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Bioenergetics of the household millipede pest, *Xenobolus carnifex* (Fabricius, 1775) (Diplopoda: Spirobolida)

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Abstract

The household millipede pest, *Xenobolus carnifex* infests organic roofing, causing heavy damage to thatched huts. Following the scheme of energy balance provided by Petrusewicz & MacFadyen (1970), bioenergetics of *X. carnifex* reared on *Aristida sativa* reed was studied at 28, 32 and 36 °C. The millipede passed through nine juvenile stadia and subsequently moulted as subadult and adult. The overall life span was 1082, 1017 and 869 days at the investigated temperatures. The millipede lost about 68 – 72 % of the ingested food as faeces and assimilated the rest with an efficiency ranging from 28 to 32 %. Over 95 % of the assimilated energy was lost on metabolism resulting in conversion of about 1 to 2 % of the ingested or 3.5 % of the assimilated energy into body tissue. The gross and net conversion efficiencies decreased with increasing temperatures as well as rates of feeding, assimilation, production and metabolism. The study has demonstrated the role of *X. carnifex* in the turnover of energy in the strange ecosystem in the rooftop of huts.

1. Introduction

Millipedes constitute one of the major groups of soil and litter fauna in temperate and tropical environments. They play an important role in energy flow, as well as in the humification of soil and circulation of minerals in terrestrial ecosystems (Kayed 1985, Crawford 1992). Some species are known as mull formers (Romell 1935). *Xenobolus carnifex* is a household pest, which infests the thatch materials used for covering roofs in India. People living in the huts endure a continuous shower of faecal pellets of the millipede from the roof; during the rainy season, adults and juveniles descend on all the household articles, food and drinking water. The millipede is exposed to harsh and desiccating conditions in its habitat and is restricted to feed on low quality, dry thatching materials. It is a slow-growing animal, which attains a final biomass > 1 g in about two years.

Temperature and photoperiod significantly influence food consumption and utilisation in arthropods (Scriber & Slansky 1981, Muthukrishnan & Pandian 1983, 1984). The present paper reports the effects of temperature on the utilisation of highly intractable reeds of *Aristida sativa* by *X. carnifex*.

2. Materials and methods

2.1. Maintenance of test animals

Freshly moulted *X. carnifex* belonging to different stadia (III to XII) were used in the present investigation. They were obtained from our laboratory culture maintained as described by Alagesan & Muthukrishnan (2003). Before commencing the feeding experiments, the selected individuals were starved for 12 hrs to ensure that their gut was empty. Except the animals belonging to stadium III all the test animals were reared individually in cylindrical plastic terraria (9 cm h x 5 cm diam.); animals of stadium III were reared in groups of two. There were five replicates for each life stage. Experimental animals were maintained in an incubator adjusted to 28, 32, or 36 ± 1 °C, 10L: 14D photoperiod and 80 ± 5 % relative humidity.

2.2. Feeding, collection of faeces and estimation of bioenergetic parameters

Reeds of *Aristida sativa* collected from 2 – 3 year old thatched roofs were cut into 3 cm long bits and dried at 70 °C to weight constancy; they were preserved in an airtight desiccator. Three to five bits of the reed were weighed in an analytical balance to an accuracy of 0.01 mg and offered as food to the millipede. The feed was kept moist by spraying 2 ml of water over it at 10:00 and 16:00 every day. Samples of feed offered every day were weighed, dried at 70 °C to weight constancy. Considering the water content of the sample feed, dry weight of the feed offered was calculated. Residual feed left over in the terraria and faecal pellets egested by the test animals were carefully collected every day before offering the feed and dried separately at 70 °C. Food consumption during a stadium or a specific feeding period was calculated in terms of dry weight by subtracting the dry weight of the residual feed collected during the stadium from the dry weight equivalent of the feed offered. The animals were weighed at the commencement and termination of each stadium or feeding experiment. Samples of freshly moulted animals were weighed and dried at 70 °C to weight constancy. Considering the water content of the animals, the dry weight equivalent of the test animals was calculated. The feeding experiment was continued till the young moulted into the next stadium. For stadia whose duration was prolonged beyond 60 days and for subadults and adults, which survived beyond 60 days, three different weight classes were selected and the feeding experiment was conducted with each weight class for 15 days. Considering the performance of the weight classes within a life stage, bioenergetics parameters for that stage were calculated. The calorific contents of food, faeces, and animals at the commencement and termination of a stadium/feeding experiment were estimated in a Parr semi-micro bomb calorimeter. Gravimetric data on food consumption (C), egestion (FU) and growth (P) were converted into Joules (J).

In the formula of Petrusewicz & MacFadyen (1970)

$$C = F+U+R+P$$

C represents the food energy consumed, P (production) the growth, R (respiration), F (faeces) and U (urine) are the energy loss through metabolic heat production, undigested faecal material and the nitrogenous excretory product, respectively. Nitrogenous excretory products mix with faecal pellets in millipedes, and hence energy assimilated (A) was calculated as the difference between C and FU. Energy expended on metabolism was calculated as the difference between A and P. Assimilation efficiency (Ae) was calculated in percentage relating A to C. Gross (Pe_1) and net (Pe_2) production efficiencies were calculated in percentage relating production to C and A, respectively. Rates of feeding (Cr), assimilation (Ar), production (Pr) and metabolism (Mr) by the different stadia were calculated by dividing the corresponding quantitative values expressed on an individual basis by the mid-body weight (Waldbauer 1968) of the millipede and the duration of the stadium/feeding period in days. The rates are expressed as kJ/g live millipede/day. Overall energy budget for the whole lifespan was prepared considering the contributions made by the different life stages of the millipede. Overall rates were calculated by dividing the sum of products of the rate and duration of each stadium by the total feeding period (see Muthukrishnan & Pandian 1983, 1984).

3. Results

3.1. Stadial duration

Freshly hatched *X. carnifex* grows and moults inside the egg capsule till attaining the III stadium in about 7 days. The duration of different juvinile stadia (III to IX) widely fluctuated between 7 and 229 days at the different temperatures. The subadult stadium (X) lasted for 287.5, 283 and 249 days at 28, 32 and 36 °C. Briefly, the life span of *X. carnifex* ranged from 869 days at 36 °C to 1017 and 1081.5 days at 32 and 28 °C.

Tab. 1 Individual consumption and utilisation of *A. sativa* reed energy (kJ/animal) by *X. carnifex* reared at 28 °C. Each value (Mean ± SD) represents the average performance of 5 animals. For abbreviations see »Materials and methods«.

Stadium	Duration (days)	C	FU	A	P	R
III	7.0 ± 0.57	0.97 ± 0.08	0.61 ± 0.06	0.36 ± 0.03	0.02 ± 0.00	0.34 ± 0.03
IV	10.0 ± 0.85	2.22 ± 0.18	1.41 ± 0.12	0.81 ± 0.79	0.04 ± 0.03	0.77 ± 0.06
V	31.5 ± 2.5	4.75 ± 0.41	3.06 ± 0.28	1.69 ± 0.13	0.10 ± 0.2	1.59 ± 0.14
VI	39.0 ± 3.4	10.2 ± 0.9	6.74 ± 0.61	3.46 ± 0.26	0.18 ± 0.2	3.28 ± 0.25
VII	41.5 ± 3.6	18.7 ± 1.5	12.6 ± 1.1	6.03 ± 0.46	0.32 ± 0.2	5.71 ± 0.44
VIII	46.5 ± 3.9	37.3 ± 3.3	25.5 ± 2.1	11.8 ± 1.0	0.85 ± 0.07	11.0 ± 1.0
IX	80.0 ± 6.3	81.4 ± 6.7	56.4 ± 4.9	25.0 ± 1.9	1.88 ± 0.14	23.1 ± 2.2
X (subadult)	287.5 ± 24.6	128.4 ± 11.3	91.9 ± 6.9	36.5 ± 3.2	2.68 ± 0.23	33.9 ± 3.1
XI (adult)	363.5 ± 29.2	164.2 ± 13.3	119.3 ± 1.0	44.9 ± 3.5	1.83 ± 0.13	43.0 ± 3.6
XII	175.0 ± 15.6	95.5 ± 8.2	70.6 ± 6.2	24.9 ± 2.2	0.74 ± 0.00	24.2 ± 2.1
Overall	1082 ± 100	543.6 ± 51.0	388.1 ± 31.1	155.5 ± 14.0	8.64 ± 0.70	146.8 ± 13.9

Tab. 2 Individual consumption and utilisation of *A. sativa* reed energy (kJ/animal) by *X. carnifex* reared at 32 °C. Each value (Mean ± SD) represents the average performance of 5 animals.

Stadium	Duration (days)	C	FU	A	P	R
III	10.0 ± 0.9	1.18 ± 0.11	0.74 ± 0.06	0.44 ± 0.44	0.02 ± 0.00	0.42 ± 0.04
IV	26.0 ± 2.1	2.16 ± 0.19	1.35 ± 0.12	0.81 ± 0.06	0.04 ± 0.00	0.77 ± 0.07
V	28.0 ± 2.3	4.84 ± 0.41	3.07 ± 0.29	1.77 ± 0.16	0.08 ± 0.00	1.69 ± 0.14
VI	33.5 ± 2.9	11.9 ± 1.0	7.65 ± 0.68	4.22 ± 0.39	0.18 ± 0.02	4.04 ± 0.39
VII	44.0 ± 4.0	20.9 ± 1.9	13.8 ± 1.3	7.12 ± 0.64	0.26 ± 0.02	6.86 ± 0.61
VIII	90.0 ± 8.3	40.8 ± 3.6	27.3 ± 2.5	13.5 ± 1.1	0.71 ± 0.50	12.8 ± 1.25
IX	228.5 ± 20.2	118.0 ± 10.1	79.2 ± 5.6	38.9 ± 3.5	2.41 ± 0.21	36.4 ± 3.5
X (subadult)	283.0 ± 25.4	212.9 ± 18.5	144.0 ± 13.3	68.9 ± 6.3	2.09 ± 0.20	66.8 ± 5.6
XI (adult)	156.5 ± 14.77	155.2 ± 13.1	109.0 ± 11.0	46.2 ± 3.5	0.74 ± 0.06	45.4 ± 4.3
XII	117.5 ± 10.6	126.6 ± 11.2	90.0 ± 7.9	36.5 ± 3.0	0.90 ± 0.08	35.6 ± 3.0
Overall	1017 ± 101	694.3 ± 61.1	476.1 ± 51.9	218.3 ± 22.7	7.43 ± 1.10	210.8 ± 21.3

Tab. 3 Individual consumption and utilisation of *A. sativa* reed energy (kJ/animal) by *X. carnifex* reared at 36 °C. Each value (Mean ± SD) represents the average performance of 5 animals.

Stadium	Duration (days)	C	FU	A	P	R
III	8.0 ± 0.71	0.90 ± 0.09	0.54 ± 0.05	0.36 ± 0.03	0.01 ± 0.00	0.34 ± 0.03
IV	22.0 ± 1.8	2.12 ± 0.17	1.38 ± 0.12	0.74 ± 0.07	0.03 ± 0.00	0.71 ± 0.14
V	29.0 ± 2.5	4.15 ± 0.39	2.80 ± 0.20	1.36 ± 0.12	0.06 ± 0.01	1.30 ± 0.11
VI	32.5 ± 2.6	8.08 ± 0.71	5.51± 0.50	2.58 ± 0.23	0.13 ± 0.01	2.45 ± 0.18
VII	44.5 ± 3.9	16.19 ± 1.34	11.1 ± 1.0	5.06 ± 0.42	2.34 ± 0.02	4.82 ± 0.42
VIII	49.0 ± 4.2	33.42 ± 2.80	23.3 ± 1.6	10.1 ± 0.8	0.56 ± 0.04	9.56 ± 0.81
IX	168.5 ± 15.8	82.42 ± 7.12	58.3 ± 3.9	24.2 ± 2.5	1.72 ± 0.13	22.5 ± 2.2
X (subadult)	249.0 ± 22.0	153.50 ± 14.45	110.4 ± 10.3	43.1 ± 4.2	1.85 ± 0.16	41.3 ± 3.6
XI (adult)	172.5 ± 15.6	229.43 ± 19.37	166.6 ± 14.8	62.8 ± 5.5	1.10 ± 0.09	61.7 ± 5.6
XII	94.0 ± 8.0	109.6 ± 10.0	80.3 ± 7.2	29.3 ± 2.5	0.48 ± 0.04	28.9 ± 2.2
Overall	869.0 ± 8.5	589.8 ± 55.9	460.2 ± 41.7	179.7 ± 20.2	6.18 ± 0.61	173.5 ± 13.0

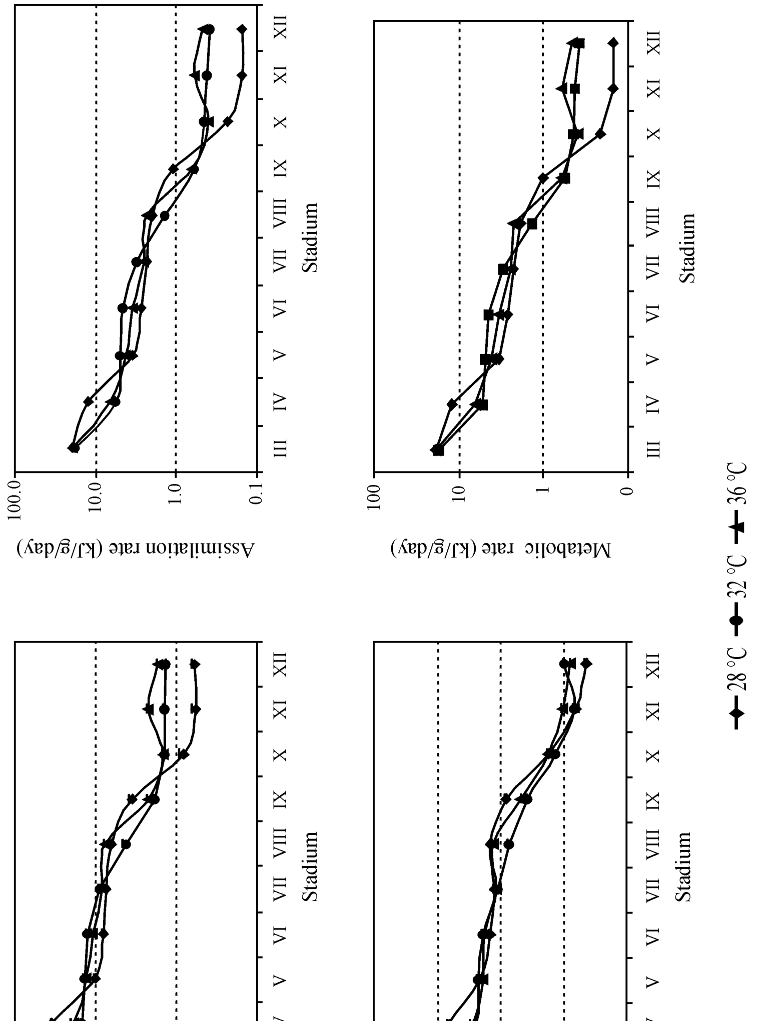

Fig. 1 Rates of feeding of *X. carnifex* at different temperatures.

3.2. Food consumption

Tabs 1, 2 and 3 provide data on food consumption and utilisation by the different stadia of *X. carnifex* at 28, 32 and 36 °C respectively. Irrespective of the temperature, with advancing life stage and corresponding increase in the duration of the stadia, food consumption during the different stadia increased. For instance, at 32 °C, food energy consumed increased from 1.18 kJ/animal in stadium III to 212.86 kJ/animal in stadium X (Tab. 2). Owing to the shorter duration, food consumption during the mature adult (XII) stadium compared with stadium XI was less. Maximum food consumption was during stadium XI at 28 and 36 °C and during stadium X at 32 °C. Irrespective of temperature, the highest feeding rate was observed during stadium III. With advancing stadium, the feeding rate of *X. carnifex* decreased at all the temperatures due to increase in the stadial duration and body weight (Fig. 1).

3.3. Assimilation

X. carnifex egested over 60 to 75 % of the ingested food energy as faeces and nitrogenous excretory material. Food energy assimilated by the different stadia increased corresponding to the increase in the food energy consumed. For instance, at 28 °C, energy assimilated increased from 0.36 kJ during stadium III to 44.86 kJ during stadium XI and subsequently decreased to 24.93 kJ during the shorter stadium XII (Tab. 1). As in the case of the feeding rate, the assimilation rate decreased with advancing stadium. The rate for stadia X, XI and XII at 28 °C was significantly less than that at 32 and 36 °C, whereas that of stadium IV was greater (Fig. 1). The juveniles assimilated the feed more efficiently than the subadult and adult stages. At the tested temperatures, assimilation efficiency during the different juvenile stadia (stadia III to IX) varied between 29.2 and 39.4 % compared with 26.1 to 32.4 % during the subadult X and mature adult stages XII (Fig. 2).

4. Production

Production of body tissue during the different stadia increased with advancing stadium; at 28 and 36 °C, maximum production was realised during the subadult stadia (X) and at 32 °C during preadult stadia (IX) (Tabs. 1 – 3). Irrespective of the temperature production rate decreased with advancing stadia. The highest rate of 1040.8 J/g/day was recorded for stadium III reared at 28 °C compared to 4.5 J/g/day for stadium XII at 28 °C (Fig. 1). Gross production efficiency (Pe_1) of *X. carnifex* ranged from 0.4 % for stadium XII at 36 °C to 2.3 % for stadium IX at 28 °C (Fig. 2). Obviously, only a very small proportion of the nutritionally poor *A. sativa* reed energy could be utilised for tissue production. Net production efficiency (Pe_2) of *X. carnifex* ranged between 1.6 to 7.5 % for the different stadia (Fig. 2).

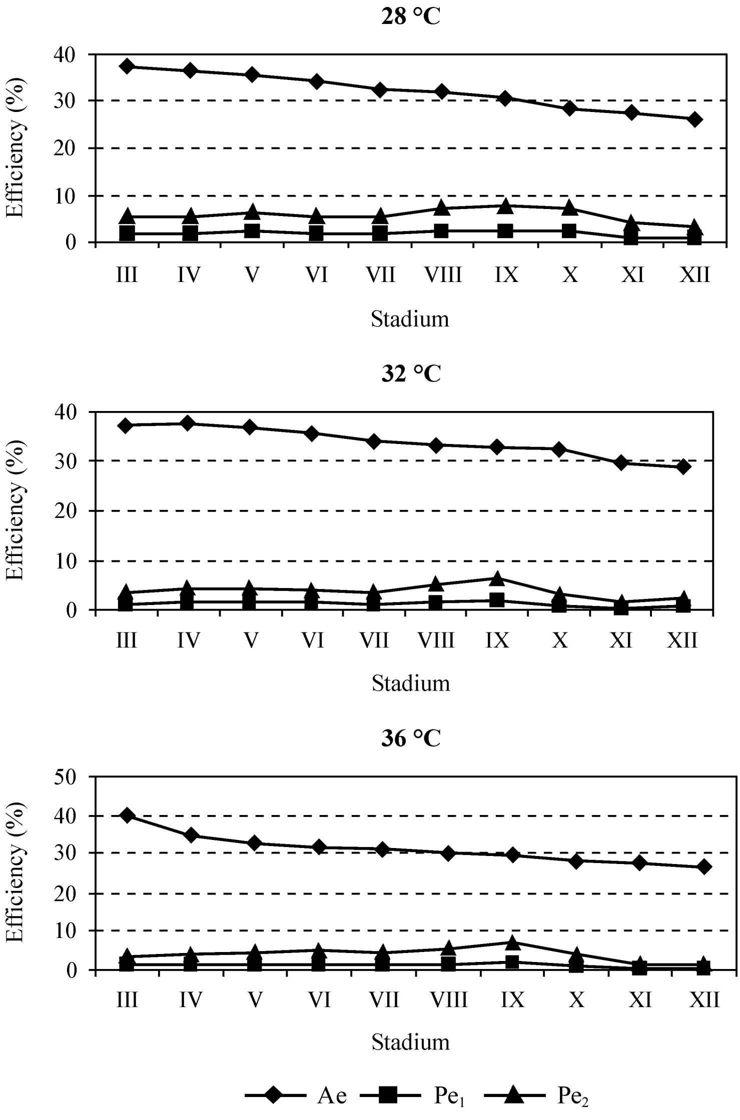

Fig. 2 Efficiencies of assimilation (Ae), gross (Pe_1) and net (Pe_2) conversion of *X. carnifex* at different temperatures.

4.1. Metabolism

A major part of the assimilated energy was expended on metabolism. Energy expended on metabolism was greater for the larger animals compared with the smaller animals. Trends obtained for metabolic rate were similar to those of assimilation rate. Whereas the Mr of stadia IV and IX was greater at 28 °C, that of stadia X, XI and XII was less compared to that at 32 and 36 °C (Fig. 1). A significant positive correlation was obtained for the relation between feeding rate and metabolic rate ($r = 0.998$; $P < 0.05$).

4.2. Overall energy budget

The overall energy budget of *X. carnifex* is given in Tab. 4. At 28 °C *X. carnifex* ingested 543.6 kJ of *A. sativa* reed at the rate of 2.476 kJ/g/day and assimilated 155.5 kJ at the rate of 0.818 kJ/g/day with an efficiency of 28.6 %. It converted 8.64 kJ at the rate of 0.048 kJ/g/day with a net production efficiency of 5.6 %. With increasing temperature, the rates of food consumption and utilisation decreased while the assimilation efficiency increased. The net production efficiency was 3.4 % at 32 and 36 °C compared with 5.6 % at 28 °C, indicating that the animal converted the feed more efficiently at lower temperature.

Tab. 4 Overall bioenergetics of *X. carnifex* fed ad libitum on *A. sativa* reed at 28, 32 and 36 °C. Each value (Mean ± SD) represents the average performance of 5 individuals. Means in a row with different superscripts (a, b, c) are significantly different at $P < 0.05$ (SNK Test). Means with the same superscript are not significantly different. C, FU, A, P and M are in kJ/animal; Cr, Ar, Pr and Mr are in kJ/g/day.

Parameter	28 °C	32 °C	36 °C
Duration (day)	$1083^{b} \pm 109$	$1017^{ab} \pm 92$	$869^{a} \pm 84$
Consumption (C)	$543.6^{a} \pm 40.0$	$694.3^{b} \pm 41.2$	$639.9^{b} \pm 40.0$
Egestion (FU)	$388.0^{a} \pm 37.0$	$476.0^{b} \pm 46.2$	$460.2^{ab} \pm 58.0$
Assimilation (A)	$155.5^{a} \pm 12.6$	$218.3^{b} \pm 11.0$	$179.7^{a} \pm 9.9$
Production (P)	$8.64^{c} \pm 0.43$	$7.4^{b} \pm 0.32$	$6.2^{a} \pm 0.38$
Metabolism (M)	$146.8^{a} \pm 14.2$	$210.8^{b} \pm 21.6$	$173.6^{ab} \pm 20.5$
Assimilation efficiency (%)	$28.6^{a} \pm 1.61$	$31.5^{a} \pm 1.03$	$30.5^{a} \pm 1.2$
Gross production efficiency (%)	$1.60^{b} \pm 0.13$	$1.10^{a} \pm 0.12$	$1.10^{a} \pm 0.10$
Net production efficiency (%)	$5.6^{b} \pm 0.44$	$3.4^{a} \pm 0.12$	$3.4^{a} \pm 0.15$
Feeding rate (Cr)	$2.48^{a} \pm 0.16$	$3.42^{b} \pm 0.31$	$4.11^{c} \pm 0.38$
Assimilation rate (Ar)	$0.818^{a} \pm 0.08$	$1.188^{b} \pm 0.16$	$1.30^{c} \pm 0.12$
Production rate (Pr)	$0.048^{a} \pm 0.0$	$0.049^{a} \pm 0.0$	$0.057^{a} \pm 0.01$
Metabolic rate (Mr)	$0.7740^{a} \pm 0.05$	$1.14^{b} \pm 0.12$	$1.25^{b} \pm 0.11$

5. Discussion

Xenobolus carnifex feeds exclusively on dead and decaying vegetation, particularly dry materials such as *A. sativa* reed used for thatching huts. As in the case of other millipedes occurring in unconventional habitats, food selection appears to be a function of habitat (Wooten & Crawford 1975). Inhabiting the roof of huts, which provides abundant and constant food supply, energy cost of foraging for the animal is almost negligible. It is amazing to note that in the present study, in the course of development from hatching to death in about 869 to 1082 days *X. carnifex* ingested 58.3 to 76.2 g of dry reed per individual at temperatures ranging from 28 to 36 °C. These estimates clearly substantiate the fact that millipedes play a dominant role in the recycling of detritus energy in the ecosystem (see Reichle 1967, O'Neill 1968, McBrayer 1973).

Cellulolytic and lignolytic bacteria that colonise the reed help in the easy digestion of the feed material by *X. carnifex* and thereby play an important role in determining the rates and efficiency of utilisation of these materials (Alagesan et al. 2003). As the feed was almost dry, water content of the feed does not seem to have a role in the regulation of food intake. As *X. carnifex* had to obtain adequate energy to sustain its activities from energetically poor thatch materials, it maintained a very high feeding rate (ranging from 52.8 to 0.6 kJ/g/day) during the different stadia. Similar differences in the »feeding level« and »weight exponent« have also been reported for the painted grasshopper, *Poecilocerus pictus* (Delvi & Pandian 1972). Relating body weight to food consumption in the millipede *Jonespeltis splendidus* (Verhoeff, 1936), Bano (1996) reported that the dry weight of food consumed by the different stadia was equal to 125 to 225 times of dry weight of their biomass. In the present study, dry weight of food consumed by *X. carnifex* averaged to 120 to 165 times of the dry biomass of the different stadia. *X. carnifex* is a slow-growing animal with the older stadia (X and XI) lasting for more than 200 days and hence its average food consumption in terms of dry biomass of the stadium is comparatively less than that of the fast growing *J. splendidus*. Overall feeding rate of *X. carnifex* in the present study ranged from 2.476 kJ/g/day at 28 °C to 4.113 kJ/g/day at 36 °C.

X. carnifex lost 60 to 75 % of the ingested feed as faeces. Crawford (1992) has described diplopods inhabiting soil-litter system as accelerators, regulators and decomposers. Van der Drift (1951), Gere (1956), Dunger (1958) and Bocock (1963) indicated that millipedes consume considerable quantities of food materials but the amount utilised is in comparison very small, thus the amount of litter converted into humus is very high. A similar role may be assigned to *X. carnifex* in the present study as it ingests vast quantity of plant detritus, feeds on most of the soft parts of the feed leaving the hard midrib and veins and transform most part of the feed as faecal pellets rich in organic constituents. The transformed materials (i.e. faecal pellets) in turn are utilised by coprophagous arthropods inhabiting the roof. Bano (1996) attributed a similar role to the soil-dwelling millipede *Jonespeltis splendidus*.

The pattern of the assimilation rate of *X. carnifex* was similar to that of the feeding rate. Younger stadia assimilated the feed at a faster rate compared with the older stadia. With the ability to assimilate the ingested feed at a faster rate, the smaller animals could allocate enough energy to tissue production and maintain a higher metabolic rate, which is characteristic of younger animals. In general the assimilation efficiency decreased with advancing development. The overall assimilation efficiency of *X. carnifex* ranged between 28.6 to 31.5 %. It was less at 28 °C compared with that at 32 or 36 °C. The millipede *Narceus americanus* (Beauvois, 1805) assimilated decaying logs with an efficiency of about 15 % (O'Neill 1968). Assimilation efficiency of the desert millipede, *Orthoporus ornatus* (Girard, 1853) fed on *Ephedra* sp. bark increased from 22 % at 20 °C to 37.6 and 33.7 % at 24 and 30 °C (Wooten & Crawford 1975). A critical analysis of the data reveals that the efficiency of *X. carnifex* is comparable with that of most the herbivorous insects and of a few millipedes such as *O. ornatus*. On the other hand efficiency of a few millipedes such as *Apheloria montana* (Bollman, 1887) is as low as 5 % (see also Gere 1956, Bocock 1963). Such a high efficiency for animals like *O. ornatus* feeding on bark or *X. carnifex* feeding on intractable materials like reed is understandably due to the symbiotic gut microflora, which produce enzymes that can break down complex polysaccharides such as lignin, xylan and cellulose.

X. carnifex expended about 95 % of the assimilated energy on metabolism. With increasing body weight, energy allocated to metabolism increased, whereas the metabolic rate decreased. A significant positive correlation coefficient ($r = 0.998$; $P < 0.05$) was obtained for the relation between feeding rate and metabolic rate of *X. carnifex,* indicating that the metabolic rate is dependent on the feeding rate. Muthukrishnan & Pandian (1983) have reported a similar relationship between the two variables for the moth *Achaea janata*. Apparently, *X. carnifex* is metabolically adapted to a wide range of temperatures.

X. carnifex is a poor converter of feed. The highest gross conversion efficiency ranging from 1.1 to 1.6 % was observed at 28 and 36 °C respectively. Considering the overall food consumption and tissue conversion, *X. carnifex* converted 0.9 to 1.5 units of energy out of 100 units of energy ingested. The cost of tissue production for *X. carnifex* appears to be very high. For instance, Blower (1974) showed that the millipede *Ophyiulus pilosus* (Newport, 1843) needed 18 – 30 units of dry weight of food for conversion in to one unit of dry weight of tissue. Kheirallah (1978) reported conversion ratios (dry wt. of food converted/dry wt. of food consumed) ranging from 0.003 to 0.009 for the different stadia of the millipede *Orthomorpha gracilis* (C. L. Koch, 1847).

Overall net conversion efficiency of *X. carnifex* ranged between 3.4 and 5.6 % (see Tab. 4). Comparable data for other millipedes are not available in literature. The low net conversion efficiency of *X. carnifex* is obviously due to the very high cost of metabolism, which is met by maintaining very high rates of feeding and assimilation. As in other animals, conversion in *X. carnifex* is a weight-dependent process. With advancing development and increasing body weight, the conversion rate decreased significantly.

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