

# Cannibalism and prey sharing among juveniles of the spider *Oedothorax gibbosus* (Blackwall, 1841) (Erigoniinae, Linyphiidae, Araneae)

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**ABSTRACT.** In a terrarium experiment, juvenile cannibalism in the dwarf spider *Oedothorax gibbosus* (Blackwall, 1841) was very high – up to 99 %. More first juveniles were cannibalised at higher initial densities, and there was no effect on this cannibalism from offering different prey species. Although in their natural environment spiderlings may more readily evade one another, this terrarium experiment demonstrates the drastic effect of juvenile cannibalism. Larger first juveniles are apparently more prevalent among the cannibals, and juvenile cannibalism among similar sized spiderlings is less frequent. Prey sharing observed between similar sized first juveniles is not a social behaviour, but is rather a forced prey sharing resulting from competition among equally strong juveniles that are unable to defend their prey items from one another. Larger first juveniles do not tolerate smaller ones sharing their prey.

**KEY WORDS :** Araneae, Erigoniinae, juvenile cannibalism, food sharing, competition.

## INTRODUCTION

According to POLIS (1981), cannibalism is killing and consuming an individual or a part of it that belongs to the same species. ELGAR & CRESPI (1992) mention different forms of cannibalism, such as cannibalism in a context of competitive interaction, during copulation and courtship behaviour, killing of offspring by one or both parents (infanticide), eating of older individuals (gerontophagy), consumption of eggs (oophagy) and cannibalism between juveniles (juvenile or sibling cannibalism). Cannibalism, including juvenile cannibalism, occurs in many taxa (ELGAR & CRESPI, 1992). Juvenile cannibalism has been reported in Arachnida (ELGAR & CRESPI, 1992), Odonata (CROWLY et al., 1987), Thysanoptera (CRESPI, 1992), Heteroptera (BANKS, 1968; NUMMELIN, 1989; ORR et al., 1990), Trichoptera (MECOM, 1972), Lepidoptera (COTTRELL, 1984; JASIENSKI & JASIENSKA, 1988), Neuroptera (DUELLI, 1981), Coleoptera (CRESPI, 1992), Hymenoptera (CRESPI, 1992), Osteichthyes (SARGENT, 1992), Amphibia (CRUMP, 1992) and Reptilia (POLIS & MYERS, 1985).

Juvenile cannibalism is known for different spider species. WAGNER & WISE (1996, 1997) described juvenile cannibalism in the wolf spiders *Schizocosa ocreata* (Hentz, 1844) and *Schizocosa stridulans* Stratton, 1984. Another record of juvenile cannibalism in wolf spiders is by SAMU et al. (1999) in the species *Pardosa agrestis* (Westring, 1861). According to the latter, different factors possibly influence the extent of juvenile cannibalism, such as differences in body weight, hunger, life phase and age. They proved that juvenile cannibalism was strongly positively correlated with both weight ratio between involved cannibals and hunger, but absolute size or age of an individual could not predict the occurrence of a juve-

nile cannibalistic event (SAMU et al. 1999). Juvenile cannibalism also occurs in the salticid *Menemerus bracteatus* (L. Koch, 1879) (RIENKS, 2000). This spider species builds nests with different clutches and therefore the juveniles have the opportunity to cannibalise on 'sibling' eggs, prelarvae and larvae. Matriphagy, the cannibalism of the female by its offspring, probably also occurs in this spider species (RIENKS, 2000). Cannibalism might be an important phenomenon in the regulation of populations (SAMU et al., 1999). Also WAGNER & WISE (1996,1997) argue that juvenile cannibalism could be an important mortality- and density-regulating factor in the studied wolf spider *Schizocosa*.

While taking care of *Oedothorax gibbosus* (Blackwall, 1841) spider cultures, we observed two first instar juveniles feeding on the same prey item, a springtail. This could represent helping behaviour in dwarf spiders (voluntary prey sharing hypothesis), or perhaps these first instar juveniles are unable to defend their prey against rival spiders (forced prey sharing hypothesis). Neither POLIS (1981) nor ELGAR & CRESPI (1992) reported helping behaviour and juvenile cannibalism in the same species. Helping behaviour is typical for social spiders, i.e. spiders with co-operation between mutually tolerant individuals (DOWNES, 1995). A number of spider species live in groups, but few of them satisfy the criterion of social behaviour : co-operation in prey capture and brood care.

KRAFFT (1971) described prey capture in the social spider *Agelena consociata* Denis, 1965. A moving prey caught in the web draws the attention of all spiders that live in this web. One or more spiders attack the prey according to the prey size and the prey is carried into the common refuge where the actual feeding starts.

Also the social spider *Mallos gregalis* (Simon, 1909) exhibits similar feeding behaviour (JACKSON, 1979). The aforementioned social spiders do not exhibit any kind of aggression during feeding. This lack of aggression is, however, not typical for all social spiders (FOELIX, 1996). A social pholcid spider found in Malaysia exhibits some communal behaviour with web repair and defence, but individuals are competitively aggressive rather than cooperative in prey capture (TOMOIJ & MARYATI, 2001). The social spider *Delena cancerides* Walckenaer, 1837 (Sparassidae) exhibits not only intra-nest tolerance and communal feeding behaviour, but also extreme aggression towards members of foreign colonies (ROWELL & AVILES, 1995).

In this publication we describe the extent of juvenile cannibalism, and the effects of initial spider density and of diet on juvenile cannibalism in the dwarf spider *Oedothorax gibbosus*. We also analyse the aforementioned observed prey sharing in this species in more detail; on the basis of experiments with first instar juveniles of different sizes we weigh up the voluntary and forced prey sharing hypotheses.

## MATERIAL AND METHODS

*Oedothorax gibbosus* individuals were caught in the nature reserve Het Walenbos in Tielt- Winge (50° 55' NL, 4° 51' EL) (Belgium), 30 km north-east of Brussels, one of the most important river-associated woodlands of Flanders. *O. gibbosus* occurs in this nature reserve in an oligo- to mesotrophic alder carr (DE KEER & MAELFAIT, 1989; ALDERWEIRELDT, 1992). The dwarf spiders were caught by hand on October 13 and 27, 2001 and on April 29, 2002. Spiders used in the first, second and third experiments were of the first generation coming from female spiders inseminated in the field or from the first laboratory generation. The spiders used in the fourth and fifth experiment were of the second laboratory generation. All spiders were kept in a climatic chamber, photoperiod L :D 16 :8 and temperature of 20°C.

Experiment 1. To determine the extent of juvenile cannibalism, all juvenile spiders hatched from the same cocoon were left together in one small plastic vial (5 cm diameter and 2.5 cm height) with a thin basal layer of plaster, regularly moistened to maintain relative humidity near 100%. We fed the spiders two springtails, *Sinella curviseta*, per day per surviving individual. We monitored the occurrence of cannibalism between juveniles from 111 cocoons, and noted the number of spiders present until those that were not cannibalised reached adulthood.

Experiment 2. Here we studied the effect of the initial density of spiders and of the diet composition on the extent of juvenile cannibalism. The spiders coming from a single cocoon were divided as follows into separate small vials of the kind described above : one spider in one vial, two spiders in one vial, three, and so on per vial until all spiders of one cocoon were used. The maximal density was seven. To investigate if diet composition has an effect on the extent of juvenile cannibalism we used four different diets. A first group of spiders received two springtails, *Sinella curviseta*, per day per surviving spider. A second group received two *S. curviseta* per spider per day, and after the second moult each spider received three fruit flies each day. This is the

so-called successive *S. curviseta*-fruit fly diet. A third group was fed with four springtails, *Isotoma viridis*, each day. A fourth group received a simultaneous *S. curviseta*-fruit fly diet; four *S. curviseta* and three fruit flies per remaining spider per day. Table 1 shows the number of vials monitored for the several density categories and diets. Again, we noted the number of surviving juveniles until the spiders that were not cannibalised reached adulthood.

TABLE 1

The number of studied cups for the studied spider density categories and diets (mono-diet *Sinella curviseta*, successive poly-diet *S. curviseta*-fruit flies, mono-diet *S. curviseta* and simultaneous poly-diet *S. curviseta*-fruit flies) in the second experiment (See Material and methods).

diet	<i>S. curviseta</i>	successive <i>S. curviseta</i> - fruit flies	<i>I. viridis</i>	simultaneous <i>S. curviseta</i> - fruit flies
1	21	5	5	7
2	25	7	9	5
3	23	4	4	7
4	20	7	6	3
5	7	5	5	5
6	7	3	5	2
7	3	2	2	2

Experiment 3. In a third experiment we used large rectangular vials (terraria) to more closely imitate the natural environment. Based on the number of cannibalised spiders per terrarium after 20 days, we determined whether more juvenile spiders were cannibalised with higher initial densities. We put between 112 and 156 recently hatched spiders from a breeding stock into each of six terraria. Each terrarium contained spiders hatched the same day from different cocoons (max number of hatched *O. gibbosus* individuals per cocoon = 40). The terraria were large rectangular plastic vials (17.5 cm length; 12.5 cm width and 6.5 cm height) with a thin basal layer of plaster and tufts of moss. These terraria were moistened regularly to maintain a relative humidity near 100%. In each terrarium there was also a culture of *S. curviseta*; because the springtails propagated, there was always an over-abundance of food. Each few days we provided dry yeast as food for the springtails.

Experiment 4. To study the extent and variation of prey sharing we observed, during five hours, recently hatched juveniles from ten cocoons in the above-mentioned small vials. Each vial initially contained ten first instar spiderlings of comparable size from the same cocoon, 15 *S. curviseta* and five *I. viridis* for prey.

Experiment 5. To investigate if prey sharing is voluntary or forced we observed, during five hours, 15 small vials, each with two first instar juvenile spiders of comparable size, and 15 vials with two first instar juvenile spiders of different sizes. In each vial there were four *S. curviseta* per spider.

Experiment 6. Is there more juvenile cannibalism between juvenile spiders of different sizes than between spiders of comparable sizes? In each of 25 small vials (5 cm diameter and 2.5 cm height) we placed two first instar juveniles of comparable size, and in another 25 vials we placed two first instar juveniles of different size. Over five

days we monitored the number of spiders present each day. *S. curviseta* individuals were added each day as necessary to maintain four springtails per spider per vial.

Data on cannibalistic performance in the second experiment were used as poisson distributed response variables in a generalized mixed linear model with log link (glimmix procedure in SAS 8.1) and backwards elimination of non-significant variables. The diet treatment was included as fixed class factors, the initial number of spiderlings and the observation period (developmental period till adulthood) as continuous variables. For analysis of the other experiments we used linear regression, and to compare percentages,  $\chi^2$ -test; these analyses were performed with Statistica.

## RESULTS

### Experiment 1 : Extent of juvenile cannibalism

Juvenile cannibalism occurred in 110 of the 111 groups of juvenile descendants from individual cocoons kept together in small vials (99%).

### Experiment 2 : Effect of initial density of juveniles and diet on juvenile cannibalism

Table 1 shows the numbers observed for the different spider density and diet categories. The degree of juvenile cannibalism depended significantly on initial density, total observation period, and the interaction between the two (Fig. 1 & 2). No variation was explained by the diet

(Fig. 1) or the interaction of diet with the continuous variables. The goodness-of-fit of the model was significant ( $\chi^2_{202} = 125$ , *NS*) and standardised residuals approached normality (Shapiro Wilk's  $W = 0.97$ ). Table 2 shows the results of the linear model. Fig. 2 shows the relative number of cannibalised spiders from the start until adulthood and clearly demonstrates that more spiders were cannibalised at higher densities.

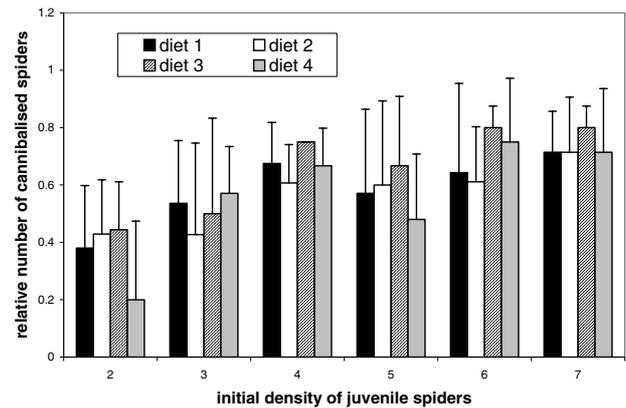


Fig. 1. – Histogram with means and standard deviations of number cannibalised spiders/total number of spiders between the four different diets and this for the different initial juvenile densities (1 = mono-diet *Sinella curviseta*, 2 = successive poly-diet *S. curviseta*-fruit flies, 3 = mono-diet *Isotoma viridis*, 4 = simultaneous poly-diet *S. curviseta*-fruit flies).

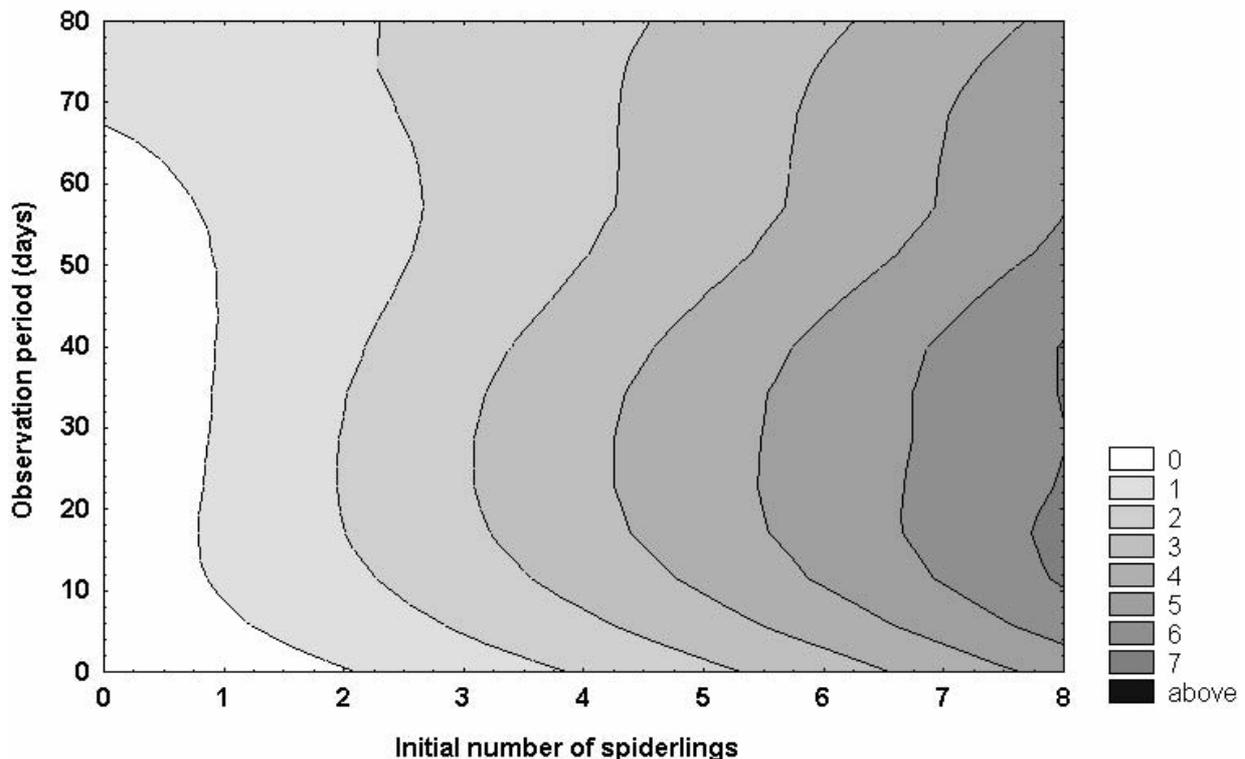


Fig. 2. – The number of cannibalised spiders of the second experiment (different grey values) is affected by the initial juvenile density, the number of observation days and the interaction between both.

TABLE 2

Statistical analysis of the effect of initial density of juveniles and diet on juvenile cannibalism (Experiment 2). Results of GLIMMIX model with stepwise backwards elimination of the non-significant contributions. Diet was treated as fixed factor; initial number of spiderlings and observation period were considered continuous variables.

Factor	num. df	den. df	F	P	R
Diet	3	202	1,12	0,343	
Initial density of spiderlings	1	202	164,37	< 0,0001	+0,866
Observation period (days)	1	202	14,24	0,0002	+0,242
Observation period x Initial density of spiderlings	1	202	19,47	< 0,0001	
Diet x Initial density of spiderlings	3	193	0,51	0,674	
Diet x Observation period	3	199	2,20	0,612	
Diet x Observation period x Initial density of spiderlings	3	196	0,53	0,661	

### Experiment 3 : Terrarium experiments

We compared the mortality of *O. gibbosus* in six separate terraria after 20 days. Because there was an overabundance of springtails, we can consider that mortality was mostly due to juvenile cannibalism. After 20 days the number of spiders in each terrarium

was drastically reduced, with mortality between 61% and 90%.

The initial number of spiders had a significant, positive effect on the extent of juvenile cannibalism (linear regression :  $F_{1,4} = 12.93$ ;  $R = +0.872$ ;  $p = 0.023$ ) (Fig. 3); this confirms the results found in the aforementioned juvenile cannibalism experiments.

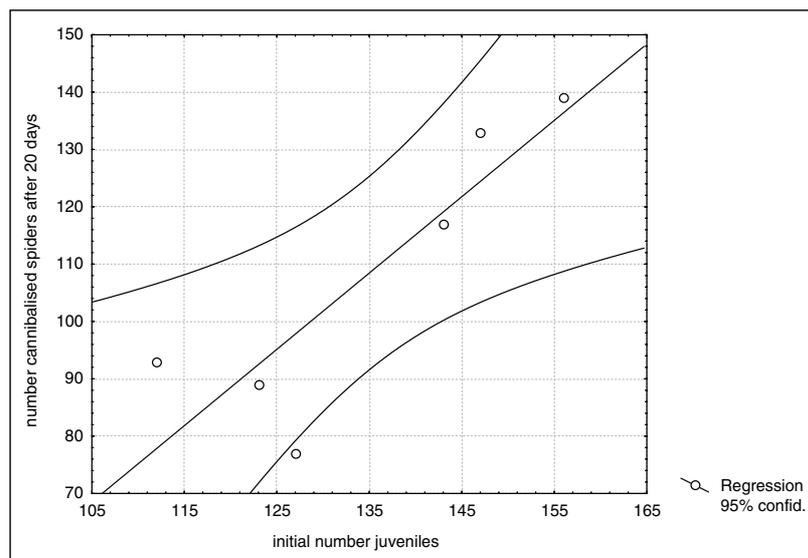


Fig. 3. – Bivariate correlation of the number of cannibalised juveniles after 20 days on the initial number of juveniles.

### Experiment 4 : Variation in and extent of prey sharing

We observed ten vials each with ten first instar juvenile spiders of comparable size during five hours. Prey sharing between juveniles of *O. gibbosus* occurred five times. One juvenile caught the prey, namely a *S. curviseta*, and tolerated another juvenile eating the same springtail. In another case the springtail was shared among three juveniles. At first, the third juvenile was driven away by the other two, but a second attempt was successful and this resulted in prey sharing among three.

Once we observed prey sharing between an *O. gibbosus* juvenile and two springtails; a juvenile spider caught an *I. viridis* springtail and shared this prey with two *S. curviseta* springtails. This is exceptional; mostly the spiders drive the springtails away while eating.

There were also five observations of scavenging; different juvenile spiders fed successively on the same prey item. One spider always caught the springtail and started to eat it. After a while the spider left the half eaten springtail; soon a second spider began to eat this springtail. Scavenging cannot be considered as helping behaviour; in the next experiment we concentrated on real prey sharing.

### Experiment 5 : Voluntary or forced prey sharing?

Observations on 15 small vials each with two first instar juveniles of comparable size and 15 vials each with two first instar juveniles of clearly different size showed that prey sharing occurred significantly more between spiderlings of comparable size (6/15) than between those of different size (0/15) ( $\chi^2_1 = 5.14$ ;  $p = 0.023$ ). Twice a small spiderling tried to eat from a prey caught by a larger

spiderling, but the latter did not tolerate this and drove the small one away.

### Experiment 6 : Are cannibals mostly bigger than their victims?

To study this we compared the occurrence of juvenile cannibalism during five days between two first instar juvenile spiders of comparable size (10/25) and between two first instar spiderlings of different size (25/25); this difference was significant ( $\chi^2_1 = 3.90$ ;  $p = 0.048$ ).

## DISCUSSION

The extent of juvenile cannibalism in the dwarf spider *Oedothorax gibbosus* is certainly very high; it occurred in 99 % of the cases in the first experiment. That juvenile cannibalism is very pronounced was also shown in the terrarium experiment (Exp. 3). After 20 days there was already a drastic decline of juvenile spiders; this mortality is most probably almost completely due to juvenile cannibalism. A slight overestimation of the extent of juvenile cannibalism is possible, because spiderlings in nature may be more able to evade one another. *O. gibbosus* spiders are, however, distributed in aggregations in alder carrs, such that the results given here are most probably a good indication for the extent of juvenile cannibalism in the field.

The second experiment showed a significant effect of initial juvenile density on the extent of juvenile cannibalism; more juveniles were cannibalised when initial density was higher. This result was confirmed by the terrarium experiment. Because we studied each case of the second experiment until adulthood of the cannibals, the number of observation days differed between cases, and the degree of juvenile cannibalistic behaviour also depended significantly on the number of observation days. Evidently, a longer juvenile development enhances chances for juvenile cannibalism. The different diets provided in the second experiment did not have a significant effect on the occurrence of juvenile cannibalism, possibly because they did not differ sufficiently in food quality.

According to the sixth experiment, it is mostly larger first juveniles that eat smaller ones, but juvenile cannibalism among similar sized juveniles also occurs. Size difference between first juveniles thus has important consequences for juvenile cannibalism, but also for the observed prey sharing in *O. gibbosus*. This is in agreement with SAMU *et al.* (1999): if cannibalism occurs among juvenile *Pardosa agrestis* spiders, the heavier spider is always the cannibal.

The fifth experiment shows that prey sharing occurs more among juveniles of comparable size; larger juveniles do not tolerate prey sharing with small ones and drive them away. This is an indication that the observed prey sharing is not voluntary; small juveniles are unable to defend their prey against rivals. This forced prey sharing is thus a consequence of the lack of a size difference between cannibalistic juveniles and is not an example of social behaviour. We observed this forced prey sharing in five of the ten cases in the fourth experiment and in six of the 15 cases with similar sized juveniles in the fifth exper-

iment. This confirms again the importance of juvenile cannibalism in *O. gibbosus*.

Some observations in the fourth experiment confirm this "involuntary sharing" hypothesis. In one of the five cases of food sharing observed there was also prey sharing among three similar sized juveniles; the third juvenile spider was first driven away but a second attempt by this spider to eat part of the prey was successful. This indicates again the inability of small first juvenile spiders to defend their prey. The observation that one juvenile spider "shared" food with two springtails also confirms that food sharing is forced and not voluntary among cannibalistic juveniles in *O. gibbosus*.

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