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# Aspects of the Ecological Energetics of the Wolf Spider *Pardosa (Lycosa) lugubris* (Walckenaer)

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*Summary.* Feeding experiments were carried out on various stages of the wolf spider *Pardosa lugubris* in order to construct an energy budget for the spider. Under the rearing conditions the spiders developed at a similar rate to those in the field. *P. lugubris* females ingest 308 cal during their life. 73.0% of this energy goes into respiration and 25.7% into production. Males ingest 98 cal of which 81.3% goes into respiration and 16.1% into production.

*P. lugubris* ingests a large proportion of the food it kills and it resembles other arthropod carnivores in having high growth efficiencies.

The annual rate of energy flow through a wolf spider population was calculated. 1.39 Kcal/m$^2$/year are "killed" of which 81.2% is ingested. Of this ingested energy 71.1% goes into respiration and 26.4% into production.

The difficulties involved in the assessment of the results of single-species energetics studies are discussed.

The annual population energy budget of *P. lugubris* is compared with that of *Pyrrhosoma nymphula*, an aquatic arthropod carnivore with a similar life-cycle to *P. lugubris*. Although the magnitudes of the various components of the energy budget are larger in *P. nymphula*, there are similarities between the two species. Thus, the amount of energy "killed" per unit of predator biomass is similar and a similar proportion of this energy is returned to the ecosystem, although proportionally more goes into decomposers in *P. lugubris*.

## Introduction

Lawton (1971) has remarked upon the dearth of studies on the ecological energetics of invertebrate carnivores. The following is an account of the ecological energetics of the Wolf Spider *Pardosa lugubris* (Walckenaer)[1]. Wolf spiders are among the largest and most conspicuous members of the terrestrial invertebrate fauna of temperate regions. *P. lugubris* occurs over the whole of western Europe. It is also found in European and Asiatic Russia (Bristowe, 1939) and in Japan (Yaginuma, 1962). It is normally found in or near woods (Dahl, 1908; Locket and Millidge, 1951) and the specimens of *P. lugubris* used in this study

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[1] This animal has normally been called *Lycosa lugubris* in the British literature (Locket and Millidge, 1951) but it has recently been agreed by European arachnologists that the use of the generic name *Pardosa* is to be preferred (G. H. Locket, pers. comm.).

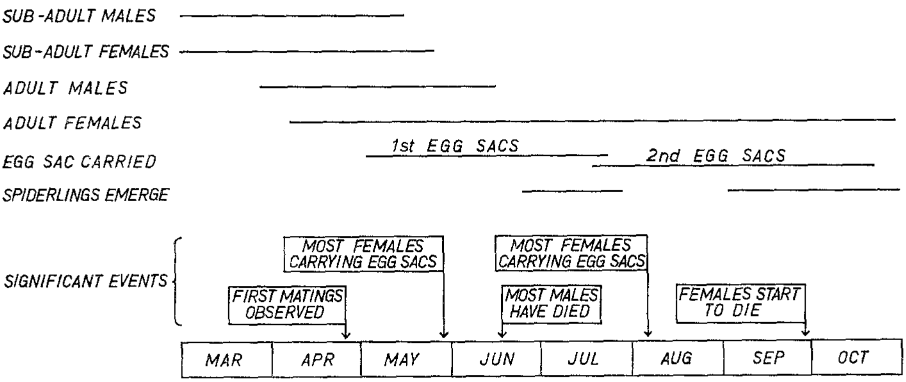

Fig. 1. Phenology of the adult stage of the life-cycle of *Pardosa lugubris*

were collected from oak woodland (*Quercus petraea*) near Glasgow University Field Station on the east bank of Loch Lomond, Scotland.

Laboratory feeding experiments were carried out on all stages of the life-cycle of *P. lugubris* in order to construct an energy budget for the animal. These results were combined with field data on density, natality and mortality (Edgar, in press, 1971a and b) to calculate a population energy budget.

## The Life-Cycle of *P. lugubris*

The life-cycle of *P. lugubris* has been discussed in detail elsewhere (Edgar, in press, 1971b) but an outline is given here to facilitate the understanding of the paper.

In Scotland *P. lugubris* overwinters twice before reaching maturity so that at any time of the year at least two distinct year groups are present. The adult females normally produce two egg sacs, one in summer and one in autumn (Fig. 1), and these are carried by the female attached to her spinnerets. The spiderlings from these egg sacs have reached the 3rd, 4th, and 5th instar stage by the time they overwinter. The spiders are normally inactive from late October to early March. During the following spring and summer these animals continue their development and by the autumn they have reached the sub-adult (penultimate) instar. The sub-adults overwinter, and moult to adult in the spring of the following year. Mating occurs soon afterwards and most of the adult males have died by mid-June. The adult females, after producing the two egg sacs, die in the autumn. The phenology of the adult stage of the life-cycle is indicated in Fig. 1. In Fig. 1 the total duration of various events and stages are indicated. For example,

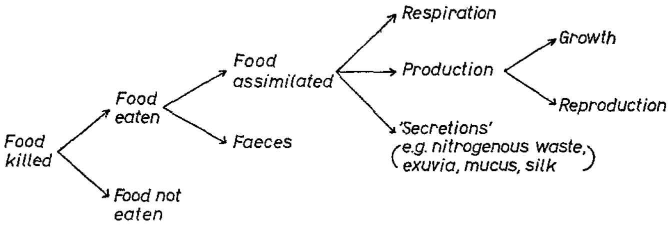

Fig. 2. The various pathways in an animal's energy budget

the period of carrying the first egg sac is indicated as being eleven weeks. This is the total period of time when females carrying first egg sacs can be found and not the time that individual spiders carry their egg sacs, which is approximately six weeks.

## Individual Energy Budget for *P. lugubris*

### 1. Introduction and Methods

The various pathways in an animal's energy budget are indicated in Fig. 2. With regard to *P. lugubris* "secretions" include nitrogenous waste materials, exuvia, and silk. In this study the quantity of food killed was known. The food not eaten was collected and the difference between the two gave an estimate of the quantity of food consumed. The amount of energy lost as faeces, nitrogenous waste and silk was considered to be negligible. The reasons for this assumption will be discussed later. Thus food consumed is equivalent to food assimilated. Exuvia were collected after moulting and their energy content determined. Production was determined by periodic weighing of the animals. Energy involved in respiration was calculated by subtracting the sum of the energy of production and of exuvia from the energy content of the food consumed. An independant determination of energy of respiration was made by measuring oxygen consumption in adult females of *P. lugubris*.

The spiders were reared in tubes 5 × 2.5 cm with a pad of plaster of Paris (calcium sulphate) in the bottom which was kept moist, thus providing the spiders with a source of water (Parry, 1954). A piece of expanded polystyrene was inserted into each tube. The spiders preferred to stand on this rather than on the moist bottom of the tube and it provided a suitable attachment site during moulting. The feeding experiments were carried out in a laboratory where the temperature ranged from 15–20° C. The spiders were fed every day (except Saturdays) and given as much food as they would take. *P. lugubris*, like other wolf spiders, undertakes the first moult within the egg sac and emerges as a second instar. The 2nd instars were fed on chironomids or small male vestigial-winged *Drosophila melanogaster* Meigen. All other instars were fed on vestigial-winged *Drosophila*. The feeding procedure was as follows: *Drosophila* were weighed individually and offered to the spiders. If the fly was not seized within an hour it was removed. In experiments dealing with adult animals, where large quantities of food were consumed, individual flies were not weighed. The number of flies eaten was noted and the quantity of food killed was calculated by multiplying this number by a previously calculated mean weight for *Drosophila*. If the *Drosophila* was eaten the remains were removed for storage at the next feeding time. The feeding procedure was repeated until the spider moulted. The spider was weighed and the food remains and exuvium dried to a constant weight in a vacuum oven at 60°C. All weighings were carried out on an E.M.B.-I Electromicrobalance. Thus for each instar the initial and final weights were known in terms of wet (live) weights, as was the quantity of *Drosophila* killed. The dry weight of the food remains and of the exuvium was also known. The dry weight/wet weight relationships for both *P. lugubris* and *D. melanogaster* were linear ($y = 0.18 + 0.29\,x$, $P < 0.001$ and $y = 0.004 + 0.223\,x$, $P < 0.001$ respectively). Both lines pass very close to the origin, and to obtain wet weight, dry weight conversion values, regression coefficients were calculated using the Model 1A method of Snedecor (Snedecor, 1956, p. 153). These were 0.27 for *P. lugubris* and 0.23 for *D. melanogaster* (see Table 2).

With a view to constructing an energy budget for *P. lugubris* the results of the feeding experiments were expressed as calorific values. Calorific determinations of *D. melanogaster*, the food remains, the spider, its egg sacs and exuvia, were made using a Phillipson Microbomb Calorimeter (Phillipson, 1964). The results are shown in Table 1. Wet weight/dry weight/calorific conversion values are given in Table 2.

In order that the population energy budget, calculated later in the paper, has some meaning, it is important that the energy budgets calculated for the various stages of *P. lugubris* in the laboratory are similar to those of field individuals. It was considered that this could be assumed to be the case if it could be demonstrated that the rate of growth and development in the laboratory was similar to that in the field. Growth and development of *P. lugubris* in the field has been reported elsewhere (Edgar, in press a). At various places in the following account of the laboratory feeding experiments, comparisons have been made using these field data.

As *P. lugubris* has a longevity of approximately two years, feeding experiments were carried out on several different stages of the life-cycle concurrently.

Table 1. *Calorific values for* Drosophila melanogaster, Pardosa lugubris, *the spider food remains, exuvia, and egg sacs*

| | Kcal/ash free (g + S.D.) | No. of determinations |
|---|---|---|
| *D. melanogaster* | 4.65 ± 0.10 | 4 |
| *P. lugubris* | 4.92 ± 0.40 | 14 |
| Food remains | 4.72 ± 0.37 | 10 |
| Exuvia | 4.20 ± 0.35 | 4 |
| Egg sacs | 5.41 ± 0.20 | 5 |

Table 2. *Wet weight, dry weight and calorific equivalents of* Drosophila melanogaster *and* Pardosa lugubris

| | Wet weight (mg) | Dry weight (mg) | Calorific equivalent (cal) |
|---|---|---|---|
| *D. melanogaster* | 1.00 | 0.23 | 1.07 |
| *P. lugubris* | 1.00 | 0.27 | 1.33 |

## 2. Energy Budget from Egg Sac Emergence until Moulting to Fifth Instar

Fifteen spiderlings from the first egg sac were reared to fifth instar. The results are given in Table 3. The mean time from egg sac emergence to fifth instar was 74 days, and as the spiderlings emerged on 22 July this would take them up to early October. In the field the spiderlings from the first egg sac have reached the fourth or fifth instar stage by October so that the rate of development in the laboratory is similar to that in the field.

## 3. Energy Budget from Moulting to Fifth Instar until Moulting to Adult

Sixty-six fourth instar spiders were collected in the spring of 1966, and all moulted to fifth instar within a few days. Eighteen of these spiders (10 males and 8 females) were reared to adult by the following spring. Six of the males were adult in instar 8 and four in instar 9 while six of the females were adult in instar 9 and two in instar 10. Comparing the weights and sizes of these animals with adult males and females in the field it was concluded that in the field males are normally adult in instar 8 and females in instar 9. Hence only the results obtained from males which were adult in instar 8 and females in instar 9 were used in the calculation of the energy budget. The results are summarized in Tables 4 and 5.

Table 3. *Results of feeding experiments on 2nd, 3rd, and 4th instars of* Pardosa lugubris *(expressed as calories unless otherwise stated ± S.D.)*

| | Food killed | Food remains | Food consumed | Initial weight | Weight increase | Exuvia | Growth efficiency (%) | Duration (days) |
|---|---|---|---|---|---|---|---|---|
| 2nd instar | 1.39 ± 0.28 | 0.39 ± 0.15 | 1.00 ± 0.22 | 0.74 ± 0.04 | 0.68 ± 0.14 | 0.05 ± 0.02 | 68.00 ± 6.94 | 24 ± 2 |
| 3rd instar | 3.94 ± 0.51 | 0.89 ± 0.26 | 3.05 ± 0.37 | 1.42 ± 0.16 | 1.42 ± 0.21 | 0.10 ± 0.03 | 46.56 ± 7.21 | 19 ± 2 |
| 4th instar | 7.47 ± 1.14 | 1.59 ± 0.34 | 5.88 ± 0.89 | 2.84 ± 0.29 | 2.06 ± 0.68 | 0.21 ± 0.03 | 35.03 ± 9.81 | 31 ± 4 |
| Total | 12.80 ± 1.52 | 2.87 ± 0.49 | 9.93 ± 1.11 | | 4.16 ± 0.75 | 0.36 ± 0.05 | 41.89 ± 7.37 | 74 ± 6 |

Table 4. *Results of feeding experiments on 5th, 6th, and 7th instar males of* Pardosa lugubris *(expressed as calories unless otherwise stated ± S.D.)*

| | Food killed | Food remains | Food consumed | Initial weight | Weight increase | Exuvia | Growth efficiency (%) | Duration (days) |
|---|---|---|---|---|---|---|---|---|
| 5th instar | 9.72 ± 4.55 | 2.62 ± 0.34 | 7.10 ± 2.22 | 4.43 ± 0.39 | 2.68 ± 1.13 | 0.36 ± 0.06 | 37.69 ± 8.84 | 36 ± 9 |
| 6th instar | 19.21 ± 3.61 | 2.87 ± 0.59 | 16.34 ± 3.15 | 7.11 ± 0.87 | 3.97 ± 1.39 | 0.59 ± 0.12 | 24.28 ± 8.32 | 55 ± 21 |
| 7th instar | 40.00 ± 4.48 | 7.18 ± 1.28 | 32.82 ± 3.60 | 11.08 ± 1.45 | 4.97 ± 1.83 | 1.28 ± 0.12 | 15.14 ± 7.52 | 226 ± 44 |
| Total | 68.93 ± 3.35 | 12.67 ± 1.13 | 56.26 ± 1.07 | | 11.62 ± 1.40 | 2.23 ± 0.46 | 20.65 ± 1.87 | 317 ± 37 |

Table 5. *Results of feeding experiments on 5th, 6th, 7th and 8th, instar females of* Pardosa lugubris *(expressed as calories unless otherwise stated ± S.D.)*

| | Food killed | Food remains | Food consumed | Initial weight | Weight increase | Exuvia | Growth efficiency (%) | Duration (days) |
|---|---|---|---|---|---|---|---|---|
| 5th instar | 9.27 ± 3.23 | 1.95 ± 0.64 | 7.32 ± 2.80 | 4.57 ± 0.13 | 3.47 ± 1.48 | 0.34 ± 0.03 | 47.40 ± 5.02 | 29 ± 6 |
| 6th instar | 18.03 ± 4.79 | 1.74 ± 1.16 | 16.29 ± 4.03 | 8.04 ± 1.27 | 4.20 ± 0.42 | 0.63 ± 0.06 | 25.78 ± 9.14 | 44 ± 8 |
| 7th instar | 20.49 ± 4.55 | 2.64 ± 0.62 | 17.85 ± 3.95 | 12.24 ± 0.90 | 4.77 ± 1.88 | 1.08 ± 0.12 | 26.72 ± 12.54 | 48 ± 11 |
| 8th instar | 47.87 ± 15.60 | 8.60 ± 2.20 | 39.27 ± 13.53 | 17.01 ± 1.71 | 9.66 ± 2.75 | 1.70 ± 0.18 | 24.60 ± 6.44 | 181 ± 36 |
| Total | 95.66 ± 15.65 | 14.93 ± 1.93 | 80.73 ± 11.92 | | 22.10 ± 2.54 | 3.75 ± 0.40 | 27.38 ± 3.66 | 302 ± 34 |

The spiders were subjected to periods at low temperatures (4° C) to simulate winter conditions. The mean length of time at 4° C was 140 ± 8 days which is similar to the duration of the inactive period in the field.

The mean number of days from 5th instar to adult was 317 ± 37 for males and 302 ± 34 for females. These spiders were collected in the field in late April and had they remained in the field they would have moulted to adult in late March or early April of the following year i.e. eleven months or 325–335 days later. Hence the rate of development in the laboratory is similar to that in the field.

### 4. Energy Budget from Moulting to Adult until Death

Adult females have two periods of active feeding, prior to producing the two egg sacs, followed by two periods when little food is taken while carrying the egg sacs. The food required during these distinct phases was calculated separately.

Five sub-adult males and five sub-adult females were collected in the spring of 1967 and fed as much food as they would take until they moulted to adult. They were then fed at a maximum rate for a further 20 days. The results are shown in Table 6. On moulting to adult the animals were paired off for short periods to allow mating to take place. Mating in the field occurs soon after moulting and previous experiments had indicated that the growth rate of unmated females is abnormal.

There was virtually no change in the weight of the males during the twenty days. In the field the weight of adult males likewise changes little throughout their life (Edgar, in press, 1971 a). Males killed 0.64 cal/day. The average life expectancy of a male is 65 days (Fig. 1). Hence the calorific equivalent of the food required from moulting until death is $65 \times 0.64 = 41.60$ cal. Adult females killed 2.93 cal/day. Thirty-five days was taken as the average time from moulting to producing the first egg sac (Fig. 1). Hence $35 \times 2.93 = 102.55$ cal are required during this period. This result was compared with field data as follows: 81.4% of the food killed by adult females is ingested (Table 11). Hence in the 35 days $102.55 \times 0.814 = 83.49$ cal is ingested. With a growth efficiency of 36.88% (Table 6), this would result in an increase in biomass equivalent to 30.63 cal. Laboratory females on moulting to adult have a calorific equivalent of 31.71 cal (Table 6) which is similar to that of females in the field carrying the first egg sac (31.51 cal) (Table 7). Hence the increase in biomass over the 35 days (30.63 cal) can be considered as energy going into the egg sac. The mean weights of 1st and 2nd egg sacs in the field are given in Table 7. A linear relationship exists between dry weight, wet weight of egg sacs ($y = 1.26 + 0.244\,x$, $P < 0.001$) and thus the mean calorific equivalents of the two egg sacs could be calculated.

Table 6. *Results of feeding experiments on adult specimens of* Pardosa lugubris *over a period of 20 days (expressed in calories unless otherwise stated ± S.D.)*

| | Food killed | Food killed/day | Food remains | Food consumed | Initial weight | Weight increase | Growth efficiency (%) |
|---|---|---|---|---|---|---|---|
| ♂ | 12.78 ± 2.20 | 0.64 ± 0.10 | 2.93 ± 0.68 | 9.85 ± 2.08 | 19.93 ± 1.87 | -0.54 ± 0.97 | |
| ♀ | 58.58 ± 2.30 | 2.93 ± 0.08 | 10.89 ± 1.12 | 47.69 ± 1.70 | 31.53 ± 5.52 | 17.59 ± 1.85 | 36.88 ± 3.90 |

Table 7. *Mean weights of females of* Pardosa lugubris *when carrying 1st and 2nd egg sacs and the mean weights of these egg sacs. Calorific equilvaents and numbers examined are given in parenthesis*

| Egg sac | Mean weight of females carrying egg sacs (mg) ± S.D. | Mean weight of egg sacs (mg) ± S.D. |
|---|---|---|
| 1st | 23.69 ± 2.73 (163)<br>(31.51) | 19.5 ± 3.5 (166)<br>(32.56) |
| 2nd | 22.54 ± 3.85 (61)<br>(29.98) | 13.6 ± 3.4 (97)<br>(24.77) |

Thus the calorific equivalent of the first egg sac (32.56 cal) is in reasonable agreement with the value (30.63 cal) calculated as being available for egg sac production from the laboratory experiments.

Taking 25 days as the time taken from emergence of the first spiderlings until production of the second egg sac (Fig. 1), then $25 \times 2.93 = 73.25$ cal would be required during this period. This represents a weight increase equivalent to $73.25 \times 0.841 \times 0.3688 = 21.99$ cal, which is in reasonably good agreement with the calorific equivalent of 24.77 cal (Table 7) for the second egg sac.

The good agreement between the estimates of energy going into egg sac production from the laboratory experiments and the calorific equivalents of the egg sacs found in the field, suggests that the calculated energy budget reasonably reflects the field situation.

There remains to be calculated for the adult female the amount of food required while carrying the two egg sacs and up to the time of death. Six weeks is taken as the mean time that the first egg sac is carried and seven weeks as that when the second egg sac is carried, including the period up to death, which occurs soon after spiderling emergence (Fig. 1). While carrying an egg sac the feeding rate is very much reduced and field samples have indicated that the weight of adult

Table 8

*Results of feeding experimetns on females of* Pardosa lugubris *carrying egg sacs*

| Spider | Initial weight (mg) | Final weight (mg) | Weight difference (mg) | Food killed (cal) | Duration of feeding expt. (days) | Food killed/day (cal) |
|---|---|---|---|---|---|---|
| 1 | 23.14 | 24.74 | 3.60 | 23.11 | 14 | 1.65 |
| 2 | 22.65 | 24.60 | 1.95 | 23.11 | 14 | 1.65 |
| 3 | 24.97 | 24.18 | −0.97 | 13.48 | 12 | 1.12 |
| 4 | 24.27 | 23.45 | −0.82 | 8.67 | 12 | 0.72 |

Mean feeding rate of spiders showing weight increase is 1.65 cal/day and mean feeding rate of spiders showing weight decrease is 0.92 cal/day. Hence 1.65 cal/day = 2.78 mg increase and 0.92 cal/day = 0.81 mg decrease. Plotting these two pairs of values and joining the points gives a zero weight increase at a feeding rate of 1.0 cal/day.

females remains relatively constant while carrying an egg sac (Table 7). Thus the total time at this reduced feeding rate is 13 weeks or 91 days.

Four females with egg sacs were fed in the laboratory and the results are given in Table 8. From these results a value of 1.0 cal/day was taken as the feeding rate required to maintain a constant body weight. Hence the amount of food killed over 13 weeks is equivalent to 91 × 1.0 = 91 cal.

## 5. Total Energy Budget for *P. lugubris*

On the basis of the above calculations a total energy budget for all the stages of *P. lugubris* can be given. In the feeding experiments from 5th instar to adult the spiders were subjected to a period at 4°C to simulate winter conditions. During their life the spiders overwinter twice, the first time as 3rd, 4th, or 5th instars. No period of cold was given to the smaller instars in the feeding experiments. They were reared to 5th instar by the autumn, which is considered to be the furthest stage they can reach by the time they overwinter, and then the further feeding experiments started with animals which had just moulted to 5th instar in early May. The sub-adults in the feeding experiments took very little food when kept at 4°C and because of this, and the fact that the small instars in the field remain almost constant in weight from October to early May (Edgar, in press, 1971a), it was assumed that the amount of food required by the small instars over the winter was negligible.

The energy budgets for the various stages of the life-cycle of males and females of *P. lugubris* are given in Tables 9 and 10. The so-called growth efficiency for adult females (36.88%), given in Table 10, should strictly be called production efficiency as most of the increase in body weight is related to gamete production.

Table 9. *Energy budget of* Pardosa lugubris *male (expressed as calories unless otherwise stated)*

| | Food killed | Food remains | Food consumed | Weight increase | Exuvia | Growth efficiency (%) |
|---|---|---|---|---|---|---|
| 2nd–5th instar | 12.80 | 2.87 | 9.93 | 4.16 | 0.36 | 41.89 |
| 5th instar–adult | 68.93 | 12.67 | 56.26 | 11.62 | 2.23 | 20.65 |
| Adult | 41.60 | 9.52 | 31.85 | 0 | 0 | |
| Total | 123.33 | 25.06 | 98.05 | 15.78 | 2.59 | 16.09 |

Table 10. *Energy budget of* Pardosa lugubris *female (expressed as calories unless otherwise stated)*

| | Food killed | Food remains | Food consumed | Weight increase | Exuvia | Growth efficiency (%) |
|---|---|---|---|---|---|---|
| 2nd–5th instar | 12.80 | 2,87 | 9.93 | 4.16 | 0.36 | 41.89 |
| 5th instar–adult | 95.66 | 14.93 | 80.73 | 22.10 | 3.75 | 27.38 |
| From moulting to adult to production of 1st egg sac | 102.55 | 19.06 | 83.49 | 30.79 | 0 | 36.88 |
| Periods of carrying two egg sacs and time up to death | 91.00 | 16.92 | 74.08 | 0 | 0 | |
| Active feeding period prior to production of 2nd egg sac | 73.25 | 13.62 | 59.63 | 21.99 | 0 | 36.88 |
| Total | 375.26 | 67.40 | 307.86 | 79.04 | 4.11 | 25.67 |

### 6. Rate of Oxygen Consumption of Adult Females of *P. lugubris*

As a check on the feeding experiments the rate of oxygen consumption of adult females was determined using a Warburg respirometer. Adult females with egg sacs were used as no growth occurs during this stage of the life-cycle (see p. 144). The egg sacs were removed 24 hr before the start of the experiment, as the spiders are abnormally active for several hours after egg sac removal, and kept overnight at 20°C and at a relative humidity of approximately 85%. The rate of oxygen consumption at 20°C was determined over a period of 11 hours. Thirty-four specimens were tested. The mean rate of oxygen consumption was $0.277 \pm 0.063$ µl $O_2$/mg wet weight/hr. Taking 1 µl $O_2 = 0.0048$ cal (Engelmann, 1961) then this is equivalent to 0.00133 cal/mg/hr.

Table 11. *Ingestion and growth efficiencies of the various instars of* Pardosa lugubris

| Stage of *P. lugubris* | | Ingestion efficiency (%) | Gross growth efficiency (%) |
|---|---|---|---|
| | 2nd instar | 71.9 | 68.0 |
| | 3rd instar | 77.4 | 46.6 |
| | 4th instar | 78.7 | 35.0 |
| Male | 5th instar | 73.0 | 37.7 |
| | 6th instar | 85.1 | 24.3 |
| | 7th instar | 82.1 | 15.1 |
| | Adult | 76.6 | |
| Female | 5th instar | 79.0 | 47.4 |
| | 6th instar | 90.3 | 25.8 |
| | 7th instar | 87.1 | 26.7 |
| | 8th instar | 82.0 | 24.6 |
| | Adult | 81.4 | 24.3 |

In the laboratory feeding experiments on females with egg sacs the weights of these females remained relatively constant. Hence the feeding rate calculated for zero weight increase (1.0 cal/individual/day), which is equivalent to an ingestion rate of 0.81 cal/day, is the energy going into respiration. The mean weight of these females was 24.3 mg compared with 23.5 mg for the spiders in the Warburg. Hence the rate of food ingestion is $\frac{0.81}{24 \times 24.3} = 0.00139$ cal/mg wet weight/hr. Thus there is good agreement between the estimates of energy of respiration obtained from the laboratory feeding experiments and the Warburg respirometry.

### 7. Growth and Ingestion Efficiencies of Various Instars of *P. lugubris*

Gross growth efficiency is defined as the ratio of the calorific equivalent of the weight increase during the instar to that of the food ingested, expressed as a percentage. The ingestion efficiency is the ratio of the food ingested to the food killed. These efficiencies are given for the various instars in Table 11. Growth efficiencies are higher in females than in males and in general the growth efficiencies decrease with each instar. A decrease in growth efficiency with age appears to be a general feature of animal metabolism (Phillipson, 1966). The ingestion efficiency is higher in females than in males and is greatest in both sexes in instar 6. No explanation can be offered for the latter fact.

## Population Energy Budget for *P. lugubris*

Mortality and natality rates for *P. lugubris* have been given elsewhere (Edgar, in press, 1971a) as have density estimates and detailed

Table 12. *Contributions of female instars of* Pardosa lugubris *to the total annual energy budget (expressed as cal/m²/year)*

| Instar | Food killed | Food not eaten | Food consumed | Growth | Exuvia |
|---|---|---|---|---|---|
| 2nd | 26.41 | 7.41 | 19.00 | 12.92 | 0.95 |
| 3rd | 25.77 | 5.82 | 19.95 | 9.29 | 0.66 |
| 4th | 32.68 | 6.96 | 25.72 | 9.02 | 0.92 |
| 5th (part) | 5.84 | 1.41 | 4.43 | 1.90 | |
| 2nd | 7.13 | 2.00 | 5.13 | 3.49 | 0.26 |
| 5th | 41.71 | 8.77 | 32.94 | 15.62 | 1.53 |
| 6th | 77.50 | 7.46 | 70.04 | 18.06 | 2.72 |
| 7th | 79.92 | 10.30 | 69.62 | 18.60 | 4.19 |
| 8th | 157.92 | 28.37 | 129.55 | 31.88 | 5.62 |
| Adult | 488.48 | 90.81 | 397.67 | 96.63 | |
| Total | 943.36 | 169.31 | 774.05 | 217.41 | 16.85 |

Table 13. *Contributions of male instars of* Pardosa lugubris *to the total annual energy budget (expressed as cal/m²/year)*

| Instar | Food killed | Food not eaten | Food consumed | Growth | Exuvia |
|---|---|---|---|---|---|
| 2nd | 26.41 | 7.41 | 19.00 | 12.92 | 0.95 |
| 3rd | 25.77 | 5.82 | 19.95 | 9.29 | 0.66 |
| 4th | 32.68 | 6.96 | 25.72 | 9.02 | 0.92 |
| 5th (part) | 5.84 | 1.41 | 4.43 | 1.90 | |
| 2nd | 7.13 | 2.00 | 5.13 | 3.49 | 0.26 |
| 5th | 41.34 | 11.13 | 30.21 | 11.41 | 1.53 |
| 6th | 75.89 | 11.32 | 64.57 | 15.66 | 2.34 |
| 7th | 140.00 | 25.14 | 114.86 | 17.39 | 4.46 |
| Adult | 93.08 | 21.42 | 71.66 | | |
| Total | 448.14 | 92.61 | 355.53 | 81.08 | 11.12 |

information on the life-cycle (Edgar, in press, 1971 b). The mortality rate was calculated from density estimates of the various stages of *P. lugubris* in one large sampling area. The mortality rate was calculated on the assumption that the population size remained constant from year to year. It was based on a density of 1.60 adult females/m² at the time when the first batch of spiderlings emerge and 0.93 at the time of the second, these producing 55.20 and 15.53 spiderlings/m² respectively. These data on density and mortality have been combined with the results of the laboratory feeding experiments to calculate the annual energy flow through the spider population. The population density in the sampling area for which the mortality rate was calculated was the

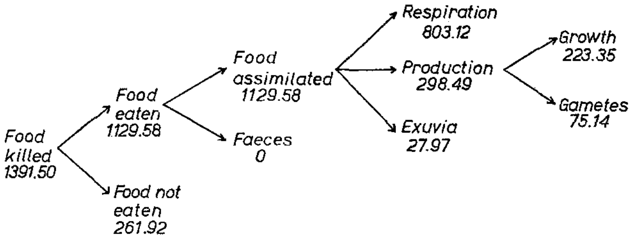

Fig. 3. Annual population energy budget for *Pardosa lugubris* (expressed in cal/m$^2$)

highest recorded in the study and hence the annual population energy budget for *P. lugubris* given here can be considered as a maximum estimate.

The calculated population energy budget was based on a slightly simplified life-cycle. Thus it was considered that all the spiderlings from the first egg sac have reached the 5th instar by the time they overwinter while those from the second egg sac have just completed the 2nd instar by this time. It was further assumed that in the spring this year group was represented only by spiders which had just moulted to the 5th instar. These simplifications probably do not result in much of an error in the total annual energy budget as 85% of the spiderlings are estimated to die before they overwinter (Edgar, in press, 1971a) and consequently they do not make a large contribution to the total energy budget compared with, say, adult females.

The contributions of the various instars to the annual energy budget are indicated in Tables 12 and 13 while the total annual energy flow through the population of *P. lugubris* is indicated in Fig. 3. Of the food killed 81.2% is ingested and of this 71.1% goes into respiration and 26.4% into production. Gamete production accounted for 25.2% of the energy of production and was taken as the energy going into the egg sacs. The energy involved in spermatozoa production was assumed to be negligible. Spider biomass was estimated as 161.80 cal/m$^2$ in early March and 189.14 cal/m$^2$ in late July. The mean of these two values (175.47 cal/m$^2$) was taken as the mean biomass of *P. lugubris*.

## Discussion

In this discussion it is proposed first to make some remarks about the methods employed in the study and then to make some general remarks about the findings.

The construction of the energy budget for *P. lugubris* was based on laboratory feeding experiments in which, except for the second instar, the spiders were fed with *Drosophila*. A criticism of this procedure could be that it is unlikely that 3rd and 4th instars in the field are catching prey as large as *Drosophila* and that such small instars, through the size limitations of their gut, would not be able to extract the maximum amount of food from the *Drosophila*. The fact that these instars ingested 78% of the food killed (Table 11) suggests that they are not in fact limited to any great extent, in the quantity of food they can extract from a *Drosophila*, by their gut capacity.

In both the laboratory feeding and respiration experiments the spiders were kept in relatively small containers under relatively uniform conditions and in such circumstances they spend much of their time motionless. One might expect that activity, and hence metabolism, under these unnatural conditions would be different from that in the field but in fact *P. lugubris* in the field also spends much of its time motionless (Edgar 1969 and unpublished data).

It was stated in the Introduction that the energy lost as faeces, nitrogenous waste and silk was considered to be negligible. These assumptions clearly require some justification. With regard to silk production Richter (1970) has shown that *P. lugubris* produces very little silk at any stage in its life-cycle.

*P. lugubris* periodically produces drops of fluid from the anus. These contain both faeces and nitrogenous waste materials. Attempts were made to estimate the quantity of material produced—by placing previously weighed circles of filter paper on the bottom of the rearing tubes and reweighing these circles of paper and the absorbed waste materials several days later. The quantities of material produced were so small in relation to the weight of the filter paper that no significant increase in weight of the filter paper could be detected. This, together with the general observation that few spots of waste material were present on the filter paper, suggests that relatively little faeces and nitrogenous waste materials are produced by *P. lugubris*. Thus, what has been assumed in this study is that all the food ingested is assimilated i.e. that the assimilation efficiency is 100%. Lawton (1970) noted that high assimilation efficiencies seemed to be a general feature of invertebrate carnivores and he recorded efficiencies in the range 83–91% for larvae of the damselfly *Pyrrhosoma nymphula* fed on different prey organisms. One special feature of *P. lugubris* which might account for the small amounts of faeces produced, even by invertebrate carnivore standards, is the method of feeding. In *P. lugubris*, as in other spiders, preliminary digestion of the prey takes place externally i.e. the prey tissues are broken down by enzymes which are pumped into them. The food taken in is consequently in a semi-fluid form and it seems reasonable to conclude that most of this ingested food is capable of being assimilated. In other words it is considered that whereas most animals ingest food, a considerable proportion of which cannot be assimilated and is voided as faeces, with *P. lugubris* this "selection" largely takes place before the food is ingested and thus, in this case, the "foot not eaten" is analogous to food not eaten plus faeces of most other animals.

The "philosophy" behind carrying out an ecological energetics study on a species is that the results obtained will allow the rôle of the species, in the community in which it lives, to be evaluated. Thus the energy budget for *P. lugubris* should, logically, be compared with those of other organisms, particularly those of the same trophic level and with similar life-cycles, of the oakland community. At present, however, no such comparable studies have been carried out, although the studies of Phillipson and his co-workers (Phillipson, 1967) on the key species of deciduous woodland should, when complete, supply such data. It should be noted in parenthesis that an animal such as *P. lugubris*, which has a fairly wide size range of life stages and exhibits some cannibalism, certainly belongs to more than one trophic level.

Thus the difficulty in assessing the importance of *P. lugubris* in the oakland community is that one has no "base-line" against which to compare the results. With a herbivore the results can always be considered against the primary productivity of the ecosystem. Such a procedure is particularly meaningful where, as in the study of Llewellyn (1969), the herbivore is restricted to one plant species, the productivity of which is known.

Another use which can be made of single species energetics data is a comparison with published energy budgets of other animals (cf. Hughes, 1970). This approach is valid at present where relatively few energetics studies have as yet been carried out and is particularly useful where, as in the paper by McNeill and Lawton (1970), it results in some generalisations and predictions being made about energy budgets in animals of different taxonomic groups and with different longevities.

Perhaps the most meaningful comparison which can be made using the *P. lugubris* data is with the results obtained by Lawton (1971) from a study of the population energetics of larvae of the damselfly *Pyrrhosoma nymphula*. Like *P. lugubris*, *Pyrrhosoma* is a carnivore with a 2-year life-cycle and its niche in the aquatic community is probably similar to that of *P. lugubris* in the oakland community.

The population energy budgets of *Pyrrhosoma* obtained by Lawton on two different years, and the energy budget for *P. lugubris*, are given in Table 14. *Pyrrhosoma* differs from *P. lugubris* in that all the food killed is ingested. The various components of the energy budget of *Pyrrhosoma* are greater in magnitude than in *P. lugubris*. In the absence

Table 14. *Annual energy budgets of* Pyrrhosoma nymphula *and* Pardosa lugubris. *Expressed as cal/m²/year. Values in parenthesis indicate ratios of various categories to food killed, expressed as percentages*

| | *Pyrrhosoma nymphula* | | | | *Pardosa lugubris* | |
|---|---|---|---|---|---|---|
| | 1966–1967 | | 1967–1968 | | | |
| Mean annual biomass | 934 | | 1421 | | 175 | |
| Respiration | 3169 | (37.4) | 3668 | (42.9) | 803 | (57.7) |
| Production | 3939 | (46.5) | 3587 | (42.0) | 298 | (21.4) |
| Exuvia | 497 | (5.9) | 303 | (3.5) | 28 | (2.0) |
| Faeces | 859 | (10.1) | 987 | (11.6) | 0 | |
| Food not eaten | 0 | | 0 | | 262 | (18.8) |
| Consumption | 8464 | (100.0) | 8545 | (100.0) | 1130 | (81.2) |
| Food killed | 8464 | | 8545 | | 1392 | |
| Adult emergence | 151 | | 1636 | | | |
| Maximum ecological efficiency | 34.0 | | 18.3 | | | |
| Production/Biomass ratio | 4.24 | | 2.53 | | 1.70 | |

of data on the primary productivity of the two communities one cannot, however, necessarily assume that the rôle of *Pyrrhosoma* in the aquatic community is greater. The values in parenthesis in Table 14 indicate the magnitude of the various components expressed as percentages of the food killed. The most striking difference between the two species is that in *Pyrrhosoma* slightly more energy goes into production than into respiration whereas in *P. lugubris* much more energy goes into respiration. As energy of respiration is lost to the ecosystem this might suggest that much more of the energy passing through the *P. lugubris* population is lost to the ecosystem. In the following discussion an attempt will be made to show that the difference between the two species in this respect is not as marked as might first appear.

There are two indices which seem particularly useful in attempting to evaluate the rôle of an animal in community energetics. The first is the ratio of the energy which is ingested by a predator to that ingested by the prey organism, expressed as a percentage. This has been called the ecological efficiency (Slobodkin, 1960) and it is a measure of how efficiently energy is transferred from one trophic level to the next (higher) trophic level. The second index is the ratio of energy returned to the ecosystem, via both predator and decomposer species, to that which is "killed" by the animal. This index gives one an indication of the overall "impact" of the organism in the community.

Dealing first with ecological efficiencies: The maximum ecological efficiencies for *Pyrrhosoma* are given in Table 14. These are "maximum" values, in that it was assumed that all mortality in *Pyrrhosoma* was yield to predators (Lawton, 1971). No value for *P. lugubris* has been given. Assuming that all mortality in *P. lugubris* was in fact yield to predators then the annual yield was calculated as 289 cal/m$^2$ (Table 14) which would give an ecological efficiency of 25.6%. However the assumption that mortality is due to predators is certainly not justified. In *P. lugubris* there is a sudden "die-off" of adult males in mid-June after mating and of females in October after producing the 2nd batch of spiderlings (Edgar, in press, 1971a). This "natural death" results in a yield to decomposers rather than predators. As adult animals make a large contribution to the annual biomass (cf. Hughes, 1970) this means that the ecological efficiency value of 25.6% is considerably too large.

A second factor which will have an influence on the ecological efficiency estimate is cannibalism. Although mechanisms exist to reduce cannibalism in *P. lugubris* (Edgar, 1969, in press, 1971b) the spider may nevertheless be the most important predator of its own species (Edgar, 1969). This means that some of the yield from the small instars goes back into the *P. lugubris* population. This would tend to reduce the estimate for ecological efficiency. The exact magnitude of these two factors, yield to decomposers and to larger specimens of *P. lugubris*, is unknown but a rough calculation suggests that they account for perhaps 70 cal/m$^2$ of the yield, which would reduce the ecological efficiency to approximately 19%.

From the aspect of how much energy "killed" remains in the ecosystem; the first similarity between the two species is the ratio of annual biomass to food killed. For *Pyrrhosoma* this is 11.0% and 16.6% in the two years of the study and 12.6% for *P. lugubris*. Therefore the two carnivores have a similar impact on their prey organisms per unit biomass.

One striking difference in the two energy budgets is that energy is lost from the aquatic ecosystem in the form of emerging adult *Pyrrhosoma* (Table 14). Adult emergence was very different in the two years, being very low in 1966–1967. This accounts for the much higher ecological efficiency in this year. Thus, in considering the energy which is made available to decomposers and predators this loss of production must be taken into account. The yield to decomposers and predators for *P. lugubris* is given by exuvia + food not eaten + yield to predators and decomposers through mortality i.e. $28 + 262 + 289 = 579$ cal/m$^2$/year. The yield to decomposers and predators for *Pyrrhosoma* is exuvia

+ faeces + yield to predators. The yield to predators, which is calculated by subtracting adult emergence and also standing stock (see Lawton, 1971) from production, was 3396 cal/m$^2$ in 1966–1967 and 1656 cal/m$^2$ in 1967–1968. Thus the yield to decomposers and predators was $497 + 859 + 3396 = 4752$ cal/m$^2$ in 1966–1967 and $303 + 987 + 1656 = 2946$ cal/m$^2$ in 1967–1968. These values give ratios of energy yield to decomposers and predators to energy "killed" of 41.6 for *P. lugubris* and 56.1 and 34.5 for *Pyrrhosoma*. Thus the ratio for *P. lugubris* is fairly similar to that of *Pyrrhosoma* in 1967–1968. The high value of 56.1 is due to the small amount of energy lost as adult emergence in 1966–1967. Thus adult emergence was only 151 cal/m$^2$ and as the mean annual biomass was 934 cal/m$^2$ it seems that this value is almost certainly abnormally low. Assuming that the 1967–1968 value is in fact more normal then the amount of energy "killed" by *Pyrrhosoma* and *P. lugubris* which remains in the ecosystem, is fairly similar.

Lawton (1971) has remarked that the energy flow through the *Pyrrhosoma* population was remarkably similar in the two years of the study. This certainly appears to be the case from a cursory examination of the data in Table 14, but as has been indicated above, when considered from the point of view of how much of the energy "killed" remains in the system or how much is transferred to the next trophic level (ecological efficiencies) which, as has been stated above, would seem to be the most meaningful indices of the impact of the animal on the ecosystem, then there are marked differences in the two years.

From the above discussion it can be concluded that the energy budgets of the terrestrial carnivore *P. lugubris* and the aquatic carnivore *Pyrrhosoma nymphula* have similarities. The amount of energy "killed" per unit of biomass is similar and a similar proportion of this energy is returned to the ecosystem, although proportionally more of this energy goes into decomposers in *P. lugubris*. Both these invertebrate carnivores are, from the numerical point of view, important predators of their respective communities but before the magnitude of their impact on the community energetics can be assessed data will be required on primary productivity, and on the energy budgets of other predators, of the respective communities.

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