

Different forms of cannibalism in the dwarf spider *Oedothorax gibbosus* (Blackwall, 1841)

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Abstract

Oedothorax gibbosus (Blackwall, 1841) (Erigoninae, Linyphiidae, Araneae) is a rare dwarf spider species bound to oligo- and mesotrophic alder marshes. There are two male morphs in this species, namely *gibbosus* with a hunch and a hairy groove on its carapace and *tuberosus* without these features. In our laboratory experiments on this dwarf spider the occurrence of juvenile cannibalism and infanticide was very high, whereas sexual cannibalism, oophagy by females and juveniles occurred less frequently. The extent of juvenile cannibalism was influenced by the male morph of the father. Juvenile cannibalism was significantly lower among the offspring of *gibbosus* fathers than among the offspring of *tuberosus* fathers, which indicates a genetic control of cannibalistic tendencies. Also other factors, like presence/absence of food, initial density of juveniles, size difference between juveniles and vulnerability of juveniles influenced the extent of juvenile cannibalism. The diets of different prey composition, on the other hand, had no significant effect on the extent of juvenile cannibalism. In *O. gibbosus* there were more female than male 'survivors' of juvenile cannibalism.

Key words: Araneae, Erigoninae, juvenile cannibalism, male dimorphism, cannibalism forms

INTRODUCTION

According to Polis (1981), cannibalism is the killing and consuming of 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, cannibalism during or after courtship and copulation (sexual cannibalism), killing of offspring by one or both parents (infanticide), eating older individuals (gerontophagy), and the consumption of eggs (oophagy). The opposite of infanticide is matrophagy, this is cannibalising the mother by its offspring (Tahari et al. 1989; Kim et al. 2000). Juvenile cannibalism is the cannibalism among juveniles (Moya-Larano et al. 2002).

Sexual cannibalism is a phenomenon that occurs in most spider families. In some spider

species sexual cannibalism was responsible for the evolution of particular courtship and copulation characteristics; the males in different spider species perform a courtship in a manner that reduces the chance to be cannibalised by the female. In some web building spiders cannibalism is the likely cause of sexual dimorphism (Elgar & Crespi 1992). Another spectacular example of sexual cannibalism is the male of the red back spider, which after penetration in the epigyne, puts its abdomen very close to the chelicerae of the female, thus offering itself as a 'nuptial gift' (Andrade 1996). Cannibalism, in this case intrasexual cannibalism, can also be a consequence of territorial disputes, such as in the Mediterranean tarantula *Lycosa tarantula* (Linnaeus, 1758) (Moya-Larano et al. 2002).

Wagner & Wise (1996, 1997) describe 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 these authors, there are different factors that possibly influence the extent of juvenile cannibalism, such as differences in body weight, hunger and life stage. Juvenile cannibalism, oophagy and matriphagy have been observed in the salticid *Menemerus bracteatus* (L. Koch, 1879) (Rienks 2000); infanticide in *S. ocreata* (Wagner, 1995); oophagy in the eresid *Stegodyphus lineatus* (Latreille, 1817) (Schneider & Lubin 1997); matriphagy in *Amaurobius ferox* (Walckenaer, 1830) (Kim et al. 2000), *Amaurobius fenestralis* (Ström, 1768) (Tahari et al. 1989) and *Diaea ergandros* Evans, 1995 (Evans et al. 1995). In some spider species cannibalism almost never occurs, such as in the non-aggressive dictynid *Mallos gregalis* (Simon, 1909) (Jackson 1979).

Polis (1981) gave some evidence that there may be a genetic component to cannibalism, which was observed in breeding strains or races with variable cannibalistic tendencies in *Trilobium* beetles and in several species of *Poeciliopsis* (guppies). Fox (1975) states that differences in the sex and age of intraspecific predators and differences in the cannibalistic propensities of closely related species strongly imply a genetic basis. The same author argues that the widespread occurrence of various adaptations that either inhibit or promote cannibalism among relatives implies the presence of selection on genes that regulate its expression. According to Wagner et al. (1999) the presence or absence of food can have an influence on the regulation of genes responsible for cannibalism in the ladybird beetle *Harmonia axyridis*.

In contrast to reports of sexual cannibalism in 49 species of 14 spider families (reviewed in Elgar & Crespi 1992), the number of publications on juvenile cannibalism in spiders is

very restricted. The only ones are the aforementioned Wagner & Wise (1996, 1997) and Samu et al. (1999) papers. Different kind of intraspecific interactions in several spider families are also mentioned by Jackson & Pollard (1990), Whitehouse & Jackson (1994), Clark & Jackson (1995) and Clark et al. (1999). As far as we know, there are no earlier reports on juvenile cannibalism in linyphiid spiders. In most cases only one form of cannibalism is studied in a spider species per publication. The purpose of this publication was to investigate the occurrence of the different forms of cannibalism in a linyphiid spider species, in the male dimorphic *Oedothorax gibbosus*. In this dwarf spider species there is a *gibbosus* male morph with a hunch on the last third of its carapace, and more in front of this hunch with a hairy groove, and there is a *tuberosus* male morph without these features. As shown by Maelfait et al. (1990) this dimorphism is based on a di-allelic gene only expressed in the male.

The different forms of cannibalism investigated in *O. gibbosus*, are juvenile and sexual cannibalism, infanticide and oophagy by females and juveniles. While taking care of spider cultures of this spider species we often observed the occurrence of juvenile cannibalism, and during copulation experiments sexual cannibalism. Therefore we expect that the occurrence of juvenile and sexual cannibalism is higher than that of the other forms of cannibalism. We also studied the effect of (a) the father morph; (b) the presence or absence of food, (c) the initial density of juveniles; and (d) diet composition on the extent of juvenile cannibalism. A difference in the amount of juvenile cannibalism between offspring with a *gibbosus* and a *tuberosus* father could be an indication for a genetic base of cannibalism. Also, the relative survival of the sexes and the male morphs was investigated.

MATERIAL AND METHODS

O. gibbosus spiders were caught in the nature reserve "Het Walenbos", a river associated

woodland 30 km north-east of Brussels in Belgium (50°55'N, 4°51'E). *O. gibbosus* lives there in an oligo- to mesotrophic alder marsh. Some spiders used in the experiments were spiderlings that emerged from the cocoons of females brought in from the field. The morph of their father was of course, unknown. Other experimental spiders originated from crossing of virgin females with either *tuberosus* or *gibbosus* males in the laboratory. All spiders were kept in a climate chamber at a photoperiod L: D 16:8 and at a temperature of 20°C.

To investigate the effect of food presence and father morph on the extent of juvenile cannibalism, all juvenile spiders coming from the same cocoon were left together in the same plastic vial (5 cm diameter and 2.5 cm height) with a thin bottom of plaster of Paris. Due to original clutch size differences spider densities in the vials varied at the start of the experiment from two to forty. The vials were moistened regularly to maintain a relative humidity near 100%. We monitored the occurrence of juvenile cannibalism for 111 cocoons. These spiders were divided into two groups: one group received each day two springtails of the species *Sinella curviseta*, the other group got no food at all. Table 1 shows the numbers of observations per food presence treatment and per male morph of the father. There were only three first juvenile instars that died of starvation without an attack on them; they were excluded from the analysis. The number of survivors was noted until the spiders that were not cannibalised reached adulthood. This was

necessary to be able to determine the sex and the male morph of the survivors (= the cannibals). Because the time needed to reach adulthood was not the same for all clutches, the length of that period was also taken into account in the statistical analysis.

In a second series of experiments we studied the effect of the initial density of spiders and of four different diets on the extent of juvenile cannibalism. Spiders coming from a cocoon were apportioned into vials of increasing densities of one, two, three, and so on spiders per vial until all juveniles of the cocoon were used. The maximal density was seven. The layout of the number of vials observed per spider density - diet combination is given in Table 2. To one group of vials two *Sinella curviseta* springtails per day per spider were added (equivalent to c. 0.28 mg fresh weight of prey). To a second group before the second moult of the spiders two *Sinella curviseta* springtails per spider per day were added (equivalent to c. 0.28 mg fresh weight of prey), and after that each day three fruit flies per spider (equivalent to c. 5.76 mg fresh weight of prey). This was the so-called successive *Sinella curviseta*-fruit fly diet. A third group was fed with four *Isotoma viridis* springtails per day per spider (equivalent to c. 0.80 mg fresh weight of prey). To a fourth group of vials a simultaneous *Sinella curviseta*-fruit fly diet was added: each day four *Sinella curviseta* springtails and three fruit flies per spider (equivalent to c. 6.32 mg fresh weight of prey). We noted again the number of spiders until the cannibals reached adulthood.

To monitor the occurrence of sexual cannibalism, 20 male-female couples were observed for three weeks. In most cases, mating took place in the first week, but multiple mating also occurred. The two partners were put together and observed during daytime and separated at night.

To study the occurrence of infanticide, the following experimental design was used: a freshly hatched juvenile was put together with its mother for six days. To investigate if the

Table 1. The number of observed vials in the first experiment of juvenile cannibalism for the different food availabilities (without/with food) and the father morph (field = unknown father from field, *gib* = *gibbosus* father, *tub* = *tuberosus* father). The total number of involved juveniles per category is included in parentheses.

Food availability	father morph		
	field	<i>tub</i>	<i>gib</i>
without food	11 (105)	40 (519)	5 (55)
with food	16 (320)	25 (517)	11 (259)
total	27 (425)	65 (1036)	16 (314)

Table 2. The number of observed vials for the different spider density categories and diets (mono-diet *S. curviseta*, successive poly-diet *S. curviseta*-fruit flies, mono-diet *S. curviseta* and simultaneous poly-diet *S. curviseta*-fruit flies) in the second experiment of juvenile cannibalism.

Initial density	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

presence or absence of food has an influence on the mother-offspring cannibalism, one replicate group received two *Sinella curviseta* springtails each day (N = 30); another group no food (N = 22).

To assess the extent of oophagy, females were put together with one of their fertilised cocoons (N = 10). These females received no food for six days beforehand.

To investigate the extent of oophagy by juveniles, juveniles were put together individually with a fertilised cocoon and were monitored during six days (N = 10). The female that produced the cocoon was removed the day before the start of the experiment.

The following statistical tests were used: the Kaplan-Meier Log Rank test (Survival Analysis) to compare two survival curves, Chi-square tests to compare proportions and ANOVA (if the assumptions for normality were fulfilled according to the Kolmogorov-Smirnov test). SPSS 10.0 and Statistica were used for these statistical tests. For the two experiments on juvenile cannibalism we used the glimmix procedure in SAS 8.1. The data of both experiments were used as a Poisson distributed response variables in a generalized mixed linear model with log link (glimmix procedure) and backward elimination of non-significant variables. To analyse the first experiment, food presence and father morph were included as fixed class factors, the initial

density of spiderlings and the observation period (developmental period till adulthood) as continuous variables. To analyse the second experiment the diet treatment was included as a fixed class factor, the initial density of spiderlings and the observation period (developmental period till adulthood) as continuous variables.

RESULTS

The extent of the different forms of cannibalism

In Table 3 the relative frequencies of occurrence of the five investigated forms of cannibalism are compared for all possible pairings by Chi-square tests. For the juvenile cannibalism ratio the data were used not yet taking into account the father morph (*gibbosus*, *tuberosus*, unknown father). Significant differences according to the Chi-square test are indicated in bold, significant differences after Bonferroni correction are indicated with an asterisk. According to these Chi-square tests, there was significantly more juvenile cannibalism than sexual cannibalism; the occurrence of infanticide was significantly more frequent than sexual cannibalism. After Bonferroni correction the difference between juvenile cannibalism and oophagy by females, as well as between infanticide and oophagy by females, was not significant anymore, probably because of the many investigated combinations. Neverthe-

less, there was clearly a trend that juvenile cannibalism and infanticide was more frequent than oophagy by females.

Sexual cannibalism only happened in three of the 20 observed couples; one of 11 *tuberosus* and two of 9 *gibbosus* males were cannibalised. The incidence of infanticide was very high; there was no significant difference in the occurrence of infanticide in the absence (21/22) and presence (23/30) of food ($\chi^2_1 = 0.28$, NS).

Effect of food presence and father morph

The Kaplan Meier test shows that the survival of juveniles with food was significantly longer than without food ($Z = 21.948$, $P < 0.05$); this is without taking into account the father morph (*gibbosus*, *tuberosus*, unknown father). The only cause of mortality here was juvenile cannibal-

ism. The survival curves of Fig. 1 clearly indicate that during the whole experiment juveniles with food had higher survival. In the absence of food almost all juveniles were already cannibalised after 20 days, whereas in the presence of food near complete cannibalism occurred after 60 days. According to a two-way ANOVA, the fecundity, calculated as the total number of hatched juveniles per cocoon, was significantly smaller in the absence of food than in the presence of food, but there was no fecundity difference attributable to father morph ($F_{1,105} = 15.78$, $P < 0.05$ and $F_{2,105} = 0.12$, NS). There was no interaction between the two variables ($F_{2,105} = 0.93$, NS).

The degree of juvenile cannibalism was significantly different between the descendants of the different father morphs and be-

Table 3. Chi-square tests between the relative frequency of the different cannibalism forms for all possible pairings (juvenile and sexual cannibalism, infanticide and oophagy by females and juveniles) (relative frequency = number of cases with cannibalism/total number of observed cases). The total number of cases is included in parentheses. For the juvenile cannibalism ratio the data were used not yet taking in account the father morph (*gibbosus*, *tuberosus*, unknown father). The P-values with an asterisk are also significant after Bonferroni correction.

group 1	group 2	relative frequency (group 1)	relative frequency (group 2)	Chi - square	P
juvenile	sexual	0.99 (111)	0.15 (20)	11.30	0.001*
juvenile	infanticide	0.99 (111)	0.85 (52)	0.42	NS
juvenile	oophagy (female)	0.99 (111)	0.10 (10)	6.95	0.008
juvenile	oophagy (juvenile)	0.99 (111)	0.40 (10)	2.37	NS
sexual	infanticide	0.15 (20)	0.85 (52)	8.35	0.004*
sexual	oophagy (female)	0.15 (20)	0.10 (10)	0.11	NS
sexual	oophagy (juvenile)	0.15 (20)	0.40 (10)	1.37	NS
infanticide	oophagy (female)	0.85 (52)	0.10 (10)	5.47	0.019
infanticide	oophagy (juvenile)	0.85 (52)	0.40 (10)	1.48	NS
oophagy (female)	oophagy (juvenile)	0.10 (10)	0.40 (10)	1.46	NS

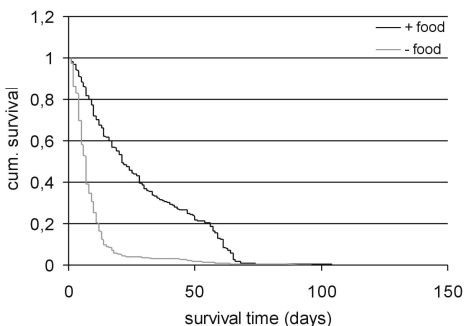


Fig. 1. Survival curves of the spiders by food presence treatment (without/with food) observed during the first experiment of juvenile cannibalism. In this graph the morph of the father was not taken into account.

tween the two food presence treatments (Table 4). The extent of juvenile cannibalism additionally depended on the initial number of spiderlings, the total observation period and the interaction between them. The linear model used did not explain the variation completely ($\chi^2_{104}=139.09$, $P < 0.05$); although standardised residuals approached normality (Shapiro Wilk's $W = 0.99$). In the absence of food juvenile cannibalism was significantly higher than in the presence of food according to the glimmix model (Table 4). The juvenile cannibalism was also significantly higher among the offspring of *tuberosus* males than among the offspring of *gibbosus* males; the juvenile cannibalism among the offspring of unknown males was in between. This is clearly visible in the survival curves (Fig. 2). This difference was more pronounced in the presence of, than in the absence of food. Fig. 3 shows the means and the standard deviations of the proportion of cannibalised spiders in a situation with and without food taking into account the father morph (*gibbosus*, *tuberosus*, unknown father).

The effect of initial density of juveniles and different diets

The degree of juvenile cannibalism depended significantly on the initial density of the spiderlings, the total observation period and the interaction between them (Fig. 4). No variation was explained by diet (Fig. 5) and by its interaction with the continuous variables. The model fitted the data well (goodness-of-fit test: $\chi^2_{202} = 125$, NS) and standardised residuals approached normality (Shapiro Wilk's $W = 0.97$). Table 5 shows the results of the linear model. It is clear from Fig. 5, that more spiders were cannibalised at higher densities.

'Survivors' and other general observations

The overall sex ratio in laboratory spider cultures of *O. gibbosus* where all spiders were reared separately - so that there could not be juvenile cannibalism- occurred to be females: males = 2:1. In the juvenile cannibalism experiments there were significantly more female than male 'survivors' (Chi-square test: $\chi^2_1 = 23.62$, $P < 0.05$); there were also more *gibbosus* than *tuberosus* male survivors, but this differ-

Table 4. Results of the glimmix model for the first experiment of juvenile cannibalism, with stepwise backwards elimination of the non-significant contributions to investigate the effect of food availability, father morph and initial spider density (food availability and father morph as fixed factors; initial density of spiderlings and observation period (days) as continuous variables)

factor	num. df	den. df	F	P	R
food availability	1	104	4.76	0.031	+0.208
father morph	2	104	5.09	0.008	+0.121
initial density	1	104	164.37	<0.0001	+0.870
days	1	104	18.74	<0.0001	+0.320
food availability* father morph	2	102	1.91	NS	
food availability*initial density	1	99	0.47	NS	
food availability*days	1	96	0.05	NS	
father morph*initial density	2	97	0.92	NS	
father morph *days	2	100	1.18	NS	
initial density*days	1	104	15.96	0.0001	
food availability* father morph *initial density	2	90	0.08	NS	
food availability*days*initial density	1	89	0.01	NS	
food availability*days* father morph	2	94	0.65	NS	
father morph *days*initial density	2	92	0.27	NS	
food availability* father morph *initial density *days	2	87	3.06	NS	

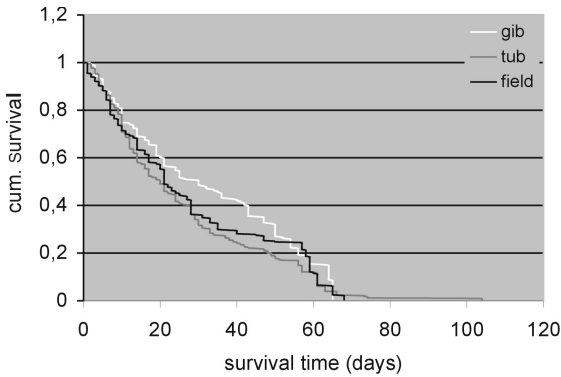


Fig. 2. Survival curves of spiders by father morph (unknown father from the field (field), *tuberosus* (tub) or *gibbosus* (gib) father) observed during the first experiment of juvenile cannibalism. This graph shows only the data of spiders in the presence of food.

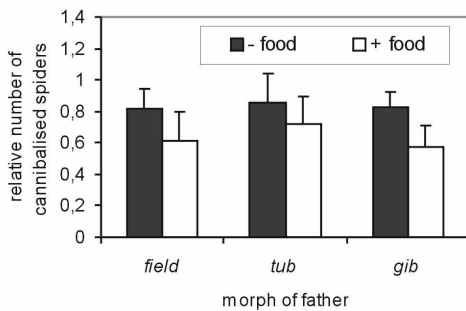


Fig. 3. Proportion of cannibalised spiders for the food presence treatment (without/with food) and father morph (unknown father from the field (field), *tuberosus* (tub) or *gibbosus* (gib) father) during the first experiment of juvenile cannibalism.

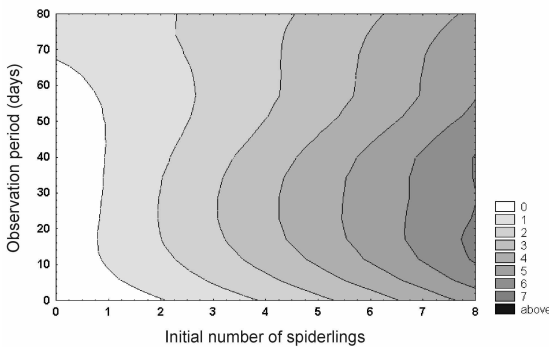


Fig. 4. The absolute number of cannibalised spiders in the second experiment of juvenile cannibalism: the effect of the initial juvenile density, the number of observation days and the complex interaction between them is clearly visible.

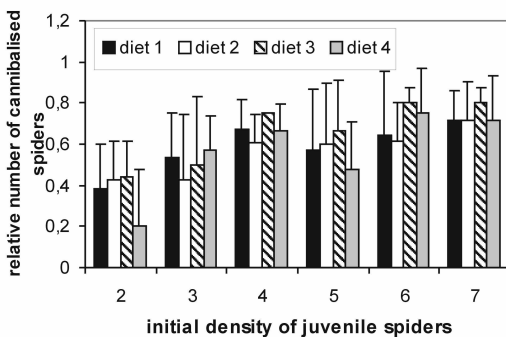


Fig. 5. Proportion of cannibalised spiders for the different initial densities of juvenile spiders and for the four different diets (1 = mono-diet *Sinella curviseta*, 2 = successive poly-diet *Sinella curviseta*- fruit fly, 3 = mono-diet *Isotoma viridis*, 4 = simultaneous poly-diet *Sinella curviseta* – fruit fly) during the second experiment of juvenile cannibalism.

Table 5. Results of the glimmix model for the second experiment of juvenile cannibalism, with stepwise backwards elimination of the non-significant contributions to investigate the effect of diet and initial spider density (diet as fixed factor; initial density of spiderlings and observation period (days) as continuous variables).

factor	num. df	den. df	F	P	R
Diet	3	202	1.12	0.343	
initial density	1	202	164.37	< 0.0001	+0.866
days	1	202	14.24	0.0002	+0.242
days*initial density	1	202	19.47	< 0.0001	
diet*initial density	3	193	0.051	0.674	
diet*days	3	199	20.20	0.612	
diet*days*initial density	3	196	0.053	0.661	

ence was not significant (Chi-square test: $\chi^2_1 = 1.19$, NS). The number of female, *gibbosus* male and *tuberosus* male survivors was 217, 62 and 48 respectively. In this dataset we pooled data across juvenile cannibalism experiments with and without food treatments.

Because of differences in developmental rate, the sizes of first juvenile instars from the same cocoon differed. In most cases larger spiders cannibalised smaller ones. Cannibalism between similarly sized juveniles occurred less frequently. Large, but weak spiderlings also fell more often as a victim of cannibalism. Recently moulted spiders, for example, were more vulnerable.

DISCUSSION

Juvenile cannibalism in *O. gibbosus* was very high; infanticide was also quite high. The extent to which the other studied forms of cannibalism occurred was very low. An overestimation of the extent of cannibalism is possible, because spiders in the field presumably have better opportunities to avoid larger conspecifics. The occurrence of *O. gibbosus*, however, is highly aggregated in their natural environment, so the results reported here are probably a good indication of the extent of the different forms of cannibalism in the field.

The frequency of occurrence of juvenile cannibalism was influenced by different factors like the presence of food, male morph of the father, initial density of juveniles, size difference between juveniles and vulnerability of

juveniles. Probably because of genetic variances the linear model used in the first experiment of juvenile cannibalism did not explain the variation completely. According to the second experiment, the different diets had no significant effect on the extent of juvenile cannibalism. It is possible that the studied food regimes (prey items) deliver a similar amount of energy to the spiders.

The difference in juvenile cannibalism among spiders with a *tuberosus* father vs. *gibbosus* father indicates a genetic background of the observed juvenile cannibalism. The male dimorphism in *O. gibbosus* has indeed a simple genetic basis (Maelfait et al. 1990; Vanacker et al. 2001). In this study we could not take into account the genotype of the females, because it is only possible to determine the genotype of females by crossings. In agreement with this result, the extent of juvenile cannibalism in offspring with an unknown father from the field was intermediate relative to that in offspring with a *gibbosus* or a *tuberosus* father. Polis (1981) already proposed a genetic control of cannibalism and according to Wagner et al. (1999) the presence and absence of food could have an influence on the regulation of the genes responsible for cannibalism. Selection could increase the extent of cannibalism under, for example, conditions of food scarcity. It is possible that the regulation of such genes is different between offspring of *tuberosus* fathers and *gibbosus* fathers. The fact that the difference in juvenile cannibalism among offspring

of the two different male morphs was more pronounced in the presence of food than in the absence of food, shows that starvation has a large effect on juvenile cannibalism that overrides the father morph effect. It is surprising that we did not find a significant difference in the occurrence of infanticide in the absence and presence of food, because this was the second most frequent form of cannibalism in *O. gibbosus*.

We already found that *tuberosus* has a shorter juvenile development (Vanacker et al. 2001), it lives longer in highly humid environment, as well as under food rich and food scarce conditions (Vanacker et al. 2003). That the offspring of *gibbosus* is less prone to juvenile cannibalism than the offspring of *tuberosus*, could be an advantage for *gibbosus* to compensate for the aforementioned advantages of *tuberosus*. Other possible advantages of *gibbosus* are the genetic dominance and the greater sexual attractiveness than *tuberosus* (Vanacker et al. 2001).

In *O. gibbosus* there were more female than male 'survivors' of juvenile cannibalism. The observed distortion in sex ratio in favour of the female sex can be partially caused by (juvenile) cannibalism. Brach (1975) already mentioned that cannibalism can distort sex ratio in favour of females in some spider species. According to Vanacker et al. (2001) *tuberosus* males are probably able to compensate for the genetic dominance of the *gibbosus* morph by a sex ratio distortion in favour of the female sex by a still unknown mechanism. Interaction between this phenomenon and juvenile cannibalism could be an explanation for the sex ratio distortion in favour of the female sex in *O. gibbosus*. Further studies are necessary. It is also interesting that in other related non-dimorphic dwarf spider species, such as *O. fuscus* (Blackwall, 1834) and *O. apicatus* (Blackwall, 1850), a higher female survival of juvenile cannibalism is absent. The sex ratio in the survivors in *O. fuscus* was 1:1, while in *O. apicatus* it was females:males = 75:25 (Vanacker, unpublished data).

Higher cannibalism in high density situations confirms the claim of Polis (1981) that juvenile cannibalism is a possible density regulator factor, which can be modulated by the size distortion of the population and food availability (Samu et al. 1999).

ACKNOWLEDGEMENTS

We are indebted to Stano Pekár and Ferenc Samu for comments on the previous version of the manuscript and to Dr. Michael L. Draney of the Department of Natural and Applied Sciences of the University of Wisconsin-Green Bay for delivering several Collembola of the species *Sinella curviseta* to start a Collembola culture in our laboratory. We also thank Etienne Bijttebier for taking care of the *Sinella curviseta* culture. We also thank Liesbeth Maes, Katrijn Deroose, Domir De Bakker, Viki Vandomme, Frederik Hendrickx, Lut Van Nieuwenhuyse, Marjan Speelmans and Wannes Heirbaut for their help to catch the dwarf spiders in the field. This paper was brought about with a PhD grant of the Foundation for Scientific Research – Flanders of the first author.

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