Cocoon production, morphology, hatching pattern and fecundity in seven tropical earthworm species – a laboratory-based investigation

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Data on the reproductive biology of seven Indian species of earthworms, viz. *Perionyx excavatus* Perrier, *Lampito mauritii* Kinberg, *Polypheretima elongata* (Perrier), *Pontoscolex corethrurus* (Muller), *Eutyphoeus gammiei* (Beddard), *Dichogaster modiglianii* (Rosa) and *Drawida nepalensis* Michaelsen are presented. The peregrine earthworms such as *Perionyx excavatus*, *Pontoscolex corethrurus*, *Dichogaster modiglianii*, and *Polypheretima elongata* are considered to be continuous breeders with high fecundity. Native *Lampito mauritii* and *Drawida nepalensis* are semi-continuous and *Eutyphoeus gammiei* discrete breeders. There is a dramatic increase in cocoon production by most earthworm species of Tripura in the summer and monsoon with a corresponding peak during April and July. Cocoon production decreased or ceased during winter. Temperature affected the incubation period of cocoons. With increase in temperature, incubation period increased in the endogeic worms, *Pontoscolex corethrurus*, *Polypheretima elongata* and *Drawida nepalensis* and decreased in the epigeic worms, *Perionyx excavatus* and *Dichogaster modiglianii*, within a temperature range between 28–32°C under laboratory conditions. There was a significant ($P < 0{\cdot}05$) positive correlation between number of hatchlings per cocoon and incubation period in *Lampito mauritii*. High rate of cocoon production, short development time with high hatching success, as well as continuous breeding strategies in the epigeic species *Perionyx excavatus* and *Dichogaster modiglianii* and the top soil endogeic species, *Pontoscolex corethrurus*, *Drawida nepalensis* and *Lampito mauritii*, indicate their possible usefulness in vermiculture. The giant anecic worm, *Eutyphoeus gammiei*, which has a very long cocoon development time, discrete breeding strategy and very low rate of cocoon production, is not a suitable species for vermiculture.

[Bhattacharjee G and Chaudhuri P S 2002 Cocoon production, morphology, hatching pattern and fecundity in seven tropical earthworm species – a laboratory-based investigation; *J. Biosci.* **27** 283–294]

1. Introduction

Population dynamics, productivity and energy flow in earthworms cannot be fully understood unless the life cycle of the earthworm is known. Studies on the life cycles of earthworms are also necessary for effective vermiculture.

Knowledge of the reproductive strategies of earthworms comes predominantly from studies on temperate species (Evans and Guild 1948; Satchell 1967; Lavelle 1971, 1979; Bouché 1972; Reynolds 1973; Phillipson and Bolton 1977; Elvira *et al* 1996; Nair and Bennour 1998; Jiménez *et al* 1999). There are reports on the earthworm resources of India including of its north-eastern states (Gates 1972; Julka 1993a,b, 2001; Julka and Senapati 1987; Bano and Kale 1991; Chaudhuri and Bhattacharjee 1999; Halder 1999, 2000). However, information is scanty regarding the biology and ecology of earthworm species from tropical regions. Dash and Senapati (1980) studied the morphology of cocoons of three tropical earthworms, *Lampito mauritii*, *Drawida willsi* and *Octochaetona surensis*, and the effect of soil moisture and temperature on the cocoon hatching process and the emergence pattern of juveniles in the field. Most studies

Keywords. Cocoon; development time; earthworm; fecundity; hatching success; temperature

on the life cycles of tropical earthworms concern the composting species *Perionyx excavatus* (Kale *et al* 1982; Reinecke and Hallatt 1989; Hallatt *et al* 1990, 1992; Edwards *et al* 1998). In *Perionyx excavatus*, Hallatt *et al* (1990) studied the growth rate, rate of maturation, cocoon production, the hatching success of cocoons, the incubation period and the number of offspring per cocoon under controlled laboratory conditions at different moisture and temperature regimes.

The aim of this study was to describe cocoon morphology, and analyse cocoon development, hatching success, dynamics of cocoon production, and fecundity in seven species of Indian earthworms. Such information could then be used to fit these earthworms into broad categories of reproductive strategies and allow selection of appropriate species for vermiculture.

2. Materials and methods

The study was carried out with seven tropical earthworm species occurring in Tripura, a north-eastern state of India. The climate is broadly divided into 3 seasons: winter (November–February), summer (March–June) and monsoon (July–October). Adult earthworms were collected by the digging and hand sorting method from pasture and dung deposit sites in Sadar subdivision of Tripura, located between latitude 22°51′–24°32′N and longitude 90°10′–92°21′E, between July and October 1998. Earthworms were acclimated in a ventilated laboratory until December 1998. Earthworms were identified by the Zoological Survey of India, Kolkata. Based on our field studies, the ecological category, habit, habitat and size relationship of these earthworms are presented in table 1.

2.1 *Culturing methods*

Earthworms were not subjected to any controlled condition in the laboratory. Clay pots (4·5 l) containing suitable food (culture medium), were used for rearing of earthworms. *Perionyx excavatus* Perrier, a surface living species, inhabits cowdung heaps, and air dried, sieved (1 mm mesh) ground cowdung (200 g) free from any foreign cocoon was used as feed for this species. *Dichogaster modiglianii* (Rosa), another surface living earthworm, is found in cowdung soil juncture and a mixture of sieved cowdung (100 g) and garden soil (100 g) was used as feed for this species. For the other geophagous species, ground, sieved pasture soil [2000 g for the giant worm *Eutyphoeus gammiei* (Beddard), 600 g for the large sized *Polypheretima elongata* (Perrier), 200 g each for the small to medium sized *Pontoscolex corethrurus* (Muller), *Lampito mauritii* Kinberg and *Drawida nepalensis* Michaelsen] was used as food for culture. Culture pots of each species received the prescribed amount of food along with two earthworms. The moisture level in the culture media was maintained close to the field soil moisture of these earthworm species (table 1) at 70–80% (*Perionyx excavatus*), 28–42% (*Dichogaster modiglianii*) and 25–35% (other species) by sprinkling water with a hand spray on alternate days. Moisture content of the substrates was measured periodically by gravimetric method. Maximum average temperature of the ventilated room (calculated from mean of actual maximum temperature) varied from 19·6 (January) to 32·4°C (April) for the year 1999.

The cultures were maintained for one year (January 1999–December 1999). During October 1999 mortality was noticed in some of the cultures containing *Eutyphoeus gammiei* that were later terminated. Death probably resulted due to stressful conditions such as comparatively small containers and low substrate volume for these giant earthworms.

2.2 *Cocoon studies*

The first experiment had five replicates for each species and was aimed at studying fecundity and dynamics of cocoon production. Cocoons were collected on 0·5 mm mesh sieve every week, using gentle washing, and their number was calculated on a per individual basis. The second experiment had three replicates for each species and was aimed at determining the approximate timing of cocoon production, incubation period and hatching pattern. The size and weight of cocoons were also measured. Before weighing, the cocoons were washed lightly in distilled water to remove debris adhering to the sticky hull. Here culture sets were carefully observed daily for cocoons, if any. The cocoons were immediately isolated and incubated. In both experiments, old culture media was replaced by the same amount of fresh media at weekly intervals, so that food was not a limiting factor.

2.3 *Incubation of cocoons*

After isolation, freshly laid cocoons were kept on moist filter paper spread over water soaked cotton (having 80% moisture) inside a petri-dish (one cocoon per dish). They were housed in the same room as the experimental pots. The maximum average room temperature during cocoon development varied from 28–32°C. Cocoons were observed daily to record any external changes during incubation and to determine whether any hatchlings emerged. Development time (incubation period) is the time lapse (in days) from cocoon formation until the first hatchling appeared. Number of hatchlings per cocoon and size of hatchlings were also recorded.

Table 1. Ecological category, habitat and size relationship of seven species of earthworms of Tripura collected between July and October (1998).

					Habitat						
Species	Family	Size (mm)	Colour	Feeding habit	Site	Vertical distribution (cm)	Soil organic matter (g%)	Soil pH	Soil temperature (°C)	Soil moisture (g%)	Ecological category
*Perionyx excavatus**	Megascolecidae	L 100–180 B 5–6	Deeply pigmented	Phytophagous	Compost heaps, leaf litter	0–15	4·5–12	6·4–7·4	20–28	10–70	Epigeic (litter species)
Lampito mauritii	Megascolecidae	L 140–160 B 5–6	Lightly pigmented	Phytogeophagous	Pasture	10–15	0·5–4·5	5·8–7·2	20–28	10–40	Top soil endogeic species
Polypheretima elongata	Megascolecidae	L 200–250 B 5–7	Unpigmented	Geophagous	Pasture	30–45	2·5–4·5	6·9–7·2	20–28	10–40	Sub soil endogeic species
*Pontoscolex corethrurus**	Glossoscolecidae	L 70–90 B 4–5·2	Lightly pigmented dorsally	Geophagous	Pasture	10–15	0·5–8·5	5·9–7·2	20–28	10–60	Top soil endogeic species
Drawida nepalensis	Moniligastridae	L 40–50 B 2–3	Lightly pigmented dorsally	Phytogeophagous	Pasture	10–15	0·5–2·5	6·5–7·0	20–26	10–40	Top soil endogeic species
*Dichogaster modiglianii**	Octochaetidae	L 25–40 B 2–3	Moderately pigmented	Phytogeophagous	Soil–cow dung juncture	0–10	2·5–8·5	5·7–7·2	20–28	10–60	Epigeic species
Eutyphoeus gammiei	Octochaetidae	L 200–400 B 7–10	Pigmented dorsally, lightly pigmented ventrally	Geophagous	Pasture (living in permanent burrow)	15–45	2·5–6·5	5·8–7·0	24–28	25–40	Subsoil anecic species

*Peregrine species. L, Length; B, breadth.

2.4 *Statistical analysis*

Significant differences, if any, in cocoon production among 3 different seasons (winter, summer and monsoon) with respect to room temperature for each earthworm species except for *Lampito mauritii* was compared by one-way ANOVA followed by critical difference (CD) at 5% level using the formula:

$$CD = t_{0\cdot05,57} \times \sqrt{\frac{2Mse}{N}}$$

($N = 60$, Mse = mean square error). In case of *Lampito mauritii*, pair-wise *t*-test was used to compare significant difference in cocoon production between summer and monsoon (cocoon production stopped during winter in this species). The correlation between the mean room temperature and incubation period for *Perionyx excavatus*, *Pontoscolex corethrurus*, *Dichogaster modiglianii*, *Drawida nepalensis*, *Polypheretima elongata* and between number of hatchlings per cocoon and incubation period for *Lampito mauritii* were tested by simple regression analysis.

3. Results

Mating was observed only in *Perionyx excavatus* on the surface of the cultures during the day.

3.1 *Cocoons: Morphology, size, development time and emergence*

Cocoons produced by *Perionyx excavatus* were rough, spindle shaped with bristles at the pointed end. In other species, cocoons are either spheroidal (*Pontoscolex* sp., *Polypheretima* sp., *Eutyphoeus* sp., *Dichogaster* sp., *Drawida* sp.) or ovoid (*Lampito* sp.) with pointed ends on either side (figures 1 and 2). Among the seven earthworm species studied, the largest cocoon (diameter 7 mm, fresh weight 103 mg) was of the giant worm, *Eutyphoeus gammiei* and the smallest cocoon (diameter 1·3 mm, fresh weight 1·5 mg) was of the smallest earthworm, *Dichogaster modiglianii* (table 2). Freshly laid cocoons of most of the earthworms were opaque, but those of *Pontoscolex corethrurus* and *Lampito mauritii* were semi-transparent. In *Lampito mauritii* 2 to 3 zygotes were clearly visible through the cocoon 4 to 5 days after cocoon laying, although one of the zygotes generally degenerated later. Blood capillaries first appeared in the cocoon of *Lampito mauritii* on the 8th day of development. The cocoon became opaque and reddish due to increase in vascularization during the 10th to 11th days of development. The hatchlings of all species of earthworms emerged through a hole made at the pointed end of the cocoon (figure 2). In most of the earthworm species, one hatchling emerged out from a single cocoon. However in *Lampito mauritii* about 53% of the cocoons produced more than one hatchling (2, rarely 3). Rare emergence of more than one hatchling per cocoon was also recorded

Figure 1. Cocoons of earthworms (from left to right: *Eutyphoeus gammiei*, *Lampito mauritii*, *Pontoscolex corethrurus*, *Polypheretima elongata*, *Drawida nepalensis*, *Perionyx excavatus* and *Dichogaster modiglianii*).

in *Drawida nepalensis* (20%) and *Polypheretima elongata* (11%).

Development time of cocoons was short in the topsoil endogeic worms, *Lampito mauritii* (15 days), *Drawida nepalensis* (25 days) and *Pontoscolex corethrurus* (29 days) and long (50 days) in the subsoil endogeic earthworm, *Polypheretima elongata* (table 2). Prolonged development time (110 days) was observed in the cocoon of the subsoil anecic worm, *Eutyphoeus gammiei*. Development time of cocoons was very short (13–14 days) in the epigeic worms, *Perionyx excavatus* and *Dichogaster modiglianii*. A significant positive linear correlation ($P < 0{\cdot}05$) between mean room temperature (28–32°C) and incubation period in *Pontoscolex corethrurus*, *Polypheretima elongata* and *Drawida nepalensis* (figure 3a–c) and a significant negative linear correlation ($P < 0{\cdot}05$) between the same variables in *Perionyx excavatus* and *Dichogaster modiglianii* were observed (figure 3d–e). Interestingly, there was a significant ($P < 0{\cdot}05$) positive correlation between number of hatchlings per cocoon and the incubation period in *Lampito mauritii* (figure 4).

Hatching success was strikingly higher in *Pontoscolex corethrurus* (85%), *Dichogaster modiglianii* (78%), *and Lampito mauritii* (60%) compared with *Polypheretima elongata* (40%), *Drawida nepalensis* (38%) and *Eutyphoeus gammiei* (20%). The mean hatching success of cocoons in *Perionyx excavatus* was 53% (table 2).

3.2 *Dynamics of cocoon production*

Pontoscolex corethrurus, *Dichogaster modiglianii*, *Polypheretima elongata* and *Perionyx excavatus* showed year-round cocoon production (continuous breeders) under laboratory conditions (figure 5). Cocoon production in *Lampito mauritii* and *Drawida nepalensis* continued from March to November (semi-continuous breeders). *Eutyphoeus gammiei* is regarded as a discrete breeder because its cocoon production was restricted to the period between March and May under laboratory conditions.

In *Lampito mauritii* cocoon production ceased and in other species it declined during winter (figure 5). In most of the species studied, there was significant increase ($P < 0{\cdot}05$, $n = 57$) in cocoon production during both summer and monsoon compared to winter (table 3). Cocoon production was significantly higher ($P < 0{\cdot}05$, $n = 57$) in the summer compared to the monsoon and winter season in *Perionyx excavatus* and *Drawida nepalensis* (table 3). In other species, viz. *Pontoscolex corethrurus*, *Polypheretima elongata*, *Dichogaster modiglianii* and *Lampito mauritii*, the difference in cocoon production during summer and rainy season was not significant ($P > 0{\cdot}05$, $n = 38$ in *Lampito mauritii* and $n = 57$ in other species). In peregrine species, *Polypheretima elongata* and *Dichogaster modiglianii*, there was no significant difference ($P > 0{\cdot}05$, $n = 57$) in cocoon production among the three seasons (table 3).

Lampito mauritii, *Polypheretima elongata*, *Drawida nepalensis* and *Dichogaster modiglianii* exhibited peaks in cocoon production twice a year, during April and July when maximum average room temperature varied from 30 to 32°C. *Perionyx excavatus*, which showed three annual peaks of cocoon production (March, July and October) had a sudden and large peak during March when maximum room temperature was 28·5°C (figure 5). *Pontoscolex corethrurus* showed a relatively steady rate of cocoon production during the major part of the year, with a single peak of production during April (figure 5). Cocoon production in earthworms declined after October when maximum average room temperature fell below 27°C, although *Pontoscolex corethrurus*, *Polypheretima elongata* and *Dichogaster modiglianii* maintained their cocoon production when the temperature was 21°C.

3.3 *Fecundity*

The highest fecundity (i.e. the number of cocoons produced per adult in one year) was recorded for the epigeic earthworm, *Perionyx excavatus*. This species produced 156 cocoons adult^{-1} year^{-1} under laboratory conditions (table 2). *Eutyphoeus gammiei* (anecic worm) had the lowest value of 1·0 cocoon adult^{-1} year^{-1}. Of the other species *Pontoscolex corethrurus* had the highest fecundity followed by *Dichogaster modiglianii*, *Lampito mauritii*, *Polypheretima elongata* and *Drawida nepalensis* (table 2).

4. Discussion

While cocoons are produced by cross-fertilization between two adult worms in many species, in others there may be self-fertilization or parthenogenesis. The shape,

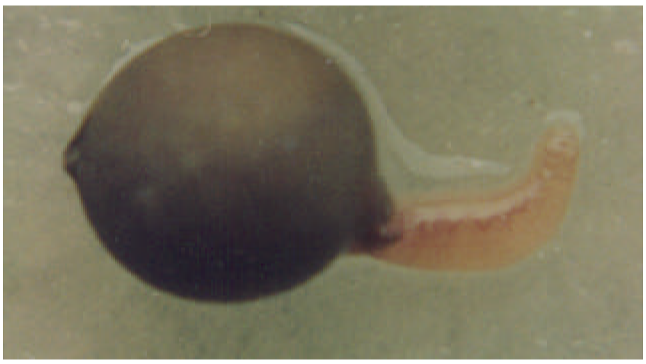

Figure 2. Emergence of hatchling from the cocoon of *Eutyphoeus gammiei*.

Table 2. Biological features of cocoons of the seven earthworm species used (means ± standard errors).

Parameter	*Perionyx excavatus*	*Pontoscolex corethrurus*	*Lampito mauritii*	*Polypheretima elongata*	*Dichogaster modiglianii*	*Drawida nepalensis*	*Eutyphoeus gammiei*
Cocoons studied (*n*)	40	40	40	40	40	40	5
Morphology	Spindle shaped	Spheroidal	Oval	Spheroidal	Pear shaped	Onion shaped	Spheroidal
Length (mm)	6·52 ± 0·44	5·0 ± 0·28	5·0 ± 0·4	3·6 ± 0·35	2·0 ± 0·28	4·6 ± 0·21	7·4 ± 0·45
Breadth (mm)	2·1 ± 0·26	3·2 ± 0·33	2·8 ± 0·17	2·8 ± 0·17	1·3 ± 0·1	3·0 ± 0·28	6·8 ± 0·33
Colour (oxidized/aged)	Dark straw	White	Light straw	Yellowish	Off-white	Reddish	Dark grey
Ornamentation	Bristles at the pointed end	Absent	Absent	Two small curved pointed ends	One end with single pointed end and other bears a circlet of bristles	Well developed pointed end on either side	Absent
Fresh weight (mg)	5·0 ± 0·4	21·0 ± 0·6	20·6 ± 0·8	30·2 ± 1·8	1·5 ± 0·04	14·4 ± 0·5	103·2 ± 1·8
Time course of cocoon production	Continuous	Continuous	Semi-continuous	Continuous	Continuous	Semi-continuous	Discrete
Cocoon production $worm^{-1}$ $year^{-1}$	156	118	43	23	68	29	1
Development time (days)	12·80 ± 0·31 (*n* = 21)	29·03 ± 1·40 (*n* = 33)	14·93 ± 0·51 (*n* = 31)	49·53 ± 1·77 (*n* = 15)	14·16 ± 0·48 (*n* = 31)	24·26 ± 1·58 (*n* = 15)	110·0 (*n* = 1)
Hatching success (%)	52·50	85	60	40	77·50	37·50	20·0
Hatchlings $cocoon^{-1}$	1·30 ± 0·11 (*n* = 21)	1·03 ± 0·02 (*n* = 33)	1·67 ± 0·11 (*n* = 31)	1·33 ± 0·12 (*n* = 15)	1·0 (*n* = 31)	1·80 ± 0·19 (*n* = 15)	1·0 (*n* = 1)
Hatchling size (mm) (length × breadth)	4·8 ± 0·52 × 1·0 ± 0·0 (*n* = 5)	6·60 ± 0·45 × 2·0 ± 0·44 (*n* = 5)	12·7 ± 1·6 × 1·4 ± 0·21 (*n* = 5)	24·0 ± 1·5 × 1·8 ± 0·17 (*n* = 5)	5·8 ± 0·33 × 1·0 ± 0·0 (*n* = 5)	7·8 ± 0·76 × 1·4 ± 0·21 (*n* =5)	50·0 × 3·0 (*n* = 5)
Room temperature during incubation (°C)	31·07 ± 0·26	30·11 ± 0·16	29·71 ± 0·27	30·38 ± 0·15	30·85 ± 0·14	30·35 ± 0·24	30·46
Room temperature during hatching (°C)	29·52 ± 0·25	29·76 ± 0·34	29·60 ± 0·49	30·61 ± 0·53	29·88 ± 0·31	29·56 ± 0·60	28·0

size, development time and hatching success of cocoons differ greatly among earthworm species. The highest and lowest size and weight of cocoons were found in the giant anecic worm *Eutyphoeus gammiei* and the smallest epigeic earthworm *Dichogaster modiglianii* respectively. Lavelle (1981) and Senapati and Sahu (1993) found a positive relationship between the size of the adults and the cocoons produced by earthworms. Edwards and Bohlen (1996) however proposed that cocoon size is not always correlated with adult size. Tufts

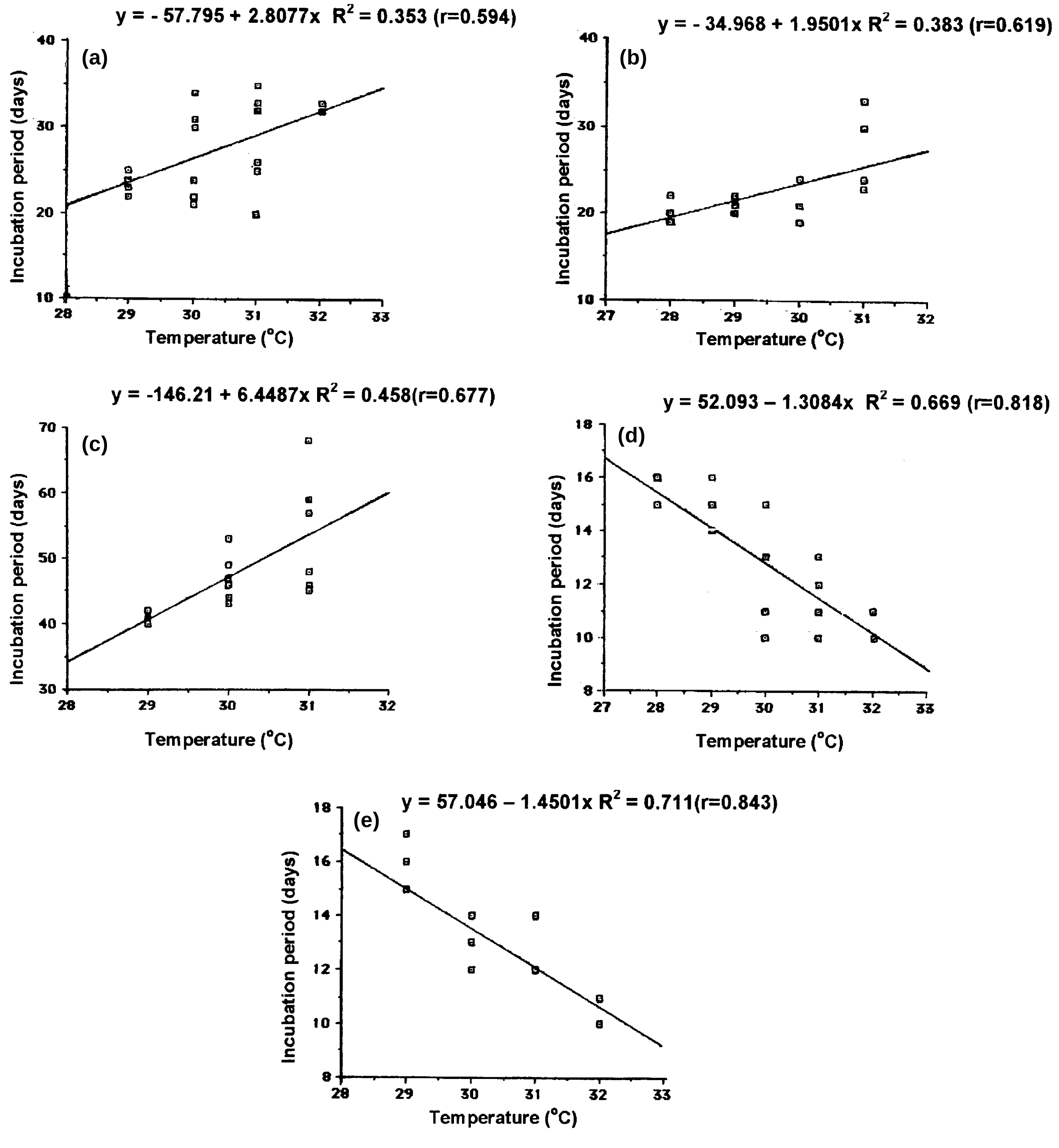

Figure 3. Linear regression analysis between temperature and incubation period in different earthworm species. (**a**) *Pontoscolex corethrurus*, (**b**) *Drawida nepalensis*, (**c**) *Polypheretima elongata*, (**d**) *Perionyx excavatus* and (**e**) *Dichogaster modiglianii*.

of bristles at the pointed ends of cocoons in *Perionyx excavatus* and *Dichogaster modiglianii* are adaptive features of these epigeic species that enable them to adhere to the litter in their surroundings. Viljoen and Reinecke (1989) reported fibrous tips at both ends of the cocoon in the African epigeic worm, *Eudrilus eugeniae*.

The development time of cocoons varies considerably among earthworm species. Among endogeic earthworms, development time of cocoons was short in topsoil endogeic worms, *Lampito mauritii* (15 days), *Drawida nepalensis* (25 days) and *Pontoscolex corethrurus* (29 days) and long in the subsoil endogeic earthworm, *Polypheretima elongata* (50 days). Development time of 28 days was reported for the cocoons of *Polypheretima elongata* (Sahu and Senapati 1991) and *Lampito mauritii* (Dash and Senapati 1980). Kaushal *et al* (1995) reported an incubation period of 30·5 days for the cocoons of *Drawida nepalensis* in moist filter paper under 25°C temperature regime. The above values on cocoon development time for these earthworms species are different from our present observation due to different methods adopted by the investigators. A prolonged development time (110 days) was found for the cocoons of the subsoil anecic worm, *Eutyphoeus gammiei*. The development time of cocoons was very short in the epigeic worms, *Perionyx excavatus* (13 days) and *Dichogaster modiglianii* (14 days). Senapati and Sahu (1993) reported a mean incubation period of 7 days for *Dichogaster bolaui*, a small, tropical, epigeic worm.

Temperature affects the incubation period of cocoons. With increase in room temperature, incubation period increased in endogeic worms, *Pontoscolex corethrurus*, *Polypheretima elongata* and *Drawida nepalensis*, and decreased in epigeic worms, *Perionyx excavatus* and *Dichogaster modiglianii*. Reinecke *et al* (1992) reported a mean incubation period of 17·8 days and 15·3 days for cocoons of *Perionyx excavatus* incubated at 25°C and at 25–37°C, respectively. They further reiterated that temperatures higher than 25°C decreased the mean incubation period in the epigeic worms *Perionyx excavatus*, *Eudrilus eugeniae* and *Eisenia fetida*. According to Holmstrup *et al* (1991) the threshold temperature for hatching should be regarded as an adaptation to the particular habitat condition in which the species lives. Increase in the incubation period with increase in the number of hatchlings per cocoon in *Lampito mauritii*

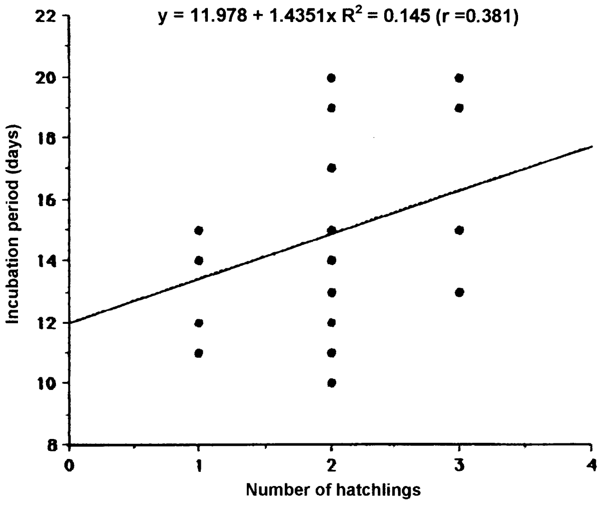

Figure 4. Linear regression analysis between number of hatchlings per cocoon and incubation period in *Lampito mauritii*.

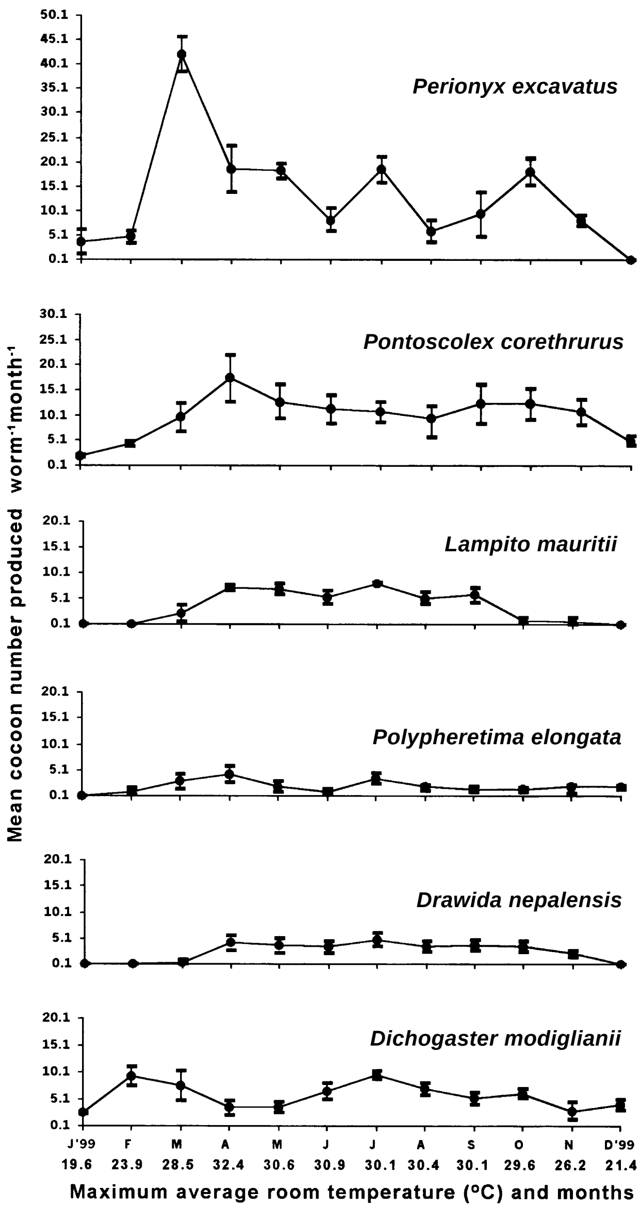

Figure 5. Number of cocoons produced (means ± SE) per worm per month for six species of earthworms.

results from delayed development due to limited resource utilization by all the embryos within the same cocoon. Edwards (1988) reported that development time of cocoons for temperate epigeic worms was 32–73 days in *Eisenia fetida*, 40–126 days in *Dendrobaena veneta*, and for tropical epigeic worms was 13–27 days in *Eudrilus eugeniae* and 16–21 days in *Perionyx excavatus*. According to Senapati and Sahu (1993) incubation period, in general, ranges from 3 to 30 weeks in temperate worms and 1 to 8 weeks in tropical worms.

Compared to the deep burrowing subsoil endogeic worm *Polypheretima elongata* and the anecic earthworm *Eutyphoeus gammiei*, hatching success was higher in the epigeic worms *Perionyx excavatus* and *Dichogaster modiglianii* and the top soil endogeic worms *Pontoscolex corethrurus* and *Lampito mauritii*, that face less competition in the surface soil with its less predictable environment. The mean hatching success of cocoons in *Perionyx excavatus* was 53%, which is close to the figure of 50% and far below that of 63·4% determined by Loehr *et al* (1984) and Hallatt *et al* (1990) respectively. Interestingly, Hallatt *et al* (1990) reported that hatching success of the cocoons of *Perionyx excavatus* was low when these were produced by newly matured non-mated worms (i.e. by self-fertilization or parthenogensis). Our value on hatching success in *Drawida nepalensis* (37·5%) is far lower than the value (84%) reported for the same species under controlled conditions by Kaushal *et al* (1995). The species we studied, with few exceptions, produced one hatchling per cocoon, although emergence of two (sometimes three) juveniles from the cocoons of *Lampito mauritii* and *Drawida nepalensis* was not rare. Dash and Senapati (1980) and Kaushal *et al* (1995) also reported rare emergence of two juveniles from cocoons of *Lampito mauritii* and *Drawida nepalensis* respectively. Mean number of hatchlings per cocoon was 3·3, 2·3 and 1·1 for the cocoons of the epigeic earthworms *Eisenia fetida*, *Eudrilus euginiae* and *Perionyx excavatus* respectively (Edwards 1988).

Earthworms are continuous or semi-continuous breeders, producing ova at most times of the year (Olive and Clark 1978). *Perionyx excavatus*, *Pontoscolex corethrurus*, *Dichogaster modiglianii* and *Polypheretima elongata* are peregrine earthworms (Fragoso *et al* 1999) that are continuous breeders with high fecundity. Continuous breeding strategies with high fecundity should be considered as adaptive features of these peregrine worms. The widely distributed native species, viz. *Lampito mauritii* and *Drawida nepalensis* (Fragoso *et al* 1999) are semi-continuous breeders and *Eutyphoeus gammiei* with restricted north-eastern distribution (Halder 2000) is a discrete breeder. In *Drawida nepalensis* which attains sexual maturity within 45 days, Kaushal *et al* (1995) reported cocoon production for only 5 months after sexual maturity. Year-round cocoon production with five cocoon peaks in *Polypheretima elongata* under field conditions was reported by Sahu and Senapati (1991). The dramatic increase in cocoon production by most earthworm species in summer and monsoon with corresponding peaks during April and July were probably due to favourable temperature conditions in Tripura at that time. The least number of cocoons were produced by these worms in the winter months due to fall in temperature. Dash and Senapati (1980) reported that under field conditions earthworms of Orissa produced cocoons, not in the harsh summer (when air temperature is around 45°C) but in the monsoon and post-monsoon seasons (air temperature < 30°C). In fact, temperatures beyond optimum levels act as cues for decreased neurosecretory activity, thus affecting cocoon production (Olive and Clark 1978).

Cocoon production (number/adult/year) varies with species and environmental conditions (Evans and Guild 1948; Satchell 1967). Among the seven earthworm spe-

Table 3. Number of cocoons produced (means ± standard errors) per earthworm species during three seasons.

Seasons and room temperature (°C)	Earthworm species					
	Perionyx excavatus	*Pontoscolex corethrurus*	*Polypheretima elongata*	*Drawida nepalensis*	*Dichogaster modiglianii*	*Lampito mauritii*
Winter (19–26)	4·17[a] ± 1·0	5·52[a] ± 0·98	1·17[a] ± 0·26	0·55[a] ± 0·25	4·92[a] ± 0·89	0·0[a]
Summer (28–31)	21·80[b] ± 3·4	12·80[b] ± 1·86	2·50[a] ± 0·64	2·92[b] ± 0·67	5·32[a] ± 1·0	5·5[b] ± 0·75
Monsoon (29–30)	12·95[c] ± 2·0	11·2[b] ± 1·51	2·02[a] ± 0·39	3·85[c] ± 0·59	7·02[a] ± 0·61	4·97[b] ± 0·78

Same letters in columns indicate non-significant variation between seasons for each species ($P > 0{\cdot}05$).
$n = 20$ for each mean value.

cies studied, highest and lowest cocoon production under fluctuating laboratory conditions (24–32°C) was by the epigeic worm *Perionyx excavatus* (156 cocoons adult^{-1} year^{-1}) and the anecic worm *Eutyphoeus gammiei* (1 cocoon adult^{-1} year^{-1}). Edwards (1988) reported production of 1014 cocoons adult^{-1} year^{-1} in *Perionyx excavatus* at 25°C which according to him is the optimum temperature for cocoon production in this species. Values of cocoon production at the rate of 19 adult^{-1} year^{-1} for *Polypheretima elongata* (Sahu and Senapati 1991), 14 adult^{-1} year^{-1} for *Lampito mauritii* (Dash and Senapati 1980) and 68 adult^{-1} year^{-1} for *Pontoscolex corethrurus* (Barois *et al* 1999) under field condition are lower than that observed in our present studies on cocoon production by *Polypheretima elongata* (23 adult^{-1} year^{-1}), *Lampito mauritii* (43 adult^{-1} year^{-1}) and *Pontoscolex corethrurus* (118 adult^{-1} year^{-1}). Senapati and Sahu (1993) postulated that size of the worms bears a negative relationship with cocoon production. Greater rate of cocoon production by small to medium sized epigeic earthworms *Dichogaster modiglianii* and *Perionyx excavatus*, and top soil endogeic worms *Pontoscolex corethrurus* and *Lampito mauritii* was due to exposure to their high mortality risk environment. Lee (1985) correlated the higher risk of mortality in early life with higher rate of cocoon production. On the contrary, large, burrowing subsoil earthworms, *Eutyphoeus gammiei* and *Polypheretima elongata* produced much fewer cocoons compared to the topsoil species studied. Jiménez *et al* (1999) also reported a very low rate of cocoon production under field conditions by *Martiodrilus carimaguensis*, a giant deep burrowing earthworm from Colombia. According to Satchell (1967) there is a clear relationship between the number of cocoons produced and their location in the soil profile. Those species that can move into deeper soil layers and are protected from adverse conditions produce fewest cocoons, whereas those living near the surface, and facing adverse conditions, produce many more cocoons. Cocoon production and time for maturation of cocoons vary with species, population density, age structure and external factors especially soil temperature, moisture and energy content of the available food (Lee 1985; Edwards and Bohlen 1996).

A relationship between reproductive strategies and ecological categories in tropical earthworms was proposed by Lavelle *et al* (1998) and Barois *et al* (1999). They distinguished four groups of earthworms. These are group 1: large native endogeic and anecic species with low fecundity (0·5–3·1 cocoons adult^{-1} year^{-1}) and only one hatchling per cocoon; group 2: medium-sized mesohumic endogeic species with intermediate fecundity (1·3–45 cocoons adult^{-1} year^{-1}); group 3: small mainly polyhumic endogeic species with intermediate fecundity (10–68 cocoons adult^{-1} year^{-1}) and usually one hatchling per cocoon; and group 4: generally small, mainly exotic and epigeic species with very high fecundity (50–350 cocoons adult^{-1} year^{-1}) and up to three hatchlings per cocoon. From our studies it appears that *Eutyphoeus* sp. belongs to group 1, *Polypheretima* sp. to group 2, *Drawida* sp., *Pontoscolex* sp. and *Lampito* sp. to group 3, *Perionyx* and *Dichogaster* sp. to group 4 categories.

Pianka (1970) on the basis of response to selection pressure, classified organisms into two categories: *r*-selected and *K*-selected species. High fecundity (i.e. high rate of cocoon production), short incubation period with high hatching success in epigeic (*Dichogaster modiglianii* and *Perionyx excavatus*) and top soil endogeic worms (*Pontoscolex corethrurus*, *Drawida nepalensis* and *Lampito mauritii*) are probably adaptive strategies of '*r*'-selected worms (Sahu and Senapati 1991) to enable them to survive drastic environmental changes, especially heat, drought and predation in the top soil. Large body size, low fecundity, long incubation period and low hatching success in the subsoil anecic worm, *Eutyphoeus gammiei* and endogeic *Polypheretima elongata* are characteristics of species with '*K*'-selection (Sahu and Senapati 1991), where the environment is predictable and benign and competition is intense (Wallwork 1983).

The giant worm, *Eutyphoeus gammiei*, that displays a very long cocoon development time and a discrete and very low rate of cocoon production, is not a suitable species for vermiculture. The more continuous and high rate of cocoon production as well as higher hatching rate in *Perionyx excavatus*, *Dichogaster modiglianii*, *Pontoscolex corethrurus*, *Drawida nepalensis* and *Lampito mauritii* indicate their possible usefulness in vermiculture-based biotechnology.

Acknowledgements

The authors express their sincere thanks to Prof. J P Roy Chowdhuri for providing laboratory facilities, Prof. Radha D Kale and Dr K E Lee for their valuable comments on the paper, Prof. D K Nanda, Department of Zoology, Calcutta University for encouragement and Dr K R Halder, Zoological Survey of India, Kolkata, for identification of earthworms, Prof B K Agarwal, Tripura University and Mr Anil Das, Department of Statistics, MBB College for statistical analysis. Financial assistance from Indian Council of Agricultural Research, New Delhi is gratefully acknowledged.

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MS received 11 July 2001; accepted 23 April 2002

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