

ORIGINAL ARTICLE

Ferenc Samu · Søren Toft · Balázs Kiss

Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae)

Received: 15 December 1997 / Accepted after revision: 10 October 1998

Abstract Cannibalistic tendencies are well known in spiders and may be a significant factor influencing population size. The wolf spider, *Pardosa agrestis*, is the dominant non-web-building spider in a wide range of central European agricultural habitats. Preliminary field observations indicated an extended reproductive period, which results in a very wide size distribution of juvenile instars. We hypothesised that if cannibalism is enhanced by differences in size, especially during periods when prey is scarce, these populations might be susceptible to cannibalism in an ecologically significant way. Laboratory studies were conducted on juvenile *P. agrestis* in arenas. We analysed the following specific aspects of cannibalism: (1) the effect of the weight ratio between the opponents; (2) the effect of weight per se, and (3) the role of hunger level in determining cannibalistic tendencies of spiders. The role of weight and hunger were analysed in separate experiments, in both cases by controlling for the other variable. The results showed that cannibalism was strongly positively correlated with both weight ratio and hunger, but absolute size/age of an individual could not predict the occurrence of a cannibalistic event. These experiments generated the plausible hypothesis that cannibalism might be an important phenomenon in the regulation of real populations, which should be tested specifically in future field experiments.

Key words Cannibalism · Wolf spider · Hunger · Size difference · Agroecosystem

F. Samu (✉) · B. Kiss
Plant Protection Institute, Hungarian Academy of Sciences
P.O. Box 102, H-1525 Budapest, Hungary
e-mail: h2367sam@ella.hu
Tel.: +36-1-1769555, Fax: +36-1-37697299

S. Toft
Department of Zoology, University of Aarhus
Bldg. 135, Universitetsparken
D-8000 Århus C, Denmark

Introduction

Cannibalistic tendencies in spiders are well documented. Indeed Bristowe (1941) has claimed that “spiders are spiders’ worst enemies”, including in his statement both true cannibalism (conspecific predation) and what is today known as intraguild predation, i.e., predation on other spider species (Polis et al. 1989). In spite of its early recognition, the ecological importance of cannibalism for spiders cannot be evaluated, because most of the research effort has focused on the study of sexual cannibalism (e.g., Ross and Smith 1979; Elgar and Nash 1988; Arnquist 1992; Prenter et al. 1994).

Non-sexual cannibalism is a widespread phenomenon in natural populations of a wide range of animal groups. This interaction has been shown to be potentially important for the regulation of populations (Polis 1981; Elgar and Crespi 1992; Crowley and Hopper 1994). Cannibalism can serve to enhance the fitness of larger animals when other prey are not available. Smaller conspecific prey might make resources (e.g. very small prey) indirectly available for the larger animals and thus effectively widen the food base for the population. Cannibalism can also have an impact on the size structure of populations. If the probability of cannibalism is correlated with the size ratio between cannibal and victim, moderate cannibalism might narrow the population size distribution, and can act as a synchronising factor. For instance, the single-age-class dominated population of predaceous copepods, found in Canadian lakes, can be attributed mostly to cannibalism (Anderson 1970). On the other hand, if the intensity of cannibalism increases with absolute size, then cannibalism might maintain or even increase size variation within a population (Crowley and Hopper 1994).

The potential costs of cannibalism include the killing of a related animal which reduces the inclusive fitness of the cannibal (Pfennig et al. 1993), and the risk of

pathogen or parasite transmission from a conspecific prey (Pfennig et al. 1998). A further important risk is that cannibal "predators" face "prey" of the same or similar predatory capabilities which makes retaliation possible (Elgar and Crespi 1992). Size difference has a strong bearing on the risks associated with a cannibalistic event, and hunger is likely to influence the risk proneness of a cannibal; both are quoted to be among the most important factors that influence the occurrence and outcome of cannibalistic attempts in a wide variety of taxa (Fox 1975; Polis 1981).

The size difference between sexes in wolf spiders (Lycosidae) is small, and sexual cannibalism is absent or infrequent. Observations of the social behaviour in a number of lycosid species revealed sophisticated display behaviour, and highly ritualised agonistic encounters, with usually no harm done to the interacting spiders (Aspey 1977a, 1977b; Nossék and Rovner 1984). By varying densities of adult *Schizocosa crassipes*, Aspey (1977b) found that agonistic interactions were adjusted so that spacing of the animals was preserved, and no cannibalism took place.

In spite of the avoidance mechanisms, both field and laboratory studies have revealed that non-sexual cannibalism might be an important phenomenon in wolf spiders. While the above-mentioned behavioural studies were mostly done on adult spiders, the picture might be different if various life stages, which coexist in natural populations, are considered. Although the smallest stages are protected against predation by conspecific reproductive females, adult males and virgin females might include spiderlings in their diet (Higashi and Rovner 1975; Wagner 1995). Juvenile wolf spiders constituted a considerable proportion of the diet in *Pardosa lugubris* and *P. pullata* in a field study by Hallander (1970). Recently, Wagner and Wise (1996) have presented very convincing field results showing that cannibalism among juveniles of the wolf spider *S. ocreata* is probably the single most important population-regulating mechanism.

One particular wolf spider species, *P. agrestis* (We-string) is perhaps the single most abundant epigeic spider in central European agricultural areas (Samu et al. 1996; Tóth and Kiss 1997). A recent study of the life history of this annual species revealed an unusually extended reproductive period, which results in a very wide and possibly bimodal size distribution of the co-existing juvenile instars (Zulka et al. 1997; Samu et al. 1998). In this paper we examine the possibility that cannibalism might be one of the factors that regulate these populations, by analysing how the frequency of cannibalism is influenced by characteristics of the population structure. Specifically, we tested, in laboratory experiments, whether (1) the probability of cannibalism is influenced by the weight ratio between encountering animals; (2) cannibalism is more frequent among smaller/younger animals than among larger/older spiders, and (3) cannibalism is more frequent among food-deprived spiders.

Methods

Around 500 juvenile *P. agrestis* were hand collected in an alfalfa field, at Nagykovácsi, near Budapest, Hungary, in October 1996. The collection was made by area-restricted hand collecting, so that the weight distribution of the animals was representative of that of the field population (for a discussion of the representativity of different sampling methods for *Pardosa* see Samu et al. 1997). The average weight of the juvenile *Pardosa* population in the field in the pre-overwintering period (obtained from an independent sample at the end of October) was 5.6 mg (SD = 2.92, range = 0.4–13.5).

Spiders were initially selected from the laboratory population and brought to standard hunger levels by feeding them ad libitum for 2 days with *Drosophila melanogaster*, which is sufficient to satiate the spiders (Toft 1995; Bilde and Toft 1998), and then starving them for a fixed period. During starvation and the experimental tests, spiders were kept at 20 °C, 16/8 h light/darkness. Cannibalism testing was done on pairs of spiders by observing them in arenas for 24 h. One day before testing, spiders were weighed, their sex and instar stage was determined, and they were checked for condition (e.g. moulting, legs missing). In cases where the weights of the spiders in a pair were close and no other distinguishing mark (e.g. sex) was available, the heavier spider was marked with a small enamel paint dot to facilitate individual recognition of animals. Spiders which moulted 24 h before or within 48 h after testing, and animals which had more than one or any of the first legs missing were excluded from the analysis. The general hunger level was also checked after each test by offering the spiders three fruit flies. If only one or none was eaten, that spider (and its pair) were excluded from the analysis. In cases where no cannibalism occurred, both spiders were re-entered into the stock population. Such animals may have been reused in another test, but this was not made sooner than a month later (during which time the animals usually moulted). Statistical tests indicated no effect of reuse. Cannibals were not used more than once.

Testing for cannibalism was carried out in 14-cm-diameter Petri dish arenas, which had a base of dampened plaster of Paris. The two experimental spiders were placed into the arena simultaneously. During the 24-h testing period, the occurrence of cannibalism was recorded. Several arenas were observed simultaneously. The observations were grouped into two experiments.

In the weight experiment ($n = 110$ pairs), the continuous independent variables were the weight of individual spiders and the resulting weight ratio of the spider pair (weight of heavier spider/weight of lighter spider). Variation in weight ratio was achieved by the random pairing of spiders of different weights. The starvation period before the weight experiment was held constant at 14 days.

In the hunger level experiments ($n = 92$ pairs), the animals were food deprived for 0, 14 or 28 days. We intended to perform the hunger experiment in a weight ratio range in which the weights of the animals were different enough to permit cannibalism, but not exceedingly different. Such spider pairs were selected so that their weight ratio fell within the lower part of the weight ratio distribution of spider pairs where cannibalism occurred in the weight experiment.

Results

The effect of weight and weight ratio

If cannibalism occurred, the heavier spider was always the cannibal. No case of size reversal was observed in any test. The weight of victims was significantly lower than that of the cannibals (Wilcoxon signed-rank test: $T = 0$, $n = 29$, $P < 0.0001$; Fig. 1a). Weight ratios of spider pairs had sufficient variation and range to test its

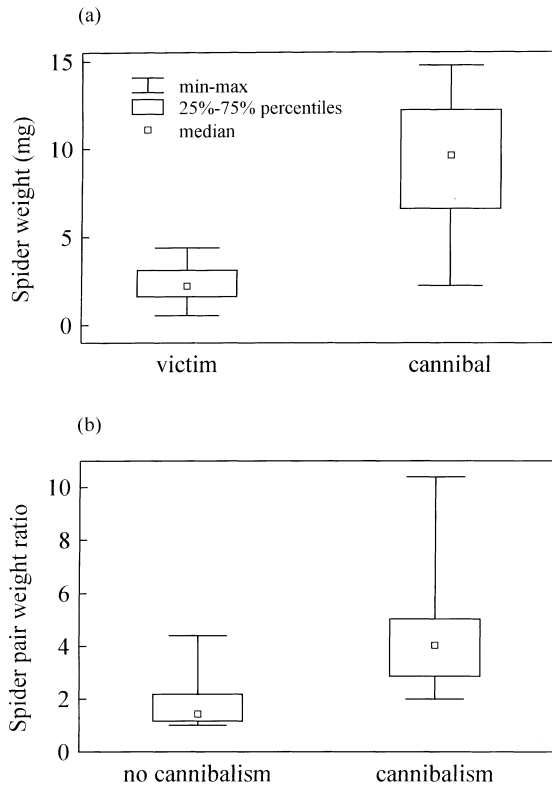


Fig. 1 **a** Weight difference in the weight experiment between spiders that became cannibals versus victims. **b** Difference in the weight experiment between weight ratios of spider pairs where testing had a neutral outcome versus cannibalism

effect on cannibalism (mean = 2.45, range = 1.01–10, $n = 110$). The weight ratios tested in the present experiment were not significantly different from weight ratios that were obtained by randomly pairing juvenile *Pardosa* individuals from a late-October sample of 189 animals taken from the same field (t -test of weight ratios: $t_{204} = 0.48$, NS; Levene test of homogeneity of variance: $F_{1,204} = 0.514$, NS). The weight ratio in cannibalistic outcomes was significantly larger than in cases where no cannibalism occurred (Mann-Whitney U -test: $U = 142$, $n_1 = 81$, $n_2 = 29$, $P < 0.0001$, Fig. 1b).

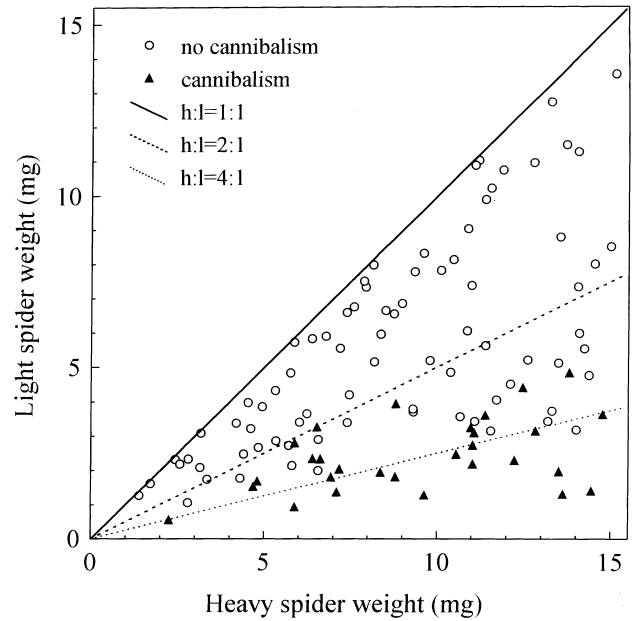


Fig. 2 Outcome of arena tests in the weight experiment. Each test is indicated by a symbol, *filled* if the outcome was cannibalism and *empty* if no cannibalism occurred. Lines were not fitted to the data: they are the isolines of the 1:1, 2:1 and 4:1 weight ratios

Figure 2 reveals that cannibalism occurred in nearly all of the cases when the weight ratio between the spiders was greater than 4:1, and no cannibalism was observed if the weight ratio was smaller than 2:1. Smaller spiders were not cannibalised if they were above 5 mg. We tested whether weight and/or weight ratio affects the outcome by logistic regression using combinations of these factors as independent variables (Table 1). If we considered the weight of one of the spiders, only the lighter spider weight was significantly correlated with the occurrence of cannibalism. The effect of the weight ratio between the opponents influenced the probability of cannibalism highly significantly. The effect of weight, controlling for weight ratio, was not significant. Thus we could not conclude that the occurrence of cannibalism would be different in various size/age classes of *P. agrestis* juveniles. The non-significance of weight

Table 1 Results of logistic regressions, where the response variable is the occurrence of cannibalism (H heavy-spider weight, L light-spider weight, R weight ratio, M whole model effect)

Model	Effect	df	χ^2	P
H	M	1	0.48	NS
L	M	1	39.206	< 0.0001
R	M	1	65.416	< 0.0001
R+H+R × H	M	3	70.062	< 0.0001
	R	1	6.456	0.011
	H	1	0.586	NS
	R × H	1	1.734	NS
R+L+R × L	M	3	68.158	< 0.0001
	R	1	3.830	0.05
	L	1	0.078	NS
	R × L	1	0.162	NS

ratio \times weight terms revealed that the weight ratio effect does not change with the absolute weight of spiders.

The influence of hunger on cannibalism frequency

The weight ratio of spiders in the hunger experiment was controlled for by selecting them so that their weight ratio distribution was as narrow as possible, and at the lower end of the possible weight ratios where we could still expect cannibalism to occur (in the hunger experiment, all pairs were above the weight ratio 2:1: mean = 2.82, range = 2.11–3.99, $n = 92$, cf. random pairing of the animals in the weight experiment: mean = 2.45, range = 1.01–10). Spider pairs in the three hunger treatments had statistically similar mean and variance of weight ratios (ANOVA: $F_{2,89} = 0.26$, NS; Levene test of homogeneity of variance: $F_{2,89} = 2.57$, NS). The occurrence of cannibalism showed a highly significant positive trend with the increase in hunger level (logistic regression: $\chi^2_1 = 51.979$, $P < 0.0001$; Fig. 3).

Discussion

In the present experiment, there was a two-fold threshold in weight ratio below which no cannibalism occurred. Cannibalism was observed more frequently when the weight ratio was larger. In cases where the experimental pairs had contrasting weights (weight ratio above 4:1), cannibalism occurred in nearly all of the tests. Field studies have suggested that size difference might be important in wolf spider cannibalism. Edgar (1970b) showed that 16% of the natural prey of *P. lugubris* were younger stages of conspecific animals. In another field study, Hallander (1970) observed that conspecific juveniles were represented in the diet of *P. lugubris* and *P. pullata* by 15% and 20%, respectively. Adult females also fed on conspecific males and in a few instances other females. Although actual size differences in these studies were not reported, we can infer the field

importance of cannibalism from the fact that it occurred most frequently between different stages or sexes. A large weight ratio can be expected to reduce the potential costs of cannibalism by decreasing the possibility of retaliation. Handling time, which is important in determining the profitability of a prey item, is predicted to decrease with increasing size difference, and thus handling time and retaliation risk together might determine the size ratio window in which conspecific prey is profitable for the predator (Dong and Polis 1992).

Cannibalism in adult wolf spiders that are essentially of similar size seems to be less frequent in the field and it is not reported from laboratory studies (Aspey 1977a; Nosssek and Rovner 1984). However, the field experiments by Wagner and Wise (1996) indicate that cannibalism between post-dispersive juvenile *S. ocreata* was common and was often seen among equal-sized hatchlings in the laboratory. Since in these cases the observed spiders were relatively homogeneous in size, it is possible that cannibalism frequency is dependent on age and size. There might be an interaction between size ratio and absolute size in such a way that cannibalism might be frequent among small animals even if there is little or no size difference, but in larger animals might only occur if the size ratio is large. The significance of absolute size is known from both odonate (Hopper et al. 1996) and coccinellid (Agarwala and Dixon 1992) larvae, though the directions were opposite in these two cases: the odonate larvae grew less cannibalistic, the coccinellids became more cannibalistic with age. In the present experiment, the most important factor was the relative weight of the opponents and the dependency of cannibalism on weight per se was not confirmed by the statistical tests. Nevertheless, since neither adult specimens nor the smallest free-living juvenile instars were involved, we think that the correct interpretation of these results should be that weight ratio is a more important factor than weight if juvenile animals are considered, but we should not exclude the possibility that the threshold weight ratio at which cannibalism becomes frequent depends on the absolute weight of the opponents.

The hunger experiments showed that starvation and cannibalism were clearly positively correlated. This observation is relevant because there is much field, laboratory and indirect evidence that spider populations are limited by food (for an overview see Wise 1993), and cannibalism might become important under such circumstances (Rypstra 1983). Cannibalism can be a way of reducing the risk of starvation. A moderate level of hunger can increase the risk proneness of a forager, and thereby alter the proportion and size of conspecifics included in the diet (Dong and Polis 1992; Elgar and Crespi 1992). Hunger is also an internal state which might lead to malnutrition and increased vulnerability of individuals. High vulnerability might result in avoidance behaviour and altered patch choice in starved animals (Hallander 1970; Dong and Polis 1992). Behavioural modifications like “freezing”, i.e. reduced activity of the potential victim confronting a potential cannibal, have

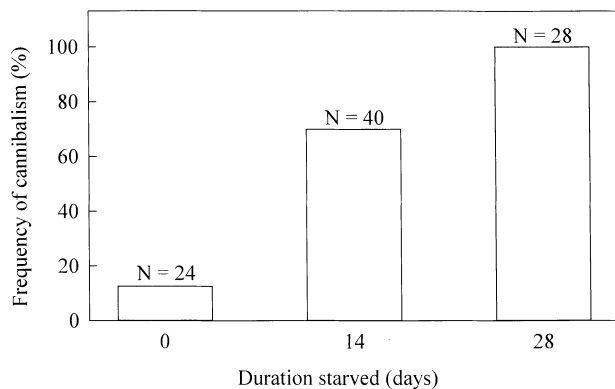


Fig. 3 Frequency of cannibalism as a function of hunger (days starved). Sample sizes are indicated above the bars

been described for odonate larvae (Crowley et al. 1987) and, at least in a potential intraguild predation situation, are likely to exist in wolf spiders (M. Persons, personal communication). However, risks associated with attacking similarly sized animals might alleviate the effect of hunger. This is exemplified in the experiments by Nosssek and Rovner (1984) on adult wolf spiders (*Lycosa* spp.), where no effect of starvation on cannibalism was found. Young animals may be more risk prone, and thus may cannibalise each other with higher frequencies because they have not accumulated sufficient reserves to survive temporal food shortages. However, size-dependent cannibalism was not evident in the present experiments with *P. agrestis*.

The importance of cannibalism should be especially important during periods when large size differences are coupled with food shortage. Studies in the laboratory (Anderson 1974) and direct field evidence (Edgar 1970a; Nyffeler and Benz 1988; Wise and Wagner 1992) suggest that wolf spiders often starve in nature. Large size differences were found among the coexisting juvenile stages of *P. agrestis* in Hungarian (Samu et al. 1998) and in Austrian (Zulka et al. 1997) populations. This was most pronounced at the end of the reproductive season in autumn. Even if the "right conditions" (i.e. broad size distribution, and high hunger level) are met, spiders should meet each other with sufficient frequency for cannibalism to occur. Encounter frequency might depend on movement behaviour, environmental heterogeneity (which might interact with this behaviour), and population density.

Field observations of individual movement patterns in *P. agrestis* and other wolf spiders showed that the 'home' ranges of individuals overlap, and there was little evidence of territorial behaviour (Hallander 1967; Vogel 1971; F. Samu and A. Szirányi, unpublished data). *P. agrestis* is highly abundant in agricultural fields in Hungary (Tóth and Kiss 1997). Both the arable fields, and the natural habitats, e.g. salt marshes, of this species are very open habitats even on the microhabitat scale, thus the lack of structural heterogeneity in the experimental arenas cannot be considered entirely unnatural. Recent mark-recapture experiments that quantified the population densities of this species (Samu and Sároszpatáki 1995; Samu and Kiss 1997) revealed four to six adult spiders/m². Since one female has a typical reproductive output of 40–60 spiderlings/cocoon (multiple cocoon production is also known), the density of juveniles can be much higher than that of the adults.

The present experiments on *P. agrestis* revealed that cannibalism is part of the biological repertoire of this species. The occurrence of cannibalism was regulated by size ratios and hunger. Field evidence on population densities, weight distribution and hunger level of wolf spiders strongly indicates that cannibalism is not an artefact observed only in the laboratory, but is rather an important phenomenon that might play a significant role in natural populations.

Acknowledgements The authors are grateful for statistical advice and useful discussions with Drs. Jacob Koella and Péter Kabai. We appreciate the helpful comments of Dr. Mark Elgar and three anonymous referees. We thank Mrs. Else Bomholt Rasmussen and Mr. Henrik Goldschmidt for their technical assistance. Funding for the project was provided by the Danish Environmental Research Programme through the Centre for Agricultural Biodiversity, and Hungarian Science Foundation (OTKA F 23627 and F 25360). F.S. was a Bolyai Fellow of the Hungarian Academy of Sciences during the preparation of the manuscript.

References

- Agarwala BK, Dixon AFG (1992) Laboratory study of cannibalism and interspecific predation in ladybirds. *Ecol Entomol* 17:303–309
- Anderson JF (1974) Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filista hibernalis* (Hentz). *Ecology* 55:576–585
- Anderson RS (1970) Predator-prey relationships and predation rates for crustacean zooplankters from some lakes in western Canada. *Can J Zool* 48:1229–1240
- Arnquist G (1992) Courtship behaviour and sexual cannibalism in the semi-aquatic fishing spider, *Dolomedes fimbriatus* (Clerck) (Araneae: Pisauridae). *J Arachnol* 20:222–226
- Aspey WP (1977a) Wolf spider sociobiology. I. Agonistic display and dominance-subordination relations in adult male *Schizocosa crassipes*. *Behaviour* 62:103–141
- Aspey WP (1977b) Wolf spider sociobiology. II. Density parameters influencing agonistic behavior in *Schizocosa crassipes*. *Behaviour* 62:142–163
- Bilde T, Toft S (1998) Quantifying food limitation of arthropod predators in the field. *Oecologia* 115:54–58
- Bristowe WS (1941) The comity of spiders. Ray Society, London
- Crowley PH, Hopper KR (1994) How to behave around cannibals: a density dependent dynamic game. *Am Nat* 143:117–154
- Crowley PH, Dillon PM, Johnson DM, Watson CN (1987) Intra-specific interference among larvae in a semivoltine dragonfly population. *Oecologia* 71:447–456
- Dong Q, Polis GA (1992) The dynamics of cannibalistic populations: a foraging perspective. In: Elgar MA, Crespi BJ (eds) *Cannibalism: ecology and evolution among diverse taxa*. Oxford University Press, Oxford, pp 13–37
- Edgar WD (1970a) Prey and feeding behaviour of adult females of the wolf spider *Pardosa amentata*. *Neth J Zool* 20:487–491
- Edgar WD (1970b) Prey of the wolf spider *Lycosa lugubris* (Walck.). *Entomol Month Mag* 106:71–73
- Elgar MA, Crespi BJ (1992) Ecology and evolution of cannibalism. In: Elgar MA, Crespi BJ (eds) *Cannibalism: ecology and evolution among diverse taxa*. Oxford University Press, Oxford, pp 1–12
- Elgar MA, Nash DR (1988) Sexual cannibalism in the garden spider *Araneus diadematus*. *Anim Behav* 36:1511–1517
- Fox LR (1975) Cannibalism in natural populations. *Annu Rev Ecol Syst* 6:87–106
- Hallander H (1967) Range and movements of the wolf spiders *Pardosa chelata* O.F. Muller and *P. pullata* Clerck. *Oikos* 18:360–364
- Hallander H (1970) Prey, cannibalism and microhabitat selection in the wolf spiders *Pardosa chelata* O.F. Muller and *P. pullata* Clerck. *Oikos* 21:337–340
- Higashi GA, Rovner JS (1975) Post-emergent behaviour of juvenile lycosid spiders. *Bull Br Arachnol Soc* 3:113–119
- Hopper KR, Crowley PH, Kielman D (1996) Density dependence, hatching synchrony, and within-cohort cannibalism in young dragonfly larvae. *Ecology* 77:191–200
- Nosssek ME, Rovner JS (1984) Agonistic behavior in female wolf spiders (Araneae, Lycosidae). *J Arachnol* 11:407–422
- Nyffeler M, Benz G (1988) Feeding ecology and predatory importance of wolf spiders (*Pardosa* spp.) in winter wheat fields. *J Appl Entomol* 106:123–134

- Pfennig DW, Reeve HK, Sherman PW (1993) Kin recognition and cannibalism in spadefoot toad tadpoles. *Anim Behav* 46:87–94
- Pfennig DW, Ho SG, Hoffman EA (1998) Pathogen transmission as a selective force against cannibalism. *Anim Behav* 55:1255–1261
- Polis GA (1981) The evolution and dynamics of intraspecific predation. *Annu Rev Ecol Syst* 12:225–251
- Polis GA, Myers CA, Holt R (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- Prenter J, Elwood RW, Montgomery WI (1994) Male exploitation of female predatory behaviour reduces sexual cannibalism in male autumn spiders, *Metellina segmentata*. *Anim Behav* 47:235–236
- Ross K, Smith RL (1979) Aspects of the courtship behaviour of the black widow spider, *Latrodectus hesperus* (Araneae, Theridiidae) with the evidence for the existence of contact sex pheromone. *J Arachnol* 7:69–77
- Rypstra AL (1983) The importance of food and space in limiting web-spider densities: a test using field enclosures. *Oecologia* 59:312–316
- Samu F, Kiss B (1997) Mark-recapture study to establish population density of the dominant wolf spider in Hungarian agricultural fields. *Bull Br Ecol Soc* 28:265–269
- Samu F, Sároszpataki M (1995) Estimation of population sizes and home ranges of polyphagous predators in alfalfa using mark-recapture: an exploratory study. *Acta Jutl* 70:47–55
- Samu F, Vörös G, Botos E (1996) Diversity and community structure of spiders of alfalfa fields and grassy field margins in south Hungary. *Acta Phytopathol Entomol Hung* 31:253–266
- Samu F, Németh J, Kiss B (1997) Assessment of the efficiency of a hand-held suction device for sampling spiders: improved density estimation or oversampling? *Ann Appl Biol* 130:371–378
- Samu F, Németh J, Tóth F, Szita E, Kiss B, Szinetár C (1998) Are two cohorts responsible for bimodal life history pattern in the wolf spider *Pardosa agrestis* in Hungary? In: Selden PA (ed) *Proc 17th Eur Coll Arachnol*. British Arachnological Society, Edinburgh, pp 215–221
- Toft S (1995) Value of the aphid *Rhopalosiphum padi* as food for cereal spiders. *J Appl Ecol* 32:552–560
- Tóth F, Kiss J (1997) Occurrence of *Pardosa* (Araneae, Lycosidae) species in winter wheat and in the field margin. *Proc 16th Eur Coll Arachnol*. Siedlce, pp 309–315
- Vogel BR (1971) Individual interactions of *Pardosa*. *Armadillo Pap* 5:1–12
- Wagner JD (1995) Egg sac inhibits filial cannibalism in the wolf spider, *Schizocosa ocreata*. *Anim Behav* 50:555–557
- Wagner JD, Wise DH (1996) Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology* 77:639–652
- Wise DH (1993) *Spiders in ecological webs*. Cambridge University Press, Cambridge, UK
- Wise DH, Wagner JD (1992) Evidence of exploitative competition among young stages of the wolf spider *Schizocosa ocreata*. *Oecologia* 91:7–13
- Zulka KP, Milasowszky N, Lethmayer C (1997) Spider biodiversity potential of an ungrazed and grazed inland salt meadow in the National Park ‘Neusiedler See-Seewinkel’ (Austria): implications for management (Arachnida: Araneae). *Biodiv Conserv* 6:75–88

Communicated by M.A. Elgar