	0	3	3	0.33
3	11	0	25	1	0	0	2	2	0.50
3	12	1	30	0	0	0	2	2	0.00
3	13	3	33	1	0	0	2	2	0.50

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Table 33 (cont'd).

Year	Month	Temper-ature (°C)	Moisture (%)	Cocoons	Imma-tures	Aclitel-lates	Clitel-lates	Popu-lation	Cocoons per clitellate
4	1	9.5	33	8	0	0	2	2	4.00
4	2	12.5	30	10	0	0	2	2	5.00
4	3	15	24	8	0	0	1	1	8.00
4	4	16	25	0	0	0	1	1	0.00
4	5	15	25	0	0	0	1	1	0.00
4	6	11	30	0	0	0	1	1	0.00
4	7	8	25	0	0	0	1	1	0.00
4	8	5	25	0	0	0	1	1	0.00
4	9	1	25	0	0	0	1	1	0.00
4	10	0	25	0	0	0	1	1	0.00
4	11	0	25	0	0	0	1	1	0.00
4	12	1	30	0	0	0	1	1	0.00
4	13	3	33	0	0	0	1	1	0.00

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Table 34. Monthly changes in modelled population structure of a cohort of class 1 *A. tuberculata*, starting on May 1 (day 1, month 1) of a typical year.

Year	Month	Temperature (°C)	Moisture (%)	Cocoons	Immatures	Aclitellates	Clitellates	Population	Cocoons per clitellate
				0	10000	0	0	10000	
1	1	10	33	0	9108	0	0	9108	---
1	2	13	30	0	8118	0	0	8118	---
1	3	15	24	0	6168	0	0	6168	---
1	4	16	25	0	4630	0	0	4630	---
1	5	15	25	0	3865	1	0	3866	---
1	6	11	30	0	3289	10	0	3299	---
1	7	8	25	0	2869	26	1	2896	0.00
1	8	5	25	0	2565	29	1	2595	0.00
1	9	1	25	0	2194	23	1	2218	0.00
1	10	0	25	0	1890	16	1	1907	0.00
1	11	0	25	0	1680	12	0	1693	0.00
1	12	1	30	0	1474	8	0	1482	0.00
1	13	3	33	0	1301	6	0	1308	0.00
2	1	10	33	0	1176	7	1	1184	0.00
2	2	13	30	2	1044	48	2	1095	0.93
2	3	15	24	3	885	132	10	1027	0.30
2	4	16	25	16	747	178	30	954	0.53
2	5	15	25	45	659	179	56	894	0.80
2	6	11	30	72	600	182	75	857	0.96
2	7	8	25	85	558	178	90	827	0.94
2	8	5	25	85	531	169	92	792	0.93
2	9	1	25	45	508	179	33	720	1.36
2	10	0	25	8	486	149	7	642	1.21
2	11	0	25	0	465	107	5	578	0.00
2	12	1	30	0	444	71	4	519	0.00
2	13	3	33	0	423	53	4	480	0.00
3	1	10	33	2	401	45	11	458	0.18
3	2	13	30	12	366	52	21	439	0.58
3	3	15	24	34	310	75	32	417	1.06
3	4	16	25	56	260	84	44	388	1.26
3	5	15	25	73	230	80	57	366	1.29
3	6	11	30	80	211	78	64	353	1.25
3	7	8	25	79	196	75	71	341	1.12
3	8	5	25	72	187	72	69	328	1.04
3	9	1	25	39	178	91	27	297	1.43
3	10	0	25	7	171	85	4	259	1.95
3	11	0	25	0	164	61	3	229	0.00
3	12	1	30	0	157	41	2	200	0.00
3	13	3	33	0	150	29	2	182	0.00

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Table 34 (cont'd).

Year	Month	Temperature (°C)	Moisture (%)	Cocoons	Immatures	Aclitellates	Clitellates	Population	Cocoons per clitellate
4	1	10	33	1	143	25	6	174	0.17
4	2	13	30	7	130	26	11	167	0.61
4	3	15	24	18	110	31	16	157	1.09
4	4	16	25	30	93	33	22	147	1.35
4	5	15	25	37	82	30	27	139	1.38
4	6	11	30	39	75	29	30	134	1.31
4	7	8	25	38	70	28	32	130	1.17
4	8	5	25	33	66	27	31	124	1.06
4	9	1	25	18	63	36	13	112	1.42
4	10	0	25	4	60	36	1	97	2.75
4	11	0	25	0	58	25	1	84	0.00
4	12	1	30	0	56	17	1	74	0.00
4	13	3	33	0	54	13	1	67	0.00
5	1	10	33	0	51	10	3	64	0.00
5	2	13	30	2	47	11	4	62	0.46
5	3	15	24	7	40	12	6	59	1.08
5	4	16	25	11	34	12	8	54	1.34
5	5	15	25	14	30	11	10	51	1.41
5	6	11	30	14	27	11	11	48	1.24
5	7	8	25	15	25	10	12	48	1.25
5	8	5	25	12	24	10	11	45	1.10
5	9	1	25	6	23	13	4	41	1.40
5	10	0	25	1	22	14	1	36	1.74
5	11	0	25	0	21	10	1	31	0.00
5	12	1	30	0	20	7	0	28	0.00
5	13	3	33	0	19	5	0	24	0.00
6	1	10	33	0	18	4	1	23	0.00
6	2	13	30	2	16	5	2	23	0.97
6	3	15	24	3	14	4	3	21	1.04
6	4	16	25	6	12	4	4	20	1.62
6	5	15	25	5	11	4	4	18	1.35
6	6	11	30	6	9	4	4	17	1.34
6	7	8	25	6	8	4	4	17	1.38
6	8	5	25	4	8	4	4	15	1.01
6	9	1	25	3	7	5	2	13	1.50
6	10	0	25	0	7	4	0	11	0.00
6	11	0	25	0	7	3	0	10	0.00
6	12	1	30	0	7	3	0	9	0.00
6	13	3	33	0	7	1	0	8	0.00

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Table 34 (cont'd).

Year	Month	Temperature (°C)	Moisture (%)	Cocoons	Immatures	Aclitellates	Clitellates	Population	Cocoons per clitellate
7	1	10	33	0	7	1	0	8	0.00
7	2	13	30	0	6	1	0	8	0.00
7	3	15	24	0	5	1	0	7	0.00
7	4	16	25	0	4	2	0	6	0.00
7	5	15	25	0	4	2	0	6	0.00
7	6	11	30	0	3	2	0	5	0.00
7	7	8	25	0	2	2	0	4	0.00
7	8	5	25	0	1	2	0	3	0.00
7	9	1	25	0	1	1	0	2	0.00
7	10	0	25	0	1	0	0	1	0.00
7	11	0	25	0	1	0	0	1	0.00
7	12	1	30	0	1	0	0	1	0.00
7	13	3	33	0	1	0	0	1	0.00

Appendix C

DATA SUMMARIES FOR INCUBATOR AND FIELD MICROCOSM STUDIES

Table 35. *L. rubellus* incubator cocoon development summary for each of five temperatures.

3°C		6°C		9°C		12°C		15°C	
DAY	SCORE	DAY	SCORE	DAY	SCORE	DAY	SCORE	DAY	SCORE
0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
31	0.00	31	0.00	28	0.00	31	0.11	31	0.50
46	0.00	48	0.00	42	0.20	49	1.22	53	2.22
63	0.00	62	0.00	54	0.40	64	1.67	63	2.50
77	0.00	74	0.00	63	0.80	76	2.11	74	2.80
89	0.00	83	0.00	75	1.20	83	2.44	83	3.00
98	0.00	95	0.00	83	1.20	95	2.78	95	3.10
110	0.11	102	0.00	95	2.00	102	2.89	109	3.30
129	0.22	114	0.00	109	2.00	114	3.00	123	3.60
144	0.22	129	0.00	122	2.20	128	3.56	137	3.70
157	0.22	152	0.80	136	2.60	142	3.67	147	3.70
171	0.33	166	1.20	150	2.80	152	3.67	161	3.80
199	0.67	180	1.80	160	3.20	166	3.78	175	3.90
209	1.00	193	2.20	174	3.40	180	3.89	186	4.00
223	1.33	211	2.40	188	3.80	211	4.00		
237	1.67	219	2.80	201	3.80				
250	1.67	232	3.00	219	4.00				
268	2.22	246	3.20						
275	2.33	267	4.00						
289	2.33								
303	2.56								
324	2.67								
338	3.11								
352	3.33								
366	3.44								
380	3.67								
394	3.78								
408	4.00								

Table 36. *D. octaedra* incubator cocoon development summary for each of five temperatures.

3°C		6°C		9°C		12°C		15°C	
DAY	SCORE	DAY	SCORE	DAY	SCORE	DAY	SCORE	DAY	SCORE
0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
31	0.00	31	0.00	29	0.88	29	1.14	31	1.33
48	0.00	48	0.25	42	1.14	42	1.67	51	2.29
62	0.00	62	0.50	54	1.38	52	2.00	63	2.86
74	0.50	74	1.00	63	1.63	66	2.33	74	3.14
89	1.50	89	1.50	75	1.88	76	2.67	88	4.00
98	1.50	98	2.00	84	2.00	90	3.11		
112	2.00	112	2.50	98	2.33	110	4.00		
126	2.00	126	2.75	108	2.67				
139	2.00	135	3.00	122	3.11				
157	3.00	143	3.44	142	4.00				
178	3.00	156	4.00						
192	3.50								
213	4.00								

Table 37. *A. tuberculata* incubator cocoon development summary for each of five temperatures.

3°C		6°C		9°C		12°C		15°C	
DAY	SCORE	DAY	SCORE	DAY	SCORE	DAY	SCORE	DAY	SCORE
0	0.00	0	0.00	0	0.00	0	0.00	0	0.00
28	0.00	28	0.00	14	1.00	14	0.00	15	0.50
46	0.38	42	0.25	26	2.00	26	0.33	31	2.00
63	0.50	54	0.50	35	2.25	35	1.00	53	2.00
77	0.63	63	0.75	47	2.75	47	2.33	63	2.75
96	0.75	82	1.25	54	3.00	54	2.67	74	3.88
110	0.88	109	1.25	66	3.25	66	3.00	83	4.00
124	1.13	122	1.25	81	3.50	81	3.33		
140	1.25	136	1.25	94	3.75	94	3.67		
154	1.75	150	1.25	108	4.00	108	4.00		
164	2.25	discontinued							
178	2.38								
192	3.13								
205	3.25								
223	3.75								
244	3.88								
258	3.88								
279	4.00								

Table 38. *D. octaedra* incubator worm summary by developmental stage.

TEMP (°C)	MOIST (%)	BEGINNING STAGE	N	ENDING STAGES IMM	ACL	CLI	DIED
3	22.5	IMM	54	33	3	0	18
		ACL	14	0	12	1	1
		CLI	27	0	0	27	0
5	17.2	IMM	54	28	1	0	25
		ACL	25	0	21	1	3
		CLI	30	0	2	21	7
5	27.8	IMM	52	39	2	0	11
		ACL	22	0	19	1	2
		CLI	28	0	0	27	1
10	15	IMM	42	27	3	0	12
		ACL	46	1	31	5	9
		CLI	4	0	0	3	1
10	22.5	IMM	39	20	4	0	15
		ACL	45	0	37	6	2
		CLI	24	0	0	21	3
10	30	IMM	32	16	9	0	7
		ACL	39	0	28	9	2
		CLI	10	0	0	8	2
15	17.2	IMM	29	12	2	0	15
		ACL	3	0	0	3	0
		CLI	22	0	0	20	2
15	27.8	IMM	28	20	2	0	6
		ACL	6	0	2	2	2
		CLI	24	0	0	20	4
17	22.5	IMM	47	25	3	0	19
		ACL	8	0	2	6	0
		CLI	42	0	0	34	8

IMM = immature, ACL = aclitellate, CLI = clitellate.
Ending stages are the fates of each of the N worms at the end of a 28-day period.

Table 39. *L. rubellus* incubator worm summary by developmental stage.

TEMP (°C)	MOIST (%)	BEGINNING STAGE	N	ENDING STAGES IMM	ACL	CLI	DIED
3	22.5	IMM	69	63	0	0	6
		ACL	9	2	3	4	0
		CLI	13	0	0	10	3
5	17.2	IMM	66	60	0	0	6
		ACL	5	0	5	0	0
		CLI	22	0	2	20	0
5	27.8	IMM	62	53	0	0	9
		ACL	4	0	4	0	0
		CLI	23	0	2	16	5
10	15	IMM	64	53	3	0	8
		ACL	20	6	12	1	1
		CLI	7	0	3	2	2
10	22.5	IMM	77	69	3	0	5
		ACL	5	0	3	2	0
		CLI	14	0	0	14	0
10	30	IMM	72	65	0	0	7
		ACL	17	0	15	2	0
		CLI	7	0	4	3	0
15	17.2	IMM	71	63	0	0	8
		ACL	12	0	9	2	1
		CLI	10	0	0	10	0
15	27.8	IMM	95	82	1	0	12
		ACL	10	0	8	2	0
		CLI	17	0	0	10	7
17	22.5	IMM	28	12	0	0	16
		ACL	4	0	1	2	1
		CLI	5	0	0	0	5

IMM = immature, ACL = aclitellate, CLI = clitellate.
Ending stages are the fates of each of the N worms at the end of a 28-day period.

Table 40. *A. tuberculata* incubator worm summary by developmental stage.

TEMP (°C)	MOIST (%)	BEGINNING STAGE	N	ENDING STAGES IMM	ACL	CLI	DIED
3	22.5	IMM	57	48	0	0	9
		ACL	10	0	10	0	0
		CLI	20	0	7	13	0
5	17.2	IMM	72	71	0	0	1
		ACL	4	0	4	0	0
		CLI	20	0	13	7	0
5	27.8	IMM	68	66	2	0	0
		ACL	12	0	12	0	0
		CLI	17	0	13	4	0
10	15	IMM	61	55	6	0	0
		ACL	29	5	24	0	0
		CLI	6	0	4	2	0
10	22.5	IMM	97	89	7	0	1
		ACL	80	6	69	3	2
		CLI	15	0	1	14	0
10	30	IMM	61	50	9	0	2
		ACL	23	0	19	2	2
		CLI	10	0	2	8	0
15	17.2	IMM	63	59	0	0	4
		ACL	36	3	28	1	4
		CLI	17	0	5	12	0
15	27.8	IMM	53	48	0	0	5
		ACL	12	0	5	7	0
		CLI	22	0	2	20	0
17	22.5	IMM	103	65	2	0	36
		ACL	43	0	17	11	15
		CLI	21	0	1	10	10

IMM = immature, ACL = aclitellate, CLI = clitellate.
Ending stages are the fates of each of the N worms at the end of a 28-day period.

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Tables 41 to 43: N DAYS = days elapsed since the previous sampling date; temperature and moisture are means over this period. Each cocoon series begins with a boldface capital letter and the number of cocoons in parentheses, and ends with a horizontal line. The numbers are mean developmental codes.

Table 41. *D. octaedra* field microcosm summary by date.

DATE	N DAYS	TEMP (°C)	MOIST (%)	BEGINNING STAGE	N	ENDING STAGES IMM	ACL	CLI	DIED	COCOON SERIES
1	183	1.5	---	IMM	161	41	0	0	120	
				ACL	11	3	3	1	4	
				CLI	4	0	1	1	2	
2	27	11.1	19.9	IMM	44	12	5	0	27	
				ACL	4	0	2	1	1	
				CLI	2	0	0	0	2	
3	28	11.9	25.4	IMM	53	32	9	0	12	
				ACL	20	0	15	1	4	
				CLI	1	0	0	0	1	**A(90)**
4	28	13.3	22.8	IMM	32	17	0	0	15	0
				ACL	24	0	9	13	2	
				CLI	3	0	0	3	0	**B(97)**
5	28	13.8	28.9	IMM	17	6	4	0	7	1.55 0
				ACL	9	0	2	6	1	
				CLI	14	0	1	11	2	**C(101)**
6	28	12.4	25.4	IMM	8	4	1	0	3	2.12 0.97 0
				ACL	9	0	2	6	1	
				CLI	19	0	0	16	3	**D(56)**
7	27	8.6	27.6	IMM	29	24	1	0	4	2.5 1.46 0.88 0
				ACL	5	0	1	3	1	
				CLI	26	0	3	10	13	**E(13)**
8	210	2.0	26.2	IMM	39	11	12	1	15	3.97 2.79 2.31 0.78 0
				ACL	5	0	1	3	1	
				CLI	14	0	0	10	4	
9	27	10.0	25.5	IMM	36	18	1	0	17	3.99 3.5 3.34 2.36 0.63
				ACL	11	0	5	4	2	
				CLI	14	0	0	10	4	**F(60)**
10	29	14.1	26.2	IMM	24	11	5	0	8	4 3.78 4 4 1.62 0
				ACL	8	0	2	4	2	
				CLI	14	0	0	11	3	**G(82)**
11	27	15.2	27.2	IMM	27	8	4	0	15	0 3.97 4 1.48
				ACL	8	0	5	3	0	
				CLI	15	0	0	13	2	**H(125)**
12	29	16.2	27.4	IMM	33	20	3	0	10	1.86 4 0 2.13
				ACL	9	0	2	6	1	
				CLI	15	0	0	13	2	**I(82)**
13	27	9.7	26.9	IMM	37	15	2	0	20	1.95 0.97 0 2.23
				ACL	5	0	0	4	1	
				CLI	20	0	0	19	1	
14	214	2.6	---	COC						3.5 2.96 1.99 3.67
15	29	9.8	---	COC						4 4 3.62 4
16	30	12.1	---	COC						3.99
17	28	15.1	---	COC						4

Table 42. *L. rubellus* field microcosm summary by date.

DATE	N DAYS	TEMP (°C)	MOIST (%)	BEGINNING STAGE	N	ENDING IMM	ACL	CLI	DIED	COCOON SERIES
1	183	1.51	---	IMM	161	0	41	0	120	
				ACL	11	3	3	1	4	
				CLI	4	0	1	1	2	
2	27	11.07	19.88	IMM	44	12	5	0	27	
				ACL	4	0	2	1	1	
				CLI	2	0	0	0	2	A(37)
3	28	11.9	25.45	IMM	53	32	9	0	12	0
				ACL	20	0	15	1	4	
				CLI	1	0	0	0	1	B(71)
4	28	13.25	22.84	IMM	32	17	0	0	15	0.91 0
				ACL	24	0	9	13	2	
				CLI	2	0	0	0	2	C(46)
5	28	13.84	28.91	IMM	12	1	4	0	7	2.63 0.39 0
				ACL	9	0	2	6	1	
				CLI	14	0	1	11	2	D(6)
6	28	12.4	25.45	IMM	8	4	1	0	3	3.03 1.49 0 0
				ACL	9	0	2	6	1	
				CLI	19	0	0	16	3	
7	27	8.57	27.55	IMM	29	24	1	0	4	4 1.94 0.13 0
				ACL	6	0	1	3	2	
				CLI	26	0	3	10	13	E(9)
8	210	2	26.22	IMM	29	11	2	1	15	0 2.8 1.92 0.3
				ACL	5	0	1	3	1	
				CLI	13	0	2	7	4	F(7)
9	27	9.97	25.51	IMM	36	18	1	0	17	0.63 2.93 3.33 2.7 0
				ACL	11	0	5	4	2	
				CLI	14	0	0	10	4	G(12)
10	29	14.11	26.16	IMM	24	11	5	0	8	1.45 3.24 3.91 3.37 0.4 0
				ACL	8	0	2	4	2	
				CLI	14	0	0	11	3	
11	27	15.23	27.18	IMM	27	8	4	0	15	3.21 3.81 4 4 2.73 0.77
				ACL	8	0	5	3	0	
				CLI	15	0	0	13	2	H(12)
12	29	16.24	27.39	IMM	33	20	3	0	10	3.73 3.86 0 2.94 2.62
				ACL	9	0	2	6	1	
				CLI	15	0	0	13	2	
13	27	9.69	26.91	IMM	37	15	2	0	20	3.89 4 1.3 4 3.5
				ACL	5	0	0	4	1	
				CLI	20	0	0	19	1	
14	214	2.57	---	COC						4 1.73 3.92
15	29	9.75	---	COC						3.41 4
16	30	12.1	---	COC						3.83
17	28	15.11	---	COC						4

Table 43. *A. tuberculata* field microcosm summary by date

DATE	N DAYS	TEMP (°C)	MOIST (%)	BEGINNING STAGE	N	ENDING IMM	ACL	CLI	STAGES DIED	COCOON SERIES
1	183	1.5	---	IMM	135	91	5	0	39	
				ACL	31	5	20	0	6	
				CLI	0	0	0	0	0	
2	27	11.1	19.92	IMM	96	76	6	0	14	
				ACL	25	2	23	0	0	
				CLI	0	0	0	0	0	
3	28	11.9	24.50	IMM	116	76	4	0	36	
				ACL	46	2	34	8	2	
				CLI	3	0	0	3	0	A(35)
4	28	13.3	22.47	IMM	79	44	4	0	31	0
				ACL	38	0	14	20	4	
				CLI	11	0	5	6	0	B(19)
5	28	13.8	29.43	IMM	45	26	0	0	19	1.72 0
				ACL	22	0	1	15	6	
				CLI	26	0	1	25	0	C(29)
6	28	12.4	24.65	IMM	47	35	0	0	12	3.31 1.47 0
				ACL	2	0	1	1	0	
				CLI	40	0	5	23	12	D(12)
7	27	8.6	28.86	IMM	59	35	3	0	21	3.9 2.06 0.6 0
				ACL	29	1	11	12	5	
				CLI	24	0	3	13	8	E(6)
8	210	2.0	25.52	IMM	36	24	5	0	7	4 3.44 1.77 0.79 0
				ACL	17	1	11	5	0	
				CLI	15	0	2	13	0	F(22)
9	27	10.0	24.62	IMM	42	27	3	0	12	0 3.95 3.15 2.63 0.22
				ACL	20	2	9	5	4	
				CLI	0	0	0	0	0	G(34)
10	29	14.1	26.09	IMM	51	25	5	0	21	1.15 4 4 4 3.12 0
				ACL	18	0	7	7	4	
				CLI	22	0	0	17	5	H(17)
11	27	15.2	27.24	IMM	57	25	3	0	29	3.73 0 4 2.46
				ACL	15	0	6	4	5	
				CLI	28	0	1	23	4	I(14)
12	29	16.2	27.30	IMM	47	17	3	0	27	4 1.05 0 4
				ACL	10	0	3	5	2	
				CLI	27	0	4	23	0	
13	27	9.7	26.90	IMM	63	34	6	0	23	3.08 0.21
				ACL	10	0	6	4	0	
				CLI	28	0	3	23	2	
14	214	2.6	---	COC	27	27	0	0	0	3.48 3.17
15	29	9.8	---	COC	6	6	0	0	0	4 3.4
16	30	12.1	---	COC	12	12	0	0	0	4

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