

Earthworm Numbers, Biomass and Respiratory Metabolism in a Beech Woodland—Wytham Woods, Oxford

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Summary. The mean annual population density of earthworms was found to be 164.6 m^{-2} during a period of detailed study between October 1971 and September 1972. In a year of less detailed study between November 1972 and October 1973 the population density was 117.5 m^{-2} (139.8 m^{-2} when the type of extraction method was allowed for). Mean biomass densities in the two years of investigation were $41.0 \text{ g preserved wet wt m}^{-2}$ (1971–1972) and 38.6 (possibly 39.2) $\text{g preserved wet wt m}^{-2}$ (1972–1973).

Comparison of the Brogden's Belt population and biomass densities with those reported from other woodlands indicates that soil type is more important than leaf litter type in determining the numerical abundance of earthworms. Population densities are lower in beechwoods on mor soils, mor soils also support significantly fewer species. As with numbers, mean biomass density in beechwoods on mor soils was significantly lower than that occurring in beechwoods on mull soils; the latter, in turn, being lower than those found in mixed deciduous woods on mull soils. Unlike population density biomass density is influenced by both soil and litter type, this is discussed by reference to mean body weights and food quality as reflected by tannin, nitrogen and carbohydrate content.

The annual respiratory metabolism of the Brogden's Belt earthworms was calculated to be between 10.7 and $13.4 \text{ l O}_2 \text{ m}^{-2} \text{ a}^{-1}$, which is equivalent to between 4.1 and 5.1% of the total soil metabolism. A production/biomass ratio of 0.49 – 0.58 was estimated, as was a net population efficiency of 22% .

Introduction

Beech (*Fagus sylvatica* L.) woodlands are widespread in Europe and are established on a variety of soil types (Baltzer, 1956; Bornebusch, 1930; Tansley, 1939; Volz, 1962). Both leaf litter and soil type have been described as major factors governing earthworms species associations, abundance and biomass (Phillipson et al., 1976; Satchell, 1967; Zajonc, 1971). In particular Reynolds (1972)

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and Zajonc (1971) have suggested that beech woodlands are not especially rich in earthworms (Lumbricidae) and relate this to litter type.

Among the published accounts of earthworm densities and biomasses in *F. sylvatica* woodland the majority depend on data collected on one or two sampling occasions (Baltzer, 1956; Füller, 1953; Lindquist, 1938; Rabeler, 1960; Rondé, 1953; Sergienko, 1969; Volz, 1962; Zajonc, 1967). Notable exceptions are the studies of Bornebusch (1930) in Denmark, Drift (1951) in the Netherlands and Nördstrom and Rundgren (1973, 1974) in Sweden.

The present work forms part of a research programme designed to investigate the ecosystem dynamics of an English *Fagus sylvatica* woodland known as Brogden's Belt, it reports on earthworm numbers, biomass and respiratory metabolism. The contribution made by Lumbricidae to total soil respiration in Brogden's Belt is evaluated and their population density and biomass are compared with results from other beech woodlands.

The Site

A description of Brogden's Belt (Nat. grid ref. SU 464077), which forms part of Wytham Woods, Oxford, is given in Phillipson et al. (1976). An account of litter fall, litter decomposition and the evolution of carbon dioxide is given in Phillipson et al. (1975).

In brief, the study site was established as a series of 10 × 10 m grid squares and covered an area of 5130 m². The rendzina type soil is shallow (6–42 cm in depth), overlies broken Jurassic limestone ('Coral rag') of the Upper Corallian strata (Arkell, 1945; Elton, 1966) and, with a single exception (pH 6.3) has a range of pH's from 7.3 to 8.0.

Methods

Sampling and Extraction. From October 1971 to September 1972 earthworms were sampled at intervals of one month and between November 1972 and October 1973 on four occasions only.

On each sampling occasion twenty two sample units, selected on a stratified random basis, were taken. The relevant material from each sample unit comprised worms sorted by hand from a soil core (obtained by means of a square metal corer, 25 cm on the side, which was forced rapidly into the substrate with blows from a sledge hammer) and worms extracted from the 25 × 25 cm sample hole by the application of 4% formalin. The formalin solution was applied via a watering can with sprinkler at 10 min intervals over a period of 30 min; 9 l of solution were used for each extraction.

In addition to the 352 sample units obtained in the above manner different types of sample were taken in the 1971–1972 period. Each month during this time 32 circular sample units (0.0189 m²) of litter were taken in a stratified random manner. These were processed in a K.L.G. infra-red extractor (Kempson et al., 1963) over a period of 10 days.

The extracted worms were preserved in 4% formalin for subsequent examination.

Number and Biomass Determination. All individuals were identified to species and counted. The identification of sample adults and juveniles was kindly checked by R.W. Sims of the British Museum (Natural History). In the few instances where juveniles could not be referred to a single species (e.g. juveniles of *Allolobophora caliginosa* and *A. longa*) they were allocated in the same ratio as the known proportions of the species of the genus found on that particular sampling occasion. The material referred to below (and in Phillipson et al., 1976) as *Dendrobaena rubida*

consists of *D. rubida tenuis* and *D. subrubicunda* in the approximate ratio 5:2 (R.W. Sims, pers. comm.).

With regard to biomass determination Satchell (1971) pointed out that worms preserved in formalin can lose up to 25% of their fresh weight over a period of a few months, and that this factor must be taken into account when considering biomass estimates. Further, Bouché (1975) has indicated the advantages of employing gut free, dry weight estimates of earthworm biomass. Although this last method is an ideal one most earlier calculations of earthworm biomass have been based on wet weights and so the same procedure was followed in the present work.

Each preserved individual was weighed, after light blotting, during 1973. Tests on worms of different sizes demonstrated that desiccation during weighing over a period of 2 min never led to a weight loss exceeding 2% of the initial weight. In the knowledge of these results it was not considered necessary to adopt a standard weighing procedure.

Approximately 20% of all worms recovered in 1971–72 were fragmented during collection and hand sorting, and within each sample about 25% of these could be matched up with certainty as complete individuals. In reporting densities in this paper, residual unmatched fragments have been regarded as representing whole worms, while the biomass reported related simply to the material actually recovered.

In spite of the use of preserved wet weights in the results section of this work the desirability of being able to express the obtained biomass data in a variety of ways is recognised. Acknowledgement of this is presented in the appendix to this paper where seasonal conversion factors (total dry weight: total preserved wet weight; dry weight of gut contents: total dry weight; dry weight (excluding gut contents): total preserved wet weight) and energy equivalents for the species studied are given.

Ancillary Measurements. From April 1969 to June 1971 field temperatures were measured at seven stations on the study area. At six of these a sucrose inversion technique (Berthet, 1960; Lee, 1969) was employed to calculate fortnightly integrated temperatures and at the seventh a Grant continuous recorder was installed. A monthly mean temperature profile was determined at each station from measurements at six vertical heights (+100 cm, +20 cm, air-litter interface, litter-soil interface, -5 cm and -20 cm). Subsequent analysis showed no significant differences between the seven stations and thereafter (July 1971 to April 1973) results were obtained only from the Grant continuous recorder.

Rainfall data were provided by the Geography Department, Oxford University.

Respiratory Metabolism. Monthly and annual respiration values for the earthworm biomass were calculated using the weight specific respiratory rates for individual species reported by Barley and Jennings (1959), Phillipson and Bolton (1976), and Satchell (1967). The weight specific values were converted from the temperature of measurement to the recorded mean monthly soil temperatures by means of Krogh's (1914) curve. They were then multiplied by the appropriate monthly biomass.

Results

Numbers

Phillipson et al. (1976) reported that of the ten species of earthworm known to occur in Brogden's Belt three (*Dendrobaena mammalis*, *Lumbricus castaneus*, and *D. rubida*) are primarily litter dwellers while two (*L. terrestris* and *A. longa*) are deep burrowers which come to the surface at night to draw down litter. Four of the remaining five species (*A. caliginosa*, *A. rosea*, *A. muldali*, and *Octolasion cyaneum*) live constantly in the mineral-organic substrate. The last of the ten species present (*A. chlorotica*) cannot be properly assigned to any of the above categories. Clearly, differential vertical distribution of the type described can, depending upon the extraction method employed, give rise to differing estimates of population density. This point is illustrated in Figures 1 a–f where estimates of single species population densities derived via two

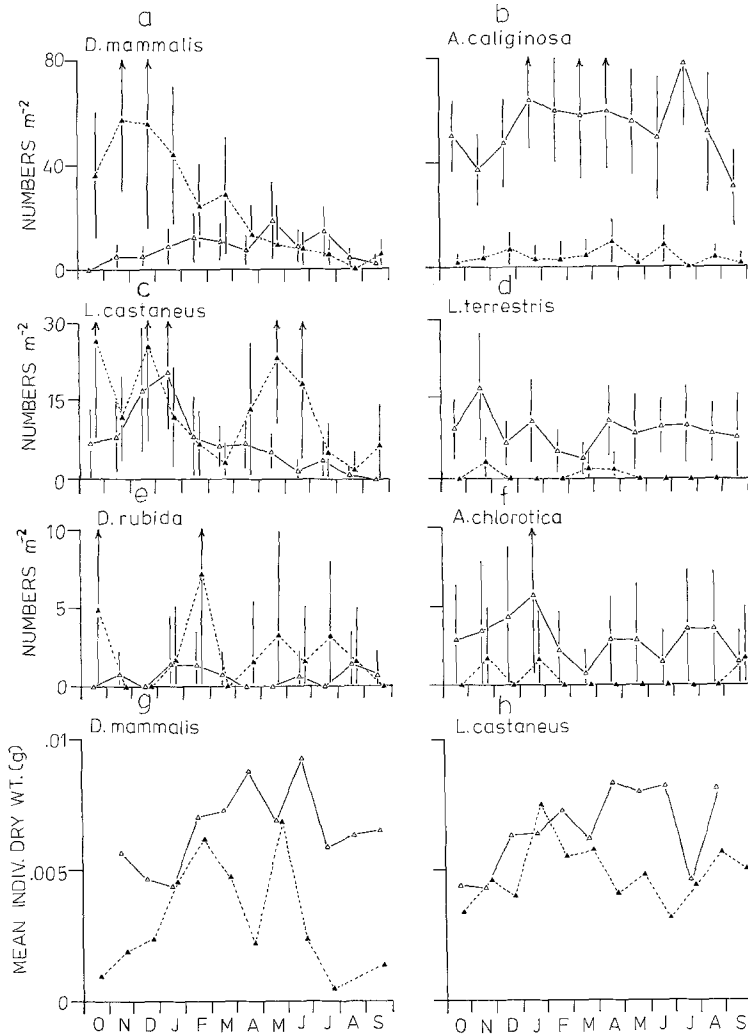


Fig. 1 a-h. Population densities and mean individual dry weights of selected species of earthworms extracted during 1971-1972 by the hand sorting/formalin method (—) and the K.L.G. infra-red process (---). Population densities (mean and 95% confidence limits are shown in a-f and mean individual dry weights in g and h

extraction methods are shown. The efficiency of the K.L.G. infra-red apparatus in extracting litter-dwelling species can be seen to be greater than that of the hand-sorting/formalin method. The low numbers of non-litter dwelling species obtained in the K.L.G. apparatus is not surprising for the soil horizons proper were not subjected to this form of extraction. It does demonstrate however that these species only occurred in small numbers in the litter, in fact *A. longa*, *A. rosea*, *A. muldali* and *O. cyaneum* never appeared in the infra-red extractions.

Figure 1g and h shows that the mean individual dry weights of the two major litter dwelling species, when extracted by the K.L.G. apparatus, were, with

one exception, always lower than those of individuals of the same species obtained by the hand sorting/formalin method. This is a clear indication that the smallest individuals of *D. mammalis* and *L. castaneus* were overlooked during hand sorting, the third litter dwelling form (*D. rubida*) was also subject to the same error.

Because of the above noted discrepancies in extraction efficiency it was (for the purpose of calculating population densities) considered appropriate to employ the highest density estimates obtained for the litter-dwelling species irrespective of the mode of extraction. Table 1 shows these monthly population densities and Figure 2 illustrates the numerical species composition of the total earthworm fauna in the period October 1971 to September 1972. Although the number of sampling occasions in the second period (1972–1973) was limited to four it is suggested that the population densities were not significantly different over the two years of study. In 1971–1972 the mean population density was 164.55 m^{-2} and in 1972–1973 it was 117.45 m^{-2} . The apparent discrepancy between the two years can be accounted for by the modes of extraction; in 1972–1973 the hand sorting/formalin methods were not supplemented by K.L.G. litter extractions. In an earlier paper (Phillipson et al., 1976) the 1971–1972 density was reported on the basis of hand sorting/formalin extraction only and amounted to 138.2 m^{-2} . It is thus possible that population density in 1972–1973 was 1.19 ($164.55/138.20$) times higher than the recorded 117.45 m^{-2} , that is 139.84 m^{-2} .

Biomass

Mean monthly biomass estimates for each species were calculated by summation of the formalin preserved weights of every individual. Table 2 shows the monthly population biomass estimates based on formalin preserved wet weights and Figure 3 illustrates the biomass composition of the total earthworm fauna according to species during the period October 1971 to September 1972. Mean biomasses in the 2 years of study were 41.02 g m^{-2} (1971–1972) and 38.63 g m^{-2} (1972–1973) and these values are in closer accord than the density figures were. This is not surprising when one recognises that the supplementary K.L.G. extraction in 1971–1972 made available more small individuals than did the hand sorting and formalin extraction. The latter extraction methods gave rise to 40.44 g m^{-2} in 1971–1972 whereas inclusion of K.L.G. extracted specimens raised this value to 41.02 g m^{-2} ; it is thus probable that the mean biomass in 1972–1973 was 1.01 ($41.02/40.44$) times greater than the recorded 38.63 g m^{-2} , that is 39.18 g m^{-2} . In addition, the biomass of the unrecovered fragments of worms can be estimated fairly crudely from segment counts of the fragments in relation to mean segment number for each species as an additional 6.09%.

Respiratory Metabolism

Respiration rates of different earthworm species have been reported on a number of occasions (Barley and Jennings, 1959; Byzova, 1965; Johnson, 1942; Phillipson and Bolton, 1976; Pomerat and Zarrow, 1936; Raffy, 1930; Ralph, 1957;

Table 1. Earthworm population densities in numbers m^{-2} (mean \pm 95% confidence limits). The values marked with an asterisk were obtained by the K.L.G. infra-red extraction method, all others by hand sorting/formalin extraction. "Confidence limits" for 1971-72 totals are derived conservatively by adding 95% limits for totals by each sampling method

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.
<i>D. mammalis</i>	36.44* \pm 23.99	56.31* \pm 27.85	54.66* \pm 39.86	43.06* \pm 26.33	24.00* \pm 15.55	28.68* \pm 21.36	12.44* \pm 11.63	18.18 \pm 14.90	8.00 \pm 6.10	13.82 \pm 9.86	3.64 \pm 3.75	4.97* \pm 5.66
<i>L. castaneus</i>	26.50* \pm 18.79	11.59* \pm 8.02	25.50* \pm 18.45	20.36 \pm 10.54	8.00 \pm 7.51	3.64 \pm 3.75	13.25* \pm 12.84	23.19* \pm 12.78	18.22* \pm 14.24	4.97* \pm 5.66	1.66* \pm 3.38	6.47* \pm 7.79
<i>D. rubida</i>	4.97* \pm 10.13	0.73 \pm 1.51	0.00 \pm 3.38	1.66* \pm 3.38	7.28* \pm 11.85	0.73 \pm 1.51	1.66* \pm 3.38	3.31* \pm 6.75	1.66* \pm 3.38	3.31* \pm 4.70	1.66* \pm 3.38	0.73 \pm 1.51
<i>L. terrestris</i>	9.45 \pm 5.65	17.45 \pm 10.25	6.55 \pm 4.19	10.91 \pm 7.71	5.09 \pm 4.03	3.64 \pm 3.04	10.91 \pm 6.71	8.73 \pm 7.17	9.45 \pm 5.21	10.18 \pm 7.44	8.73 \pm 5.68	8.00 \pm 8.12
<i>A. longa</i>	5.82 \pm 5.60	8.00 \pm 5.69	3.64 \pm 3.75	5.09 \pm 3.38	7.27 \pm 4.76	1.45 \pm 2.09	0.00	5.09 \pm 3.38	2.91 \pm 2.80	0.73 \pm 1.51	0.73 \pm 1.51	2.18 \pm 3.32
<i>A. caliginosa</i>	50.18 \pm 13.73	37.09 \pm 13.57	47.27 \pm 16.74	64.00 \pm 18.71	59.64 \pm 20.56	57.45 \pm 24.15	58.91 \pm 21.94	55.27 \pm 20.51	49.45 \pm 23.68	79.27 \pm 25.49	51.64 \pm 23.06	30.55 \pm 14.67
<i>A. rosea</i>	38.55 \pm 22.82	32.00 \pm 20.19	33.45 \pm 22.53	42.18 \pm 22.50	22.55 \pm 10.65	30.55 \pm 21.67	48.00 \pm 23.17	35.64 \pm 22.43	38.55 \pm 21.53	37.82 \pm 26.14	37.82 \pm 17.32	15.27 \pm 13.40
<i>A. muldali</i>	10.18 \pm 12.68	6.55 \pm 4.19	5.82 \pm 6.01	5.82 \pm 5.16	9.45 \pm 13.79	13.82 \pm 10.34	22.55 \pm 25.69	26.91 \pm 17.30	18.91 \pm 17.87	9.45 \pm 12.32	10.91 \pm 8.01	8.00 \pm 7.51
<i>O. cyaneum</i>	5.09 \pm 3.38	10.18 \pm 7.44	2.18 \pm 2.49	1.45 \pm 2.09	2.91 \pm 3.56	4.36 \pm 3.23	8.73 \pm 5.68	16.73 \pm 9.91	5.82 \pm 5.16	13.09 \pm 10.19	12.36 \pm 12.18	7.27 \pm 5.24
<i>A. chlorotica</i>	2.91 \pm 3.56	3.64 \pm 4.34	4.36 \pm 4.48	5.82 \pm 5.16	2.18 \pm 2.49	0.73 \pm 1.51	2.91 \pm 2.80	2.91 \pm 3.56	1.45 \pm 2.09	3.64 \pm 3.75	3.64 \pm 3.75	1.45 \pm 2.09
Total 1971-72	190.09 \pm 74.88	183.54 \pm 66.58	183.43 \pm 79.60	200.35 \pm 71.93	148.37 \pm 62.88	145.06 \pm 61.58	179.36 \pm 67.30	195.96 \pm 61.23	154.42 \pm 67.28	176.28 \pm 64.47	132.79 \pm 54.00	84.89 \pm 42.83
Total 1972-73	105.45 \pm 43.83 (1973)	93.09 \pm 38.41 (1972)				151.27 \pm 40.24 (1973)				120.00 \pm 45.92 (1973)		

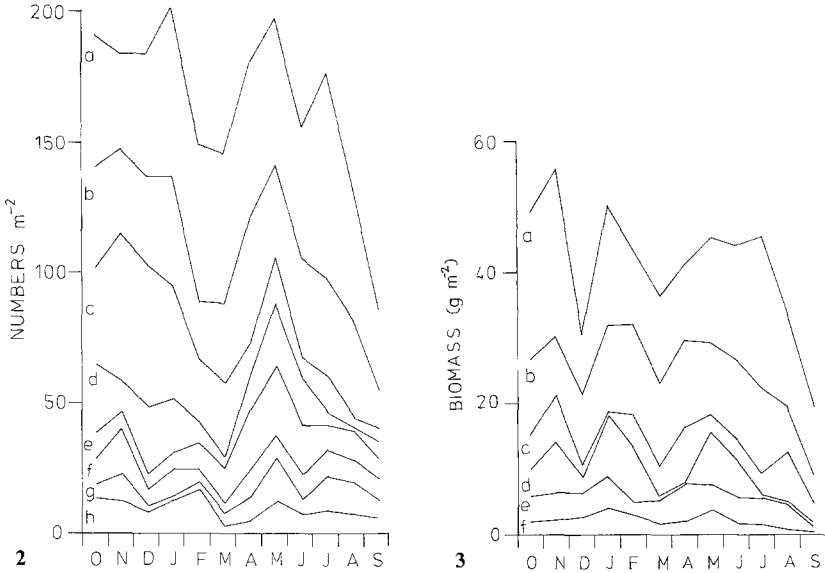


Fig. 2 a-h. Species contributions by number to the total earthworm fauna between Oct. 1971 and Sep. 1972. **a** *A. caliginosa*; **b** *A. rosea*; **c** *D. mammalis*; **d** *L. castaneus*; **e** *A. muldali*; **f** *L. terrestris*; **g** *O. cyaneum*; **h** *A. longa* + *A. chlorotica* + *D. rubida*

Fig. 3 a-f. Species contributions by biomass to the total earthworm fauna between Oct. 1971 and Sep. 1972. **a** *L. terrestris*; **b** *A. caliginosa*; **c** *O. cyaneum*; **d** *A. longa*; **e** *A. rosea*; **f** *L. castaneus* + *D. mammalis* + *A. chlorotica* + *A. muldali* + *D. rubida*

Satchell, 1967). In some instances only adult respiration rates were evaluated (Byzova, 1965), in others both juveniles and adults were considered (Phillipson and Bolton, 1976).

To calculate the respiratory metabolism of the earthworms in the present study a single weight specific rate was chosen for each species. These values were used in conjunction with the biomass estimates to calculate monthly respiratory metabolism per unit area. Table 3 lists the weight specific rates used in these calculations and indicates the source from which the original data were taken. Note that the weight specific rates have been corrected by means of Krogh's (1914) curve to accord with the mean monthly field temperatures.

Because measurements of field temperatures ceased in April 1973 it was not possible to calculate respiratory metabolism for the period November 1972 to October 1973. However, in view of the similarity in earthworm biomasses between the two separate years and the not dissimilar climatic conditions in the two periods of study (see Table 4) it is suggested that respiratory metabolism was very much the same in 1971-1972 and 1972-1973.

Table 5 shows the mean monthly respiration values per square metre for each of the species studied in 1971-1972 and indicates that the annual respiration of the total earthworm fauna was equivalent to 10.748 l O₂ m⁻². It should be recalled that this estimate is based on weight specific rate per gramme live weight and biomass in grammes preserved weight, it is therefore a minimum estimate and could be 25% higher, i.e. 13.435 l O₂ m⁻² a⁻¹.

Figure 4 shows the annual course of respiratory metabolism and the contribu-

Table 2. Earthworm biomasses in g preserved wet wt m⁻² (mean \pm 95% confidence limits). See Table 1 for significance of asterisks and confidence limits applied to 1971-72 totals

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.
<i>D. mammalis</i>	0.21* \pm 0.14	0.68* \pm 0.39	0.83* \pm 0.59	1.28* \pm 0.89	1.00* \pm 0.74	0.90* \pm 0.67	0.38 \pm 0.36	0.79 \pm 0.54	0.48 \pm 0.35	0.49 \pm 0.36	0.10 \pm 0.11	0.03 \pm 0.07
<i>L. castaneus</i>	1.04* \pm 0.90	0.67* \pm 0.71	1.37* \pm 0.97	1.64 \pm 0.91	0.75 \pm 0.79	0.31 \pm 0.31	0.75* \pm 0.84	1.61* \pm 1.26	0.65* \pm 0.72	0.29* \pm 0.43	0.11* \pm 0.23	0.04* \pm 0.05
<i>D. rubida</i>	0.10* \pm 0.21	0.02 \pm 0.05	0.00	0.13* \pm 0.26	0.50* \pm 0.84	0.04 \pm 0.07	0.10* \pm 0.20	0.18* \pm 0.38	0.08* \pm 0.16	0.14* \pm 0.21	0.05* \pm 0.09	0.03 \pm 0.06
<i>L. terrestris</i>	22.37 \pm 19.65	25.06 \pm 16.24	9.22 \pm 8.29	18.24 \pm 18.66	11.19 \pm 14.82	13.53 \pm 13.45	11.84 \pm 10.83	15.91 \pm 18.86	17.20 \pm 16.25	23.04 \pm 25.02	13.53 \pm 12.50	10.32 \pm 14.77
<i>A. longa</i>	4.11 \pm 4.35	7.84 \pm 9.00	2.54 \pm 4.00	9.52 \pm 8.21	8.39 \pm 6.70	0.41 \pm 0.62	0.00	7.75 \pm 7.15	5.64 \pm 6.39	0.58 \pm 1.21	0.34 \pm 0.71	0.59 \pm 0.85
<i>A. caliginosa</i>	11.54 \pm 3.83	9.62 \pm 3.67	10.66 \pm 4.83	13.20 \pm 4.12	13.67 \pm 5.43	12.40 \pm 5.04	13.13 \pm 6.11	11.10 \pm 4.56	12.05 \pm 4.16	12.86 \pm 4.33	7.04 \pm 3.89	4.26 \pm 2.79
<i>A. rosea</i>	3.96 \pm 2.40	4.15 \pm 2.92	3.56 \pm 2.86	4.98 \pm 2.94	2.08 \pm 1.11	3.61 \pm 2.78	5.73 \pm 3.01	3.85 \pm 2.74	4.11 \pm 2.17	4.15 \pm 3.17	3.83 \pm 1.90	0.93 \pm 0.93
<i>A. muldali</i>	0.12 \pm 0.14	0.09 \pm 0.08	0.01 \pm 0.08	0.10 \pm 0.09	0.16 \pm 0.21	0.27 \pm 0.20	0.45 \pm 0.45	0.48 \pm 0.34	0.19 \pm 0.17	0.10 \pm 0.12	0.11 \pm 0.09	0.05 \pm 0.04
<i>O. cyaneum</i>	5.22 \pm 5.65	7.05 \pm 6.65	1.77 \pm 3.53	0.16 \pm 0.26	4.82 \pm 6.90	4.73 \pm 4.96	8.41 \pm 7.75	2.64 \pm 4.47	3.14 \pm 4.01	3.13 \pm 2.66	7.58 \pm 9.04	2.90 \pm 2.66
<i>A. chlorotica</i>	0.31 \pm 0.51	0.58 \pm 0.68	0.33 \pm 0.47	0.72 \pm 0.66	0.51 \pm 0.59	0.14 \pm 0.29	0.47 \pm 0.54	0.77 \pm 0.92	0.26 \pm 0.48	0.47 \pm 0.53	0.39 \pm 0.47	0.19 \pm 0.27
Total 1971-72	48.98 \pm 23.54	55.76 \pm 23.27	30.35 \pm 12.17	49.97 \pm 22.94	43.07 \pm 20.79	36.34 \pm 16.33	41.26 \pm 20.40	45.08 \pm 24.02	43.80 \pm 21.16	45.25 \pm 29.91	33.08 \pm 20.13	19.34 \pm 18.14
Total 1972-73	50.53 \pm 21.96 (1973)	20.59 \pm 9.17 (1972)				48.17 \pm 23.25 (1973)				35.24 \pm 18.16 (1973)		

Table 3. The weight specific oxygen consumption rates used in calculating earthworm annual metabolism (1971-1972)

		Oxygen consumption ($\mu\text{l g}^{-1}$ fresh wt h^{-1})												Source of metabolic data	Orig temp of measurement $T^\circ\text{C}$
		10°C	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.		
Litter $T^\circ\text{C}$	-	9.3	4.8	4.8	2.45	2.45	5.75	7.1	8.65	9.35	13.3	12.95	10.20		
Krogh's (1914) factor - to convert $R_{10^\circ\text{C}}$ to ambient $T^\circ\text{C}$	-	0.91	0.50	0.50	0.37	0.37	0.58	0.68	0.87	0.92	1.42	1.38	1.00		
<i>D. mammalis</i>	112.0	101.92	56.00	56.00	41.44	41.44	64.96	76.16	97.44	103.04	159.04	154.56	112.00	Phillipson and Bolton (1976)	10.0
<i>L. castaneus</i>	155.8	141.78	77.90	77.90	57.65	57.65	90.36	105.94	135.55	143.34	221.24	215.0	155.80	Phillipson and Bolton (1976)	10.0
<i>D. rubida</i>	112.0	101.92	56.00	56.00	41.44	41.44	64.96	76.16	97.44	103.04	159.04	154.56	112.00	Phillipson and Bolton (1976)	10.0
Soil $T^\circ\text{C}$	-	9.5	5.5	5.0	3.1	2.6	4.8	6.2	7.7	8.5	11.8	11.8	9.8		
Krogh's (1914) factor - to convert $R_{10^\circ\text{C}}$ to ambient $T^\circ\text{C}$	-	0.93	0.55	0.51	0.40	0.38	0.50	0.60	0.74	0.82	1.21	1.21	0.97		
<i>L. terrestris</i>	21.6	20.09	11.88	11.02	8.64	8.21	10.80	12.96	15.98	17.71	26.14	26.14	20.95	Satchell (1967)	15.0
<i>A. longa</i>	27.0	25.11	14.85	13.77	10.80	10.26	13.50	16.20	19.98	22.14	32.67	32.67	26.19	Satchell (1967)	15.0
<i>A. caliginosa</i>	40.2	37.39	22.11	20.50	16.08	15.28	20.10	24.12	29.75	32.96	48.64	48.64	38.99	As <i>L. terrestris</i> Barley and Jennings (1959)	15.0
<i>A. rosea</i>	71.8	66.77	39.49	36.62	28.80	27.28	35.90	43.08	53.13	58.88	86.88	86.88	69.65	Phillipson and Bolton (1976)	10.0
<i>A. muldali</i>	78.6	73.10	43.23	40.09	31.60	29.87	39.30	47.16	58.16	64.45	95.11	95.11	76.24	Phillipson and Bolton (1976)	10.0
<i>O. cyaneum</i>	69.4	64.54	38.17	35.39	27.76	26.37	34.70	41.64	51.36	56.91	83.97	83.97	67.32	imm. <i>A. rosea</i> Phillipson and Bolton (1976)	10.0
<i>A. chlorotica</i>	72.7	67.61	39.99	37.08	31.60	27.63	36.35	43.62	53.80	59.61	87.97	87.97	70.52	Phillipson and Bolton (1976)	10.0
														As large imm. <i>A. rosea</i>	

Table 4. Monthly mean temperatures and rainfall

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Σ
1971-1972													
Litter T° C	9.3	4.8	4.8	2.45	2.45	5.75	7.1	8.65	9.35	13.3	12.95	10.2	
Soil T° C (5 cm deep)	9.5	5.5	5.0	3.1	2.6	4.8	6.2	7.7	8.5	11.8	11.8	9.8	
Rainfall (mm)	74.2	61.3	24.0	60.5	50.8	63.2	45.8	49.8	55.8	23.3	29.8	31.0	569.5
1972-1973													
Litter T° C	8.75	5.25	5.05	1.25	—	4.85	5.8	—	—	—	—	—	
Soil T° C (5 cm deep)	8.5	5.6	5.2	2.0	—	4.0	4.9	—	—	—	—	—	
Rainfall (mm)	25.9	65.8	74.0	24.4	15.0	10.8	42.4	71.2	109.3	60.0	28.8	32.7	572.8

Table 5. Earthworm respiratory metabolism (1971-1972) in ml O_2 m^{-2} mh^{-1}

	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.		
<i>D. mammalis</i>	15.924	27.418	34.581	39.464	28.842	43.497		
<i>L. castaneus</i>	109.704	37.579	79.402	70.342	30.093	20.841		
<i>D. rubida</i>	7.583	0.806	0	4.008	14.421	1.933		
<i>L. terrestris</i>	334.363	214.353	75.594	117.250	63.941	108.716		
<i>A. longa</i>	76.782	83.825	26.022	76.495	59.913	4.118		
<i>A. caliginosa</i>	321.022	153.143	162.586	157.918	145.379	185.435		
<i>A. rosea</i>	196.720	117.996	96.993	106.707	39.493	96.422		
<i>A. muldali</i>	6.526	2.801	2.088	2.351	3.326	7.895		
<i>O. cyaneum</i>	250.653	193.751	46.604	3.305	88.464	122.113		
<i>A. chlorotica</i>	15.594	16.700	9.104	16.927	9.808	3.786		
Σ	1334.871	848.372	532.974	594.767	483.680	594.756		
	Apr.	May	Jun.	Jul.	Aug.	Sep.	Σ	Per cent contrib. to total resp.
	20.837	57.271	35.611	57.980	11.499	2.419	375.343	3.49
	57.208	162.367	67.083	47.735	17.596	4.487	704.437	6.55
	5.484	13.049	5.935	16.566	5.750	2.419	77.954	0.73
	110.481	189.156	219.321	448.086	263.134	155.667	2300.062	21.40
	0	115.205	89.906	14.098	8.264	11.126	565.754	5.26
	228.021	245.687	285.961	465.380	254.765	119.590	2724.887	25.35
	177.731	152.186	174.238	268.251	247.566	46.638	1720.941	16.01
	15.280	20.770	8.817	7.076	7.784	2.745	87.459	0.81
	252.139	100.879	128.662	195.543	473.550	140.564	1996.227	18.57
	14.761	30.821	11.159	30.761	25.525	9.647	194.593	1.81
	881.942	1087.391	1026.693	1551.476	1315.433	495.302	10747.657	

Fig. 4a-e. Species contributions to the respiratory metabolism of the total earthworm fauna between Oct. 1971 and Sep. 1972. **a** *A. caliginosa*; **b** *L. terrestris*; **c** *O. cyaneum*; **d** *A. rosea*; **e** *L. castaneus* + *A. longa* + *D. mammalis* + *A. chlorotica* + *A. muldali* + *D. rubida*

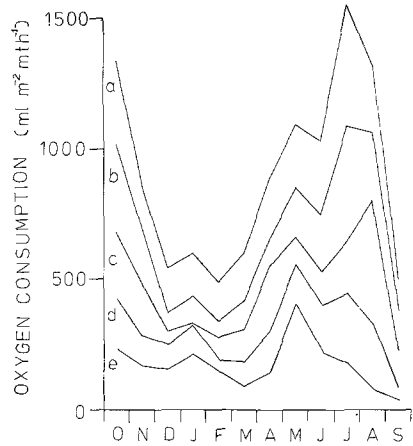


Table 6. The relative annual contributions by the different earthworm species to numbers, biomass and respiratory metabolism

Species	Numbers		Biomass		Respiratory metabolism	
	% contribution	Rank	% contribution	Rank	% contribution	Rank
<i>D. mammalis</i>	15.41	3	1.46	7	3.49	7
<i>L. castaneus</i>	8.28	4	1.87	6	6.55	5
<i>D. rubida</i>	1.40	10	0.28	10	0.73	10
<i>L. terrestris</i>	5.52	6	38.89	1	21.40	2
<i>A. longa</i>	2.17	8	9.69	4	5.26	6
<i>A. caliginosa</i>	32.45	1	26.72	2	25.35	1
<i>A. rosea</i>	20.88	2	9.13	5	16.01	4
<i>A. muldali</i>	7.51	5	0.44	9	0.81	9
<i>O. cyaneum</i>	4.57	7	10.47	3	18.57	3
<i>A. chlorotica</i>	1.80	9	1.04	8	1.81	8

tion made to it by the different species. It is clear that the influence of temperature on respiratory metabolism is considerable.

The Relative Contributions by Different Species to Numbers, Biomass and Respiratory Metabolism

It is well known that the relative importance of animal taxa to community structure and function varies according to the criteria used for assessment. The earthworms of Brogden's Belt are no exception and the relative importance of each species to total earthworm numbers, biomass and respiratory metabolism is shown in Table 6. The rank order of species in the numbers column differs from the given by Phillipson et al. (1976). This is explained by the inclusion of K.L.G. extracted specimens in the present calculations with the result that the small litter dwelling species *D. mammalis* and *L. castaneus* have increased their numerical proportional abundance.

When all three parameters (numbers, biomass and metabolism) are taken into consideration the ten species from Brogden's Belt can be ranked in order

of importance as *A. caliginosa* > *L. terrestris* > *A. rosea* > *O. cyaneum* > *L. castaneus* > *D. mammalis* > *A. longa* > *A. muldali* > *A. chlorotica* > *D. rubida*. In all cases the first three named species were responsible for more than 50% of the total earthworm contribution.

Discussion

It is not the intention of this paper to explore in detail the population dynamics of individual species but it should be noted from Figure 1 that different species exhibit different annual courses with respect to their population densities. For example, the population density curve for *D. mammalis* is unimodal whereas that for *L. castaneus* shows a tendency towards trimodality.

Of greater importance for the purposes of this discussion are the general levels of abundance of the total earthworm fauna. The mean population densities recovered in this beechwood study were 164.6 m^{-2} in the first, and detailed, period of study (1971–1972) and 117.5 m^{-2} (possibly 139.8 m^{-2}) in the second, less detailed, study period (1972–1973). These densities are among the highest recorded from beechwoods, in particular they both exceed the mean values quoted by Zajonc (1971) for nine types of temperate woodland. Comparison with the 81 individual temperate woodland earthworm densities given in Zajonc (1971) reveals that a density of 164.6 m^{-2} is only exceeded eight times and places in question the suggestion that beech woodlands are not especially rich in earthworms. It is possible that the combination of three extraction methods used in 1971–1972 was more effective than those employed in other studies. This explanation is unlikely to account for the observed differences, however, in that only ten of Zajonc's (1971) eighty-one records exceed the 117.5 m^{-2} recorded by the hand sorting/formalin extraction methods in 1972–1973. Significant to the line of reasoning that many *Fagus sylvatica* woods are not poor in numbers of earthworms is the omission by Zajonc (1971) of the studies by Bornebusch (1930) and Lindquist (1938). For seven beechwoods on mull soils in Denmark Bornebusch (1930) recorded earthworm densities of $73\text{--}220 \text{ m}^{-2}$ (mean $131.1 \pm \text{S.D. } 54.1$), similarly for seven beechwoods on mull in Sweden Lindquist (1938) reported densities of $90\text{--}184 \text{ m}^{-2}$ (mean $128.9 \pm \text{S.D. } 33.0$). In contrast three beechwoods on mor soils studied by Bornebusch (1930) produced $23\text{--}81$ earthworms m^{-2} (mean $44.3 \pm \text{S.D. } 31.9$) and two Swedish beechwoods on mor gave rise to densities of 67.4 and 89.8 m^{-2} (Nordström and Rundgren, 1973). It would thus appear that soil type is more important than dominant tree leaf litter in determining earthworm abundance; that this is so can be clearly seen in Table 7. Student's *t* test for the difference between the means of two small samples showed that earthworm densities in beechwoods on mor soils are significantly less than those in mull soils ($t=6.88$, d.f. = 34, $P < 0.001$). Mor soils also support significantly fewer species ($t=3.13$, d.f. = 47, $0.001 < P < 0.005$). The densities found in Brogden's Belt were not significantly different from the densities recorded from other beechwoods on mull soils ($t=1.13$, d.f. = 24, $0.20 < P < 0.40$).

The mean density of earthworms in beechwoods on mor soils (25.54 , $n=27$) is in general accord with the mean densities noted by Zajonc (1971) for taiga forest (17.4 and 23.0 m^{-2}), mountain spruce and fir (11.0 m^{-2}), pine forest

Table 7. Comparison of earthworm densities, biomasses and species numbers in beechwoods on mor/"acid" and mull/"basic" soils

Authority	Mor soils <i>or</i> pH <5.5			Authority	Mull soils <i>or</i> pH >5.5			
	No. m ⁻²	g m ⁻² (fresh wt.)	No. spp.		No. m ⁻²	g m ⁻² (fresh wt.)	No. spp.	
Baltzer (1956)	6	1.40	2	Baltzer (1956)	54	14.59	6	
	24	9.22	3		51	14.78	5	
	4	4.39	1		52	14.23	4	
	22	13.62	2		41	11.65	5	
	4	1.83	1		33	18.78	4	
	25	10.78	1		54	42.57	4	
	38	4.42	3		38	22.14	3	
	37	13.77	3		28	11.16	3	
	22	10.61	2		99	37.40	4	
	12	4.83	2		86	30.73	7	
	18	6.54	3		Bornebusch (1930)	177	53.10	3
	30	4.38	2			93	27.90	—
	Bornebusch (1930)	29	1.45			1	73	5.90
81		5.40	4	220		—	—	
23		1.15	1	155		—	1	
Drift (1951)	30	—	2	110	—	2		
Fuller (1953)	36	16.00	4	90	—	—		
Nordstrom and Rundgreen (1973)	67.4 89.8	12.39 25.60	6 8	Lindquist (1938)	90	16.89	5	
Rabeler (1960)	7.0	7.20 ^a	2		116	75.58	5	
	10.5		6		94	28.71	7	
	3.5		2		150	—	6	
	14.0		5		127	—	—	
	10.5		4	141	—	5		
19.5	5	184	48.04	5				
Sergienko (1969)	8.0	6.10	5	Present study	164.6	41.02	10	
Volz (1962)	—	3.05	—		117.5	38.63	10	
	—	2.86	—					
Zajonc (1967)	18.5	12.00	4					
Mean	25.54	7.78	3.11	Mean	101.47	29.15	4.91	
Standard deviation	22.19	5.93	1.83	Standard deviation	51.86	17.78	2.20	

^a Estimated by Zajonc (1971)

(48.2 m⁻²) and steppe forests (55.2 m⁻²). In beechwoods on mull soils the mean density (101.47 m⁻²) is more akin to the means reported for lowland mixed forests (135.9 m⁻²), Central European (90.8 m⁻²), East European (90.7 m⁻²) and Caucasian (129.0 m⁻²) oakwoods. The importance of soil type in determining earthworm abundance is clear and it would seem that beechwoods on mull soils support similar densities of earthworms to those found in other types of deciduous woodland on mull soils.

In Brogden's Belt the mean biomasses were 41.02 g and 38.63 g preserved

wet weight m^{-2} ; allowing for a twenty-five per cent loss in fresh weight due to preservation these figures could be as high as 51.28 and 48.29 g live weight m^{-2} . Table 7 shows the separation of beechwood earthworm biomasses according to soil type. As with numbers, mean biomass in beechwoods on mor soils (7.78 g m^{-2}) was significantly lower than the 29.15 g m^{-2} of mull soils ($t=5.01$, d.f.=21, $P<0.001$). The preserved wet weight biomasses found in Brogden's Belt were not significantly different from those recorded from other beechwoods on mull soils ($t=0.893$, d.f.=17, $0.20 < P < 0.40$) nor were the estimated live weight biomasses ($t=1.64$, d.f.=17, $0.01 < P < 0.20$).

The mean biomass of earthworms in beechwoods on mor soils (7.78 g m^{-2}) is similar to those noted by Zajonc (1971) for taiga forests (2.8 and 8.4 g m^{-2}) and mountain spruce and fir (5.3 g m^{-2}) but lower than those reported for pine (73.8 g m^{-2}) and steppe (30.0 g m^{-2}) forests. In mull soils the mean beechwood earthworm biomass (29.15 g m^{-2}) is very like that reported for all beechwoods (30.3 g m^{-2}) by Zajonc (1971) but considerably lower than those quoted for lowland mixed forests (68.3 g m^{-2}), Central European (85.2 g m^{-2}), East European (50.4 g m^{-2}) and Caucasian (70.8 g m^{-2}) oakwoods. The Brogden's Belt preserved wet weight biomasses, which are relatively high for beech, are exceeded by thirty of the eighty-one individual records for temperate woodlands given in Zajonc (1971). The estimated live weight biomasses (51.28 and 48.29 g m^{-2}) are exceeded twenty-six times out of eighty-one. Unlike population density it would appear that earthworm biomass per unit area is affected by both soil and litter type.

The mean individual body sizes of earthworms in beechwoods do not reflect the influence of soil and litter type on biomass because on mor and mull soils they are very similar at 0.30 and 0.29 g. The effect in this type of woodland is therefore on absolute numbers. However, since earthworm numbers in beechwoods are much the same as those found in other woodlands on similar soil types and yet the biomasses are different, it follows that the effects of various litter types on biomass should be reflected in mean individual body sizes. Using the data reviewed by Zajonc (1971) it can be shown that in coniferous forests and beechwoods the mean body weights are 0.34 g in both cases and compare favourably with the 0.30 and 0.29 g calculated from Table 7. In deciduous forests other than beech the mean individual body weights are 0.62 g (range 0.54 to 0.94 g). Clearly, acting as it does through individual body weights, litter type has a profound influence on the level of earthworm biomass supported on similar soil types.

Satchell (1967) implicated food as a population determinant for earthworms by pointing out that population size increased when food was supplied experimentally to the Broadbalk plots at Rothamsted. He also suggested that nitrogen could be limiting for *L. terrestris* populations in Merlewood Lodge Wood in the north-west of England. Food limitation could operate by imposing a ceiling on absolute numbers only when mean individual weights remain constant. When mean body weights differ the carrying capacity must be determined in terms of biomass. The present findings show that mean body weights do vary between sites on similar soil types at similar latitudes and suggest that differences in leaf quality rather than leaf quantity are of importance in determining the level of biomass that can be supported by such sites.

Interactions between leaf quality and earthworms have been investigated on a number of occasions. Lindquist (1941), Bornebusch (1953) and Satchell and Lowe (1967) have all demonstrated that earthworms exhibit a preference for the leaves of particular species and that beech leaves and conifer needles are low in the order of preference. Brown et al. (1963) found that beech leaves contain a high proportion of condensed tannins and Edwards and Heath (1975) showed that such leaves become progressively less palatable through the growing season due to an increase in polyphenolic materials. The tannins remain at a high level for several months after leaf fall but gradually reduce under the influence of weathering and soil micro-organism enzyme systems (Bocks et al., 1963; Satchell and Lowe, 1967; Edwards and Heath, 1975). In Brodgen's Belt the annual decomposition of litter is equal to the annual litter input (Phillipson et al., 1975) and from this it can be concluded that although tannin content will delay the consumption of freshly fallen beech litter by earthworms it will not, in the long term, prevent it. It is unlikely therefore that polyphenolic substances are the ultimate determinant of the earthworm carrying capacity of a particular site.

Satchell and Lowe (1967) have shown a variety of factors other than tannins to be broadly correlated with leaf palatability, for example soluble carbohydrate and nitrogen content. Wittich (1953) also found that earthworms showed a preference for leaves with a high nitrogen content. In this context it is of interest to note the mean values for the per cent dry weights of soluble carbohydrate and nitrogen found by Satchell and Lowe (1967) in the seven most preferred leaf species and the seven least preferred of the 14 species studied by them. For soluble carbohydrates the ratio of the means was 1.99:1.0 in unweathered leaves and 2.02:1.0 in weathered leaves while for nitrogen the ratio was 2.01:1.0. These ratios are similar to those shown by the earthworm biomasses quoted by Zajonc (1971) for lowland mixed forests versus beech, oak and coniferous woodlands, namely 1.72:1.0. The same relationship holds for the mean individual biomasses of 0.62 and 0.34 g noted earlier, i.e. 1.8:1.0. There is thus strong circumstantial evidence that litter quality as measured by soluble carbohydrate and nitrogen content could play a large part in determining earthworm biomass levels. However, it is still necessary to account for the nearly four-fold difference between earthworm biomasses found in beechwoods on mor and mull soils. It is highly unlikely that the nutrient content of beech leaves produced by trees on mull and mor soils show a four-fold difference, nor is it probable that the total quantity of litter produced on the two soil types varies by this amount. Another possible explanation is that by Handley (1954) who suggested that the organic nitrogenous material in mor is less easily digested than that in mull but it is difficult to visualize that this would apply to leaves of the same tree species. However, it is possible that the chemical characteristics of the two soil types are such that the micro-organisms which can deal with polyphenols are less abundant in mor soils and that the tannins persist much longer than in mull soils. The persistence of polyphenolic substances in beech leaves on mor as opposed to mull soils would lead to a continued unpalatability of the leaves thereby giving rise to reduced quantities of soluble carbohydrates and nitrogen available to earthworms.

The annual course of earthworm respiratory metabolism in Brodgen's Belt

was different to that of population density and biomass. Monthly respiration values varied more than threefold while monthly densities and biomass varied much less. As can be seen from Tables 4 and 5 temperature had a considerable influence on metabolism.

The annual respiratory metabolism of the total earthworm fauna, calculated on the basis of preserved wet weight, was estimated to be 10.748 l m^{-2} . Allowing for a 25% weight loss during preservation the metabolism could have been as high as $13.435 \text{ l m}^{-2} \text{ a}^{-1}$. Conversion of these annual oxygen consumption values to energy equivalents ($4.775 \text{ cal ml}^{-1} \text{ O}_2$ (Heilbrunn, 1947) $\approx 19.979 \text{ J ml}^{-1} \text{ O}_2$) indicates that the energy expenditure of the Brogden's Belt earthworms in 1971–1972 was between 214.727 kJ ($\approx 51.319 \text{ kcal}$) $\text{m}^{-2} \text{ a}^{-1}$ and 268.409 kJ ($\approx 64.150 \text{ kcal}$) $\text{m}^{-2} \text{ a}^{-1}$. These values are close to the $63.8 \text{ kcal m}^{-2} \text{ a}^{-1}$ quoted by Macfadyen (1963) for Bornebusch's (1930) beech mull site 15.

Phillipson et al. (1975) showed the annual carbon dioxide evolution from Brogden's Belt to be $239.481 \text{ l CO}_2, \text{m}^{-2} \text{ a}^{-1}$ and Phillipson et al. (1977) calculated that oxygen consumption by the soil would have been $263.429 \text{ l O}_2 \text{ m}^{-2} \text{ a}^{-1}$ ($5263 \text{ kJ m}^{-2} \text{ a}^{-1}$). The Brogden's Belt earthworms in 1971–1972 were thus responsible for between 4.08 and 5.10% of total 'soil' respiration, a contribution which is 30–50 times greater than that made by nematodes on the same site (Phillipson et al., 1977). This finding is in sharp contrast to the situation, as evaluated by Macfadyen (1963), in Bornebusch's beech mull 15 where nematode contribution to total faunal metabolism was 1.44 times greater than that attributed to earthworms. The 4.08 to 5.10% contribution by earthworms to total soil respiration in Brogden's Belt is very like the 4% suggested by Barley (1964) for a population of *A. caliginosa* in an Australian pasture. On the other hand it is only half of the 8% estimated by Satchell (1967) for *L. terrestris* in Merlewood Lodge Wood where litter input was assumed to be $300 \text{ g dry wt m}^{-2}$; 500 g m^{-2} is not unusual for such woods.

Details of production by the earthworms in Brogden's Belt will be reported in a future publication. For the present it is possible to estimate production from the known energy equivalents of respiratory metabolism by substituting them in the regression equation for poikilotherms given in McNeill and Lawton (1970). The equation is $\log P = 0.8233 \log R - 0.2367$, where P is production and R is respiration (in $\text{kcal m}^{-2} \text{ a}^{-1}$), and gives rise to an estimate of earthworm production of 62.052 to $74.569 \text{ kJ m}^{-2} \text{ a}^{-1}$ (14.838 to $17.831 \text{ kcal m}^{-2} \text{ a}^{-1}$).

Using the conversion values presented in the appendix it can be shown that the mean preserved wet weight biomass of 41.02 g m^{-2} represents $6.22 \text{ g dry weight}$ (exclusive of gut contents) m^{-2} . Following Bolton and Phillipson (1976) this has an energy equivalent of 128.01 kJ m^{-2} . Given these data it is possible to estimate the production/biomass (P/B) ratio for the Brogden's Belt earthworms; it is of the order of 0.49 to 0.58. Net population efficiency [$(P/A) \times 100$ or $(P/P+R) \times 100$] may be estimated as 21.7 to 22.4%.

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Appendix

Conversion Factors for Use with Earthworm Biomass Data

Species	Total dry wt $\times 100$										Dry wt of gut contents $\times 100$													
	Oct.	Nov.	Jan.	Apr.	May	Jul.	Aug.	Sep.	Oct.	Nov.	Jan.	Apr.	May	Jul.	Aug.	Sep.	Oct.	Nov.	Jan.	Apr.	May	Jul.	Aug.	Sep.
<i>D. mammalis</i>	—	18.03	17.90	17.57	—	20.62	—	28.94	—	13.58	15.41	19.53	—	21.96	—	0.0	—	13.58	15.41	19.53	—	21.96	—	0.0
<i>L. castaneus</i>	18.85	—	18.15	18.24	—	17.92	18.38	—	—	—	—	22.30	—	11.99	10.37	—	—	—	—	22.30	—	11.99	10.37	—
<i>D. rubida</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>L. terrestris</i>	16.97	—	18.92	17.50	—	19.27	—	17.71	29.97	—	24.73	29.21	—	31.86	—	11.39	—	—	—	29.97	—	31.86	—	11.39
<i>A. longa</i>	20.69	—	20.82	—	22.30	17.98	—	24.26	17.14	—	25.80	—	33.30	—	0.0	0.0	—	—	—	17.14	—	33.30	—	0.0
<i>A. caliginosa</i>	22.95	—	23.27	23.01	—	23.77	—	21.80	24.94	—	23.45	27.87	—	22.79	—	0.0	—	—	—	24.94	—	22.79	—	0.0
<i>A. rosea</i>	24.67	—	27.59	25.75	—	23.83	—	23.61	21.43	—	36.21	28.98	—	21.27	—	0.0	—	—	—	21.43	—	21.27	—	0.0
<i>A. multitali</i>	20.50	—	26.22	29.02	—	19.98	—	19.39	27.51	—	43.71	55.71	—	20.37	—	0.0	—	—	—	27.51	—	20.37	—	0.0
<i>O. cynaeum</i>	24.26	—	25.85	25.25	—	26.52	—	15.42	53.12	—	57.34	51.14	—	47.58	—	0.0	—	—	—	53.12	—	47.58	—	0.0
<i>A. chlorotica</i>	21.50	—	23.30	23.48	—	23.74	—	26.94	7.60	—	28.04	32.59	—	24.42	—	0.0	—	—	—	7.60	—	24.42	—	0.0

Species	Dry wt (excluding gut) $\times 100$										Energy equivalents (kJ g ⁻¹)																				
	Oct.	Nov.	Jan.	Apr.	May	Jul.	Aug.	Sep.	Oct.	Nov.	Jan.	Apr.	May	Jul.	Aug.	Sep.	Immatures					Adults									
																<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g	<i>W</i> -g
<i>D. mammalis</i>	—	15.60	15.14	14.12	—	16.10	—	28.94	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
<i>L. castaneus</i>	15.17	—	15.34	14.17	—	15.78	16.47	—	—	18.459	23.274	—	—	17.518	23.287	—	—	—	—	—	—	—	—	—	—	—	—				
<i>D. rubida</i>	—	—	—	—	—	—	—	—	—	18.221	23.968	—	—	17.594	22.614	—	—	—	—	—	—	—	—	—	—	—	—				
<i>L. terrestris</i>	11.88	—	14.17	12.25	—	13.06	—	15.71	—	17.209	22.718	—	—	16.649	23.107	—	—	—	—	—	—	—	—	—	—	—	—				
<i>A. longa</i>	17.14	—	15.43	—	14.82	17.98	—	24.26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>A. caliginosa</i>	17.10	—	17.72	16.51	—	18.23	—	21.80	21.414	13.063	23.061	20.056	—	12.235	22.204	—	—	—	—	—	—	—	—	—	—	—	—				
<i>A. rosea</i>	19.10	—	17.49	18.28	—	18.58	—	23.61	22.075	13.272	23.479	21.924	—	13.418	23.483	—	—	—	—	—	—	—	—	—	—	—	—				
<i>A. multitali</i>	14.65	—	14.61	12.55	—	15.25	—	19.39	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>O. cynaeum</i>	11.31	—	11.00	12.27	—	13.73	—	15.42	18.885	11.520	22.388	19.128	—	11.666	22.442	—	—	—	—	—	—	—	—	—	—	—	—				
<i>A. chlorotica</i>	19.79	—	16.73	15.83	—	17.92	—	26.94	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				

W-g = dry wt - gut contents, *W*_{tot} = total dry wt, *W*_{af} = ash free dry wt

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