Energy cost of exuviae production of spiders*

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Summary

The percentage of growth production represented by exuviae production has been studied under laboratory conditions for six species of spiders from an Ivory Coast savannah: one theraphosid (*Scodra griseipes* Pocock), four lycosids (*Orinocosa celerierae* Cornic, *Hippasa lamtoensis* Dresco, *Brevilabus gillonorum* Cornic, *Pardosa injucunda* (O. P.-C.)) and one ctenid (*Anahita aculeata* (Simon)). Exuviae production represents 5.2-16.2% of growth production for the whole postembryonic development, depending on the species and sex. It even reaches 50% of growth production in the adult female theraphosid which moults throughout its life.

The results are compared with those given in the literature.

The loss of energy associated with the exuviae lost after moulting is therefore far from being negligible compared with the energy invested in life tissues. The growth production must take into account all components among which exuviae cannot be excluded.

If only the corporeal growth production is considered in an energy budget, the percentage of ingested energy devoted to total growth production is underestimated.

Introduction

Spiders moult during their postembryonic development and some of them continue to do so throughout their life. The exuviae are shed after moulting and represent a loss of energy which must be taken into account in growth production estimation. The total (gross) growth production (Pg) thus includes the corporeal (net) growth production (Pc) and exuviae production (Pe), with the addition of silk production in weaving species.

During the drawing up of spider energy budgets (Blandin & Célérier, 1981), exuviae production has been studied regularly and its cost calculated in growth production. The results obtained in six species from Lamto savannah (Ivory Coast) are presented here and compared with those given in the literature.

Material and methods

Experiments have been conducted under laboratory conditions on one theraphosid (*Scodra griseipes* Pocock), four lycosids (*Orinocosa celerierae* Cornic, *Hippasa lamtoensis* Dresco, *Brevilabus gillonorum* Cornic, *Pardosa injucunda* (O. P.-C.)) and one ctenid (*Anahita aculeata* (Simon)).

The spiders were reared individually in plastic boxes in which caps of wet absorbent cotton-wool maintained a relative humidity close to saturation. These cages were kept in controlled temperature cabinets under constant conditions: a temperature of 26 ± 2°C corresponding with the annual mean in Lamto, a light cycle of LD 12:12 and an ambient relative humidity of 80%. The spiders were fed with *Drosophila,* crickets, green and blue flies and their larvae.

Calorific determinations were made by burning the material after drying it by lyophilisation, using a Parr 1411 Oxygen Bomb Calorimeter. During post-embryonic development, exuviae were individually collected, dried, weighed then burned, all instars being included for each species.

The spiders were weighed after each moult, before

*This paper was presented at a symposium on spider ecology and behaviour held at Furzebrook Research Station in June 1985.

Species	The most frequent instar at which adult stage reached ♀ (*n*)	♂ (*n*)	Mean duration of postembryonic development (days) ♀	♂	Mean live weight at imaginal moult (mg ± S.D.) ♀ (*n*)	♂ (*n*)
1972	11 (7)	10 (4)	496	393	7070.0 ± 225.3 (3)	
Scodra griseipes						4960.0 ± 483.7 (11)
1974	(6) 10	(7)	487	469	7001.0 ± 1052.5 (5)	
Orinocosa celerierae	(29) 12	(26)	215		1222.2 ± 30.5 (38)	
F	8 (13)		121		53.4 ± 3.0 (13)	
Hippasa lamtoensis S	9 (2)		252		71.4 ± 8.9 (4)	
Anahita aculeata	(14) 10	(15)	170		137.0 ± 8.9 (13)	82.8 ± 4.2 (14)
F			202			
Brevilabus gillonorum	(16) 11	(23)			74.4 ± 2.2 (14)	61.2 ± 1.5 (20)
S			335			
F			52			
Pardosa injucunda	(6) 7	(11)			21.9 ± 4.6 (3)	17.2 ± 2.3 (8)
S			94			

Table 1: Mean quantitative features of postembryonic development of those specimens of each species which reached the adult stage at the most frequent instar. F and S = fast and slow development. Mean durations of postembryonic development are obtained by the sum of the mean durations for each instar, calculated from the data of all animals reared. Number of animals examined is given in parentheses.

Species	Energy equivalents of exuviae J/mg dry weight ash free ± S.D. (*n*)	Energy equivalents of spiders J/mg dry weight ash free ± S.D. (*n*)	Number of spiders burned
Scodra griseipes	19.39 ± 0.10 (2)	24.53 ± 0.23 (44)	91
Orinocosa celerierae	19.75 (1)	22.68 ± 0.53 (12)	128
Hippasa lamtoensis	21.44 ± 0.44 (2)	24.81 (1)	23
Anahita aculeata	20.81 ± 0.07 (2)	24.28 (1)	21
Brevilabus gillonorum	21.13	23.96 ± 0.38 (2)	50
Pardosa injucunda	—	22.43 (1)	37

Table 2: Mean energy equivalents of exuviae and spiders, all instars included, during postembryonic development. Number of pellets burned is given in parentheses (dry weight of each pellet about 150-200 mg).

feeding, and weight gains (live material) were given by differences between successive measurements. Production estimation during each instar is consequently calculated to the nearest decimal place, and the loss of energy during the fasting period before moulting is ignored as is the expenditure linked with it. In order not to disturb the animals too much, we have indeed preferred to restrict the repeated manipulations which would have been necessary.

The weights of dried material and the corresponding calorific values have been estimated for each species of spider from mean data established on reference groups, distinguishing different instars whenever possible (Blandin & Célérier, 1981).

Results and Discussion

Characteristics of species

The species studied differ in their weight, life cycle and biology. The female of *Scodra griseipes* moults throughout its life cycle, while females of the other species and all of the males do not moult after reaching the adult stage. *Hippasa lamtoensis, Orinocosa celerierae* and *Scodra griseipes* are weaving species, while *Brevilabus gillonorum, Pardosa injucunda* and *Anahita aculeata* deposit only occasional threads while moving.

There is variation within each of the six species in the duration and number of moults required to reach the adult instar. The weight reached at the imaginal moult can be multiplied by one to three (except in *Scodra griseipes*). In *Brevilabus gillonorum, Hippasa lamtoensis* and *Pardosa injucunda* there are groups of individuals with either slow or fast development. At the same instar the weight is equivalent, but slow development may lead to more instars than in fast development and to adults of larger size. The postembryonic growth of *Scodra* developed in different ways in two rearings, the one started in 1972 and the other in 1974. Therefore it seemed preferable to consider each rearing separately.

Fortunately, in each species and for each sex, adulthood was attained in one instar more frequently than in the others. Quantitative features of the species studied are given in Table 1: the number of moults

	Instar	1	2	3	4	5	6	7	8	9	10
Pc	1972 ♂	124.6	291.7	585.9	936.5	2571.7	3752.8	6750.3	7849.0	10721.9	
	1972 ♀									9841.9	14919.2
	1974 ♂	162.4	477.7	814.1	1839.8	3291.5	3963.3	8333.7	10345.3	4837.4	
	1974 ♀									18220.3	
Pe	1972 ♂	11.4	19.2	40.1	74.5	154.8	340.0	725.9	1384.9	2204.5	
	1972 ♀									2361.0	3503.5
	1974 ♂	13.4	24.8	47.7	97.4	210.2	410.8	775.5	1469.1	2122.3	
	1974 ♀									2594.1	
Pg	1972 ♂	154.1	347.0	705.5	1191.6	3407.5	4387.3	7770.7	9979.9	13560.3	
	1972 ♀									12836.8	19694.2
	1974 ♂	193.9	542.3	919.7	2050.4	3824.9	4699.3	9999.6	12704.8	7461.8	
	1974 ♀									21997.5	

Table 3: Growth production (in joules) during each instar of postembryonic development in *Scodra griseipes*. Pc = corporeal production, Pe = exuviae production, Pg = Pc + Pe + Ps (silk production) = total growth production. Values of Pc are obtained from mean live weights at beginning of each instar, converted to dry weights, then to energy equivalents. Values of Pe are calculated from mean dry weights of exuviae at each instar converted to energy equivalents.

ranges from 7 to 12, the live weight of individuals from 17.2 mg to more than 7 g, and the duration of postembryonic development from under two months to more than one year.

Energy equivalents of material

The mean energy equivalent during postembryonic development of immatures, all instars included, ranges from 22.43 to 24.81 J/mg dry weight ash free (Table 2) depending on the species, the average being 23.78 ± 0.99 J/mg dry weight ash free. The calorific value of exuviae measured, all instars included, for each of five of the species varies from one species to another (Table 2); on average, for all species studied, it is 20.50 ± 0.89 J/mg dry weight ash free.

The data given in the literature for energy equivalents of spiders (Blandin & Célérier, 1981) show the variability between various species and even in the same species. However, the results are not exactly comparable, the material sometimes being dried and burned under different conditions. The widest range of values is observed for the exuviae. Therefore, the

Species / Instar			1	2	3	4	5	6	7	8	9	10	11
	Pc		15.2	28.3	26.3	59.0	135.7	248.9	411.0	583.9	1016.9	1806.3	2781.5
O.c.	Pe		0.8	1.6	3.9	7.7	13.7	25.3	46.6	87.3	147.4	254.1	413.2
♂, ♀	Pg		16.0	29.9	30.2	66.7	149.4	303.4	516.0	744.3	1288.3	2278.8	3655.4
	Pc	F	7.5	12.1	25.1	31.8	61.5	128.3	162.3				
		S								146.2			
		F											
H.l.	Pe		0.3	0.4	0.8	1.6	3.4	7.1	14.6				
♂, ♀		S								27.2			
		F	13.2	16.9	33.8	44.5	79.8	155.6	198.5				
	Pg												
		S	13.3	19.4	36.2	54.8	96.4	173.6	234.7	239.7			
		♂						66.3	106.4	138.4	159.8		
	Pc		—	2.7	7.8	18.0	29.6						
		♀						94.2	115.3	205.7	405.5		
		♂							8.1	15.4	28.5		
A.a.	Pe		—	0.3	0.5	0.8	1.9	3.9					
		♀							9.4	16.0	31.9		
		♂						70.2	114.5	153.8	188.3		
	Pg		—	3.0	8.3	18.8	31.5						
		♀						98.1	124.7	221.7	437.4		
		♂										41.7	
	Pc		2.3	6.2	14.4	25.2	40.3	45.0	75.0	100.7	126.3		
		♀										146.2	
		♂											
B.g.	Pe		0.5	0.6	1.2	2.6	4.0	6.8	10.3	15.6	21.4	28.9	
		♀											
		♂										70.6	
	Pg		2.8	6.8	15.6	27.8	44.3	51.8	85.3	116.3	147.7		
		♀										175.1	
		♂					26.3	37.3					
	Pc		3.1	6.1	11.7	18.4							
		♀					28.7	57.2					
		♂					4.1	6.2					
P.i.	Pe		0.3	0.5	0.9	1.9							
		♀					3.8	6.6					
		♂					30.4	43.5					
	Pg		3.4	6.6	12.6	20.3							
		♀					32.5	63.8					

Table 4: Growth production (in joules) during each instar of postembryonic development in *Orinocosa celerierae (O.c.)*, *Hippasa lamtoensis (H.l.)*, *Anahita aculeata (A.a.)*, *Brevilabus gillonorum (B.g.)* and *Pardosa injucunda (P.i.)*. F and S = fast and slow development, Pc = corporeal production, Pe = exuviae production, Pg = total growth production. In weaving species (*O.c.* and *H.l.*) Pg = Pc + Pe + Ps (silk production), in wandering species (*A.a.*, *B.g.* and *P.i.*) Pg = Pc + Pe. Values obtained as in Table 3.

values found here are similar to most of those obtained in other spiders, principally Lycosidae (Célérier, 1971; Edgar, 1971; Steigen, 1975; Humphreys, 1977; Workman, 1978; Hebar, 1980). The values found by these authors range from 17.58 to 25.32 J/mg dry weight ash free, depending on the species. On the other hand, Pühringer (1979) measured an energy equivalent of 1.2 cal(= 5.0 J)/mg dry weight for the exuviae of *Araneus folium* Schrank, whereas in the lycosid *Lycosa watsoni* Gertsch, La Salle *et al.* (1984) found 9.2 cal/mg dry weight ash free, which is equivalent to 38.5 J.

Exuviae production as a percentage of growth production

The different components of production have been calculated (Tables 3, 4). The total growth production (Pg) and the percentage of this production represented by the exuviae in each instar (Pe/Pg) may then be obtained for the different species (Table 5).

The part of the total production lost in the form of exuviae is generally greatest at the end of development. It increases steadily in *Hippasa lamtoensis* whereas it shows fluctuations in the other species; this phenomenon was also observed by Humphreys (1978) in the lycosid *Geolycosa godeffroyi* (L. Koch), and has been established in other spider species, as shown in Table 6 where the values of the percentage Pe/Pg have been calculated from the data of the authors (Célérier, 1971; Edgar, 1971; Hebar, 1980). In several cases, for the first exuviae formed after emerging from the egg sac, the relative loss of energy is more important than in the following moults. This fact is found again in *Xysticus ninnii* Thorell studied by Hebar (1980): the loss caused by exuviae in the production of the first instar measured by this author is 33% and falls below 10% for the following instars, during the first half of development. The most important relative loss in the production of an instar is found in certain males. For example, the imaginal exuviae of the male of *Brevilabus gillonorum* represent 41% of the growth production in the last instar of development, whereas during previous instars the losses caused by exuviae vary from 7.8 to 17.9%. In this species, corporeal growth production during the instar before the imaginal moult has clearly diminished compared with that of previous instars, whereas the exuviae production was the highest of the development (Blandin & Célérier, 1981). In *Pardosa lugubris* (Walck.) reared by Edgar (1971) the proportion Pe/Pg reaches 20.5% in the last instar of male development, while it does not exceed 13% during the previous instars. Similarly the imaginal exuviae of the *Xysticus ninnii* male studied by Hebar (1980) represent 39% of the growth production in the last instar of postembryonic development, whereas the losses of the previous instars are clearly smaller.

Exuviae production expressed as a percentage of total growth production of the whole postembryonic development clearly varies according to the species and the sex (Table 7). The values of the proportion Pe/Pg range from 5.2 to 16.2%. Exuviae production expressed as a percentage of corporeal growth production (Pe/Pc) allows us to extrapolate individual data to the level of populations of the species (Blandin & Célérier, 1981). In the species studied here the values of this percentage range from 6.6 to 19.30% (Table 7).

On the whole, our results agree with those in the

Species	Instars		1	2	3	4	5	6	7	8	9	10	11
	1972	♂	7.4	5.5	5.7	6.3	4.5	7.8	9.3	13.9	16.3		
S.g.		♀									18.4	17.8	
	1974	♂	6.9	4.6	5.2	4.8	5.5	8.7	7.8	11.6	28.4		
		♀									11.8		
O.c.	♂, ♀		5.0	5.4	12.9	11.5	9.2	8.3	9.0	11.7	11.4	11.2	11.3
		F	2.3	2.4	2.4	3.6	4.3	4.6	7.4				
H.l.	♂, ♀	S	2.3	2.1	2.2	2.9	3.5	4.1	6.2	11.4			
		♂						5.6	7.1	10.0	15.1		
A.a.		♀	—	10.0	6.0	4.3	6.0	4.0	7.5	7.2	7.3		
		♂										40.9	
B.g.		♀	17.9	8.8	7.7	9.4	9.0	13.1	12.1	13.4	14.5	16.5	
		♂					13.5	14.3					
P.i.		♀	8.8	7.6	7.1	9.4	11.7	10.3					

Table 5: Exuviae production expressed as a percentage of total growth production (Pe/Pg) during each instar of postembryonic development (in %). F and S = fast and slow development. *S.g.* = *Scodra griseipes, O.c.* = *Orinocosa celerierae, H.l.* = *Hippasa lamtoensis, A.a.* = *Anahita aculeata, B.g.* = *Brevilabus gillonorum, P.i.* = *Pardosa injucunda.*

Species	*T. saeva*		*P. lugubris*		*X. ninnii*		*G. godeffroyi*
	♂	♀	♂	♀	♂	♀	♂, ♀
Instar							
0					33.33		
1	2.27				7.90		8.2
2	3.07		6.85		8.81		15.6
3	5.62		6.58		4.65		10.0
4	3.63		9.25		19.11		12.0
5	4.68	3.88	11.84	8.92	25.82	12.70	11.2
6	4.26	5.04	12.94	13.04	39.22	18.27	11.6
7	9.48	6.43	20.48	18.46		15.48	15.6
8		9.71		14.96			18.3
9							14.6
10							17.9
11							14.7
12							19.7
13							21.4
14							23.9

Table 6: Exuviae production expressed as a percentage of total growth production (Pe/Pg) during each instar of post-embryonic development in different species of spiders, from data in the literature. Values calculated from the data of Célérier (1971) for *Tegenaria saeva*, of Edgar (1971) for *Pardosa lugubris*, of Hebar (1980) for *Xysticus ninnii*, and of Humphreys (1978) for *Geolycosa godeffroyi*.

literature, where exuviae production as a percentage of growth production ranges from 6.2 to 20.6% (Table 8). Results obtained from the data of Pühringer (1979) are not taken into account because this author found a calorific value which is abnormally low for the exuviae (1.2 cal(= 5.0 J)/mg dry weight!). The proportion Pe/Pg appears to present the lowest values (less than 7%) in the lycosid *Hippasa lamtoensis* and in the agelenid *Tegenaria saeva* Blackwall. These two species are the only spiders among those examined which, from the beginning of development, are compelled to invest in a capture web for their food. The production of silk costs a lot of energy (Célérier, 1971; Blandin & Célérier, 1981). This point could illustrate different strategies of energy allocation between weaving spiders which capture their prey exclusively by a trap web and those called "wandering" spiders.

The peculiarity of the theraphosid *Scodra griseipes* is that the adult females go on moulting: their weight reaches 7.5 to 14 g on average (live weight) between the 10th and 15th instar, then it varies much less during the following instars. During the first part of adult life the production lost by the exuviae represents an amount of energy almost equivalent to that which is invested in living tissues (Table 9).

La Salle *et al.* (1984), who measured the energy cost of the loss of exuviae in *Lycosa watsoni* (not as a proportion of the growth production, but according to the weight of individuals), insist on the importance of taking account of exuviae production. However, these authors referred only to Edgar's studies (1971), and ignored the spider energy budgets in which the exuviae production was studied and added to the corporeal growth production, in order to evaluate total growth production (Célérier, 1971; Humphreys, 1978; Workman, 1978; Hebar, 1980). Edgar (1971), who measured the energy represented by exuviae during postembryonic development in *Pardosa lugubris*, did not take it into account in the calculation of growth production, considering the exuviae as "secretions" in addition to nitrogenous waste, silk or mucus. Growth production evaluated only by corporeal growth production was thus underestimated by 16.4% in the male and 15.7% in the female, during the whole post-embryonic development. Growth efficiency was consequently underestimated and represented the proportion of ingested energy allocated exclusively to corporeal growth production and not to total growth production.

Conclusions

In spiders the loss of energy due to exuviae after moulting may exceed 20% of the growth production during postembryonic development, but varies according to the species and the sex. The loss is far more important in the case of the female of a mygalomorph, which continues to moult during adult life: then it reaches nearly 50% of the production for the first period of adult life.

In order to calculate the growth production of a

Weaving species			**Pc** (J)	**Pe** (J)	**Pe/Pc** (%)	**Pg = Pc + Pe + Ps** (J)	**Pe/Pg** (%)
S.g.	1972	♂	33584.4	4955.3	14.8	41503.9	11.9
		♀	47623.6	8615.3	18.1	60474.6	14.3
	1974	♂	34065.2	5171.2	15.2	42396.7	12.2
		♀	47448.1	5643.0	11.9	56932.4	9.9
O.c.		♂, ♀	7113.0	1001.6	14.1	9078.4	11.0
H.l.	♂, ♀	F	428.6	28.2	6.6	542.3	5.2
		S	574.8	55.4	9.6	868.1	6.4
Wandering species						**Pg = Pc + Pe**	
A.a.		♂	529.0	59.4	11.2	588.4	10.1
		♀	878.8	64.7	7.4	943.5	6.9
B.g.		♂	477.1	91.9	19.3	569.0	16.2
		♀	581.6		15.8	673.5	13.7
P.i.		♂	102.9	13.9	13.5	116.8	11.9
		♀	125.2	14.0	11.2	139.2	10.1

Table 7: Exuviae production (Pe) expressed as a percentage of corporeal growth production (Pc) and of total growth production (Pg) in the complete postembryonic development of *Scodra griseipes* (*S.g.*), *Orinocosa celerierae* (*O.c.*), *Hippasa lamtoensis* (*H.l.*), *Anahita aculeata* (*A.a.*), *Brevilabus gillonorum* (*B.g.*), and *Pardosa injucunda* (*P.i.*). F and S = fast and slow development. Pe, Ps, Pc, Pg = production of exuviae, silk, corporeal growth and total growth.

Species	Pe/Pg (%) ♂	Pe/Pg (%) ♀	Author
Agelenidae			
Tegenaria saeva	6.2	6.9	Célérier, 1971
Lycosidae			
Pardosa lugubris	14.1	13.1	Edgar, 1971
Pardosa palustris	11.1	15.9	Steigen, 1975
Geolycosa godeffroyi	13.3		Humphreys, 1978
Trochosa terricola	10.4		Workman, 1978
Alopecosa cuneata	16.8	9.6	
Thomisidae			Hebar, 1980
Xysticus ninnii	20.6	14.7	

Table 8: Exuviae production expressed as a percentage of total growth production during postembryonic development in spiders, calculated from data in the literature.

spider, it appears that it is important to take into account all the components, in particular exuviae production, the value of which is far from being negligible.

Acknowledgements

My thanks to Professor M. Lamotte for his helpful advice and criticism of the French manuscript, and to Mr M. Brusson and Mrs G. Lewis who helped with the translation.

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Pc (KJ)	Pe (KJ)	Pg = Pc + Pe + Ps (KJ)	Pe/Pc (%)	Pe/Pg (%)
41.7	41.2	87.2	98.8	47.3

Table 9: Estimation of exuviae production expressed as a percentage of corporeal growth production and of total growth production during adult life (from instars 10 to 15) of females of *Scodra griseipes* (individuals born in 1974). Pc, Pe, Ps, Pg = production of corporeal growth, exuviae, silk and total growth.

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