ENERGY LOST TO THE EXUVIAE DURING MOLTING OF *LYCOSA WATSONI* GERTSCH (ARANEAE: LYCOSIDAE)

MARK W. LASALLE[1], ARMANDO A. DE LA CRUZ[1], GARY L. MILLER[2]

ABSTRACT

The loss of carbon compounds during molting for *Lycosa watsoni* was determined as percentage of total weight and total calories lost. The mass of exuviae from 20 spiders, from 1.3 to 4.7 mm carapace width ranged from 0.18 to 5.40 mg dry weight and from 4.4 to 10.6% of the total weight of spiders. The mass of exuviae as a % of body weight increased in the amount of material lost during successive molts and was linearly related to carapace width ($y = 3.17 + 1.3x$) and body weight ($y = 5.51 + 0.06x$). The caloric content of exuviae was 8.7 ± 1.86 cal./mg dry weight and could amount to between 1.57 and 46.98 cal per molt over the range of spider sizes studied. Similar trends were observed from comparable data reported for the lycosid spider, *Pardosa lugubris.*

RESUMEN

La pérdida de compuestos del carbón durante la muda de *Lycosa watsoni* fué determinada como porcentaje del peso total y el total de las calorias perdidas. La masa de exuvia de 20 arañas con carapachos de 1.3 a 4.7 mm de ancho, fluctuó de 0.18 a 5.40 mg de peso seco, y de 4.4 a 10.6% del peso total de las arañas. La masa de exuvia como un porciento del peso del cuerpo, aumentó en la cantidad del material perdido durante sucesivas mudas, y estaba linealmente relacionado a la anchura del carapacho ($y = 3.17 + 1.3 x$) y al peso del cuerpo ($y = 5.51 + 0.06 x$). El contenido calórico de la exuvia fué de 8.7 ± 1.86 ca./mg de peso seco, y pudiera ser una cantidad entre 1.57 y 46.98 ca. por muda en la fluctuación de tamaño de las arañas estudiadas. Tendencias similares fueron observadas con comparables datos reportados de la araña lycosi, *Pardose lugubris.*

During the molting process of arthropods carbon compounds are lost in the form of the discarded exuviae. The amount of material lost may be substantial as suggested by the fact that some animals have behavioral mechanisms for recovering some of the lost energy. Dondale (1965) observed newly molted *Philodromus rufus* Walckernaer (Thomisidae) sucking protein laden molting fluid from discarded exuviae, and the grass shrimp *Palaemonetes pugio* Holthus is known to ingest discarded exuvia, not necessarily its own (Sikora 1977).

Knowledge of the amount of energy lost to exuvia for a species may be important in constructing complete energy budgets for communities. Attempts to measure this have been made for several groups of arthropods including insects (Borutzky 1939, Teal 1957, Lawton 1971), isopods (Strong

---

[1]Department of Biological Sciences, Mississippi State University, Drawer GY, Mississippi State, MS 39762 USA.
[2]Department of Entomology, Mississippi Entomological Museum, Mississippi State University, Drawer EM, Mississippi State, MS 39762 USA.

and Daborn 1979, Luxmore 1982) and spiders (Hagstrum 1970, Edgar 1971, Humphreys, 1977). Generally overlooked, however, are the importance of changes in energy loss with successive molts. Only Edgar (1971) looked at all instars of the animal. Such changes may result from increases in later molts in the proportional amounts of the exoskeleton required to support the larger body. This paper reports the change in the amount of energy lost to exuvia during successive molts of *Lycosa watsoni* Gertsch (Lycosidae), and compares this loss with that determined from reanalysis of the data of Edgar (1971) for *Pardosa lugubris*.

Methods

Specimens of varying sizes were collected from a brackish water marsh island in St. Louis Bay, Mississippi on 10 April and 22 May 1982. Each spider was kept in a separate wide mouth jar, 0.4 liter capacity for large spiders and 0.3 liter for small spiders. All of the jars were kept in a covered 39 liter aquarium to maintain conditions of high humidity. Spiders were provided with water ad libitum and fed small insects and other spiders ca. every 2 days. The jars were checked daily and spiders which had molted were immediately removed and sacrificed by freezing.

The greatest width of the carapace was measured (nearest 0.5 mm) from the discarded exuviae with a hand held 2 mm rule. The exuviae and spider were dried to constant weight at 80° C in a Thelco oven (Model 15) and weighed on a Mettler balance (Model H20T) ($\pm$0.0001 g). The sum of these 2 weights was used as the total weight of the spider prior to molting. The percentage of the total body weight represented by exuviae (percent exuviae) was calculated. Regression analyses of percent exuviae with carapace width and with total body weight were performed.

Caloric content of the exuviae and of whole spiders was determined by combustion in a Phillipson microbomb calorimeter (Phillipson 1964). A Benzoic acid standard was used. Ash-free dry weight (AFDW) was determined by ashing the remaining material from each bomb sample in a Lindberg Hevi-duty muffle furnace at 550° C for 1 h. Corrections for heat generated by the fuse wire and the acid generated during bombing were made for each sample. The exuviae and spiders collected during the study were dried, pooled, and ground to obtain enough material for analysis. The means, standard deviations, and coefficients of variation (CV) of 3 samples of both materials were calculated.

Using the data reported by Edgar (1971) on spider and exuviae caloric equivalents for *Pardosa lugubris* we calculated the biomass (mg) of spiders and exuviae and obtained values of percent exuviae from these data. The mean initial spider biomass of each instar and the mean exuvial biomass of the previous instar were summed to give total body weight. Values were obtained for both male (2nd through 7th instar) and female (2nd through 8th instar) spiders. Regression analyses of percent exuviae with instar and with total body weight were performed.

Results

Twenty individuals of *Lycosa watsoni* molted after 1 month. Table 1 summarizes the data for carapace width, spider and exuvial weight, percent

exuviae, and caloric content of exuviae. Carapace width ranged from 1.3 to 4.7 mm. This range included the 4th to 5th instars and pentultimate stages of both male and female spiders. *Lycosa rabida*, a spider similar in size to the species used in this study, is known to have 11 instars (Redborg 1982). Total body weight ranged from 4.1 to 59.9 mg dry weight. Values of percent exuviae increased from 4.4 to 10.6% (Fig. 1). The regression results for carapace width versus percent exuviae were $Y = 3.17 + 1.3X$, $r^2 = 0.63$. The slope of the line was significantly different from zero ($t = 5.83$; $df = 18$; $P<0.05$). The regression results for total body weight versus percent exuviae were $Y = 5.51 + 0.06X$, $r^2 = 0.42$. The slope of the line was significantly different from zero ($t = 3.82$; $df = 18$; $P<0.05$).

The mean caloric content of whole spiders was 10.9 ± 0.22 cal/mg dry weight (11.7 cal/mg AFDW) with a CV of 2.0%. The mean percent ash was 6.67 ± 0.17%. The mean caloric content of spider exuviae was 8.7 ± 1.86 mg/cal dry weight (9.2 cal/mg AFDW) with a CV of 21.4%. The mean percent ash was 4.8 + 0.85%. The CV for the benzoic acid standard was 3.9%.

For comparison, values reported by Edgar (1971) for spider and exuvial weight, percent exuviae, and caloric content of exuviae are shown for male and female *Pardosa lugubris* in Table 2. Total body weight ranged from 0.30 to 3.26 mg for male spiders and from 0.30 to 5.41 mg for female spiders. Values of percent exuviae increased from 3.4 to 8.0% for males and to 6.4% for females (Fig. 2). The regression results for instar versus percent

TABLE 1. CARAPACE WIDTH, TOTAL BODY WEIGHT, EXUVIAE WEIGHT, PERCENT EXUVIAE AND CALORIC CONTENT OF EXUVIAE FOR *Lycosa watsoni*.

Carapace width (mm)	Total body wt. (mg)	Exuviae wt. (mg)	Exuviae as % of total	Caloric content of exuviae (cal/mg)
1.3	4.05	0.18	4.4	1.57
1.6	5.76	0.35	6.1	3.05
1.8	7.96	0.50	6.3	4.35
1.9	7.77	0.40	5.1	3.48
2.0	9.40	0.53	5.6	4.61
2.2	9.50	0.53	5.6	4.61
2.5	8.95	0.73	8.2	6.35
2.5	22.69	1.18	5.2	10.27
2.7	15.95	1.20	7.5	10.44
2.8	25.14	1.41	5.6	12.27
3.0	20.06	1.34	6.7	11.66
3.4	24.10	2.13	8.8	18.53
3.6	28.78	2.50	8.7	21.75
3.8	40.22	3.10	7.7	26.97
3.9	33.61	2.60	7.7	22.60
4.0	51.31	3.70	7.2	32.19
4.1	37.64	2.90	7.7	25.23
4.3	59.87	4.60	7.7	40.02
4.4	50.84	5.40	10.6	46.98
4.7	52.90	5.40	10.2	46.98

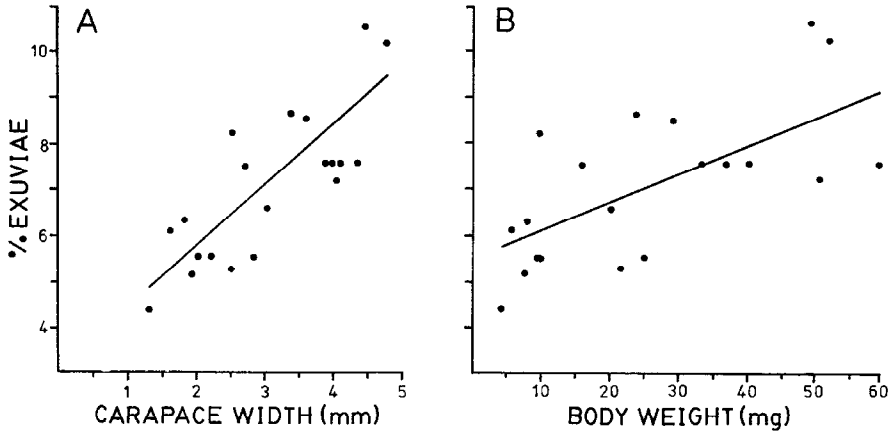

Fig. 1. Scatter plots and fitted regression line for *Lycosa watsoni*. A = Plot of carapace width versus percent exuviae, B = Plot of body weight versus percent exuviae.

exuviae were $Y = 1.19 + 0.81X$, $r^2 = 0.76$ for males and $Y = 2.00 + 0.53X$, $r^2 = 0.89$ for females. Both curves had slopes significantly different from zero ($t = 4.09$; $df = 4$ and $t = 7.20$; $df = 5$ respectively; $P<0.05$). The regression results for total body weight versus percent exuviae were $Y = 2.71 + 1.40X$, $r^2 = 0.85$ for males and $Y = 3.29 + 0.61X$, $r^2 = 0.90$ for females. Both curves had slopes significantly different from zero ($t = 5.53$; $t = 4$ and $t = 7.40$; $df = 5$ respectively; $P<0.05$). Edgar (1971) reported a mean caloric content value of 4.92 ± 0.40 kcal/gAFDW for spiders and 4.20 ± 0.35 kcal/gAFDW for exuviae.

TABLE 2. CALCULATED VALUES OF TOTAL BODY WEIGHT, EXUVIAE WEIGHT, PERCENT EXUVIAE AND CALORIC CONTENT OF EXUVIAE FROM DATA ON *Pardosa lugubris* (EDGAR 1971).

Instar	Total body wt. (mg)	Exuviae wt. (mg)	Exuviae as % of total	Caloric content of exuviae (cal/mg)
2	0.30	0.01	3.4	0.05
3	0.60	0.03	3.4	0.10
Males				
4	0.94	0.04	4.6	0.21
5	1.52	0.07	4.8	0.36
6	2.37	0.12	4.1	0.59
7	3.26	0.26	8.0	1.28
Females				
4	0.97	0.04	4.4	0.21
5	1.70	0.07	4.1	0.34
6	2.61	0.13	4.9	0.63
7	3.67	0.22	6.0	1.08
8	5.41	0.35	6.4	1.70

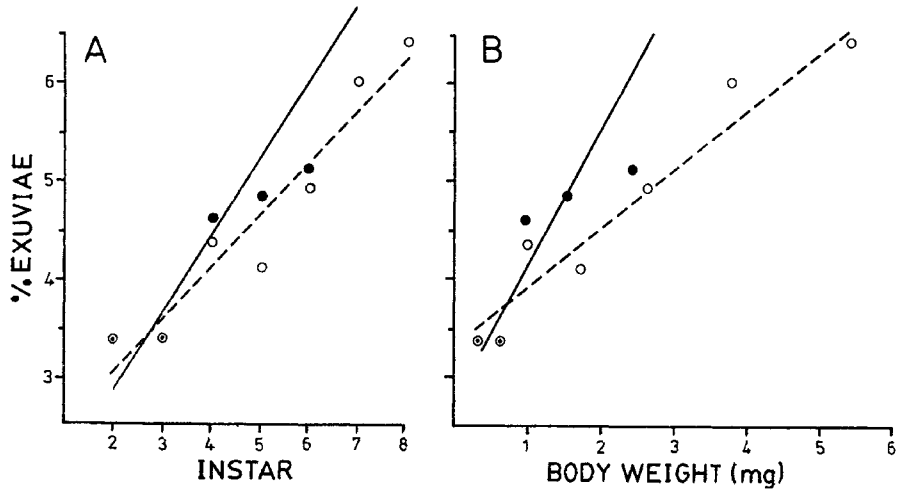

Fig. 2. Scatterplots and fitted regression lines for *Pardosa lugubris*. A—Plot of instar versus percent exuviae. B—Plot of body weight versus percent exuviae. Closed circles—males, open circles—females. First 2 points in both graphs are common to both data sets. Values for 7th instar male spiders in both graphs are off scale and, therefore, omitted.

TABLE 3. REPORTED VALUES OF ENERGY LOSS TO EXUVIAE (MG DRY WT., % TOTAL WT. AND CAL/MG WT.) FOR SEVERAL ARTHROPODS.

Taxa	Mg/dry wt.	Exuviae as % of total	Cal/mg dry wt.
Araneae			
Lycosa watsoni Gertsch (this study)	0.18-5.4	4.4-10.6	8.7
Pardosa lugubris (Walckenaer)[1]	0.01-0.35[a]	3.4-8.0[a]	4.2[b]
Tarentula kochi Keyserling[2]	0.05-0.60		
Geolycosa godeffroyi (L. Koch)[3]			5.5
Odonata			
Pyrrhosoma nymphula (Sulyer)[4]		5.0-16.0	4.5
Diptera			
Anatopynia dyari (Coquillett)[5]		9.0-11.5	
Chironomus plumosus (Linnaeus)[6]		$\bar{X}$ = 16.8[c]	
Isopoda			
Idotea baltica (Pallas)[7]			1.5
Seriolis polita Pfeffer[8]		40.0	
Seriolis cornuta Studer[8]		45.0	

[1]Edgar (1971), [2]Hagstrum (1970), [3]Humphreys (1977), [4]Lawton (1971), [5]Teal (1957), [6]Borutsky (1939), [7]Strong and Daborn (1979), [8]Luxmore (1982).
[a]Calculated from original data
[b]Cal/mg AFDW
[c]unknown

Discussion

The amount of energy lost as a result of molting in terms of dry weight, percent of total biomass, and calories per unit biomass has been reported for several groups of arthropods (Table 3). Values of percent exuviae obtained in the present study for *Lycosa watsoni* are similar to those of other spiders and insects. The high values reported for isopods undoubtedly reflect their proportionally heavier exoskeleton. Consideration of these values with respect to size of animals is only possible with the damselfly, *Pyrrhosoma nyphula,* the midge *Anatopynia dyari* and the spider *Pardosa lugubris.* In all 3 cases values of percent exuviae increased with size.

When the data (reanalysed) for *Pardosa lugubris* (Edgar 1971) and the *Lycosa watsoni* of this study are compared, similar trends are observed. The better fit of the regressions for *Pardosa* can be attributed to the use of mean values of body weight and exuviae weight. There is an increase in the amount of material lost with successive molts. This is a result of an increase in the size of apodemes and other cuticular processes as the animal grows. Additionally, the chelicera may become heavier in order to handle larger prey.

The caloric content observed for *Lycosa watsoni* may be twice that reported for other spiders. As the spider grows the amount of energy lost at molting ranged from 1.57 cal (carapace width of 1.3 mm) to 46.98 cal (carapace width of 4.7 mm), whereas the range for *Pardosa lugubris* was 0.06 cal (2nd instar) to 1.28 cal and 1.70 cal for male and female spiders respectively. The lower values for *Pardosa* reflect not only lower caloric content but also the smaller overall size of the spider.

The material lost as a result of the molting process in arthropods can be a major loss of energy especially when summed over the life span of the animal. The observed trend of increased loss over time should, therefore, be considered in any energy budget study. Failure to consider this loss may contribute to errors in calculating values of net production.

Acknowledgements

We wish to thank Augustus Mamaril and Keith Weaver for assistance in collecting spiders in the field and to Luis Lagera for computational assistance. Special thanks to Dr. Allen R. Brady and Patricia R. Miller for help in the identification of the spider. Partial funding for this study was provided by the Department of Biological Sciences, Mississippi State University.

References Cited

Borutzky, E. V. 1939. Dynamics of *Chironomus plumosus* in the profundal of Lake Beloie. Proc. Kossimo Limmnol. Stat. 22: 156-95.

Dondale, C. D. 1965. A spiders's first meal after molting. Canadian Ent. 97: 446.

Edgar, W. D. 1971. Aspects of the ecological energetics of the wolf spider *Pardosa* (*Lycosa*) *lugubris* (Walckenaer). Oecologia (Berl.) 7: 136-54.

Hagstrum, D. W. 1970. Physiology of food utilization by the spider *Tarentula kochi* (Araneae: Lycosidae). Ann. Ent. Soc. America 63: 1305-8.

HUMPHREYS, W. F. 1977. Variables influencing laboratory energy budgets of *Geolycosa godeffroyi* (Araneae). Oikos 28: 225-33.

LAWTON, J. H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). J. Anim. Ecol. 40: 385-423.

LUXMOORE, R. A. 1982. Molting and growth in Serolid isopods. J. Exp. Mar. Biol. Ecol. 56: 63-85.

PHILLIPSON, J. 1964. A miniature bomb calorimeter for small biological samples. Oikos 15: 130-9.

REDBORG, K. E. 1982. Interference by the mantispid *Mantispa uhleri* with the development of the spider *Lycosa rabida*. Ecol. Ent. 7: 187-96.

SIKORA, W. B. 1977. The ecology of *Palaemonetes pugio* in a southeastern salt marsh ecosystem with particular emphasis on production and trophic relationships. Ph.D. Thesis. University of South Carolina. 129 p.

STRONG, K. W., AND G. R. DABORN. 1979. Growth and energy utilization of the intertidal isopod *Idotea baltica* (Pallas) (Crustacea: Isopoda). J. Exp. Mar. Biol. Ecol. 41: 101-23.

TEAL, J. M. 1957. Community metabolism in a temperate cold spring. Ecol. Monogr. 27: 283-302.

CLARIFICATION OF THE COLOMBIAN HARVESTMAN GENUS *CARMENIA*, WITH A REVIEW OF THE NEW WORLD GAGRELLINAE (OPILIONES: GAGRELLIDAE)

JAMES C. COKENDOLPHER
Department of Biological Sciences
Texas Tech University
Lubbock, TX 79409 USA

ABSTRACT

The placement of *Carmenia* Roewer in the Gagrellinae (Gagrellidae) is verified. The genus and its single species are redescribed and illustrated. The similarity of *Carmenia bunifrons* Roewer to Sclerosomatinae and Gagrellinae from eastern Asia is noted. The New World genera of Gagrellinae and the South American species formerly placed in the Leiobuninae (Gagrellidae) are biefly discussed. The North American genus *Trachyrhinus* Weed is transferred to the Gagrellinae.

RESUMEN

Se verifica la inclusión de *Carmenia* Roewer dentro de los Gagrellinae (Gagrellidae), y se redescribe la única especies en dicho género. *Carmenia bunifrons* Roewer muestra similaridades con algunos Sclerosomatinae y Gagrellinae asiáticos. Los géneros de Gagrellinae del Nuevo Mundo, y las especies sudaméricanas previamente referidas a los Leiobuninae (Gagrellidae) son tratados brevemente. El género norteaméricano *Trachyrhinus* Weed es transferido a los Gagrellinae.