

Interdemic variation of cannibalism in a wolf spider (*Pardosa monticola*) inhabiting different habitat types¹

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Running title

Varying cannibalism rates in a wolf spider

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Abstract. 1. Cannibalism was investigated in the wolf spider *Pardosa monticola* (Clerck) using spiders collected from four populations with varying densities, inhabiting two different coastal dune habitat types. Sampled individuals were randomly paired and immediately tested for their cannibalism propensity.

2. The occurrence of cannibalism was found to be influenced by the size (cephalothorax width) of both the smaller and the larger spider of a pair. Larger size differences enhanced cannibalism.

3. Cannibalism rates were not significantly different in spiders from high-density compared to low-density populations. Cannibalism rates showed however large variability between habitat types, with higher rates in spiders from dune grasslands than from dune slacks. This is suggested to result from differences in prey availability throughout the growing season between both habitat types.

4. Different size classes of spiders did not use different microhabitats, indicating that microhabitat segregation as a cannibalism avoidance behaviour is absent in this species.

Key words. Coastal dunes, interdemic variation, Lycosidae, metapopulation, microhabitat segregation, prey availability.

Introduction

Cannibalism has been reported from many different and very diverse taxa, and is often identified as a potentially important factor in population regulation (e.g. Fox, 1975; Polis, 1981; Fincke, 1994; Wagner & Wise, 1996; Claessen *et al.*, 2004). In spiders, cannibalistic behaviour is known to occur in several species and in all life stages (Elgar & Crespi, 1992), but most studies have focused on sexual cannibalism (e.g. Elgar, 1991, 1992; Andrade, 1996; Fromhage *et al.*, 2003; Morse, 2004). Although occasional observations of non-sexual cannibalism in the field (e.g. Hallander, 1970) indicate that this mechanism may have a noticeable impact on natural spider population dynamics, knowledge about its ecological importance is still very much lacking (Samu *et al.*, 1999).

Both proximate and ultimate factors have been found to influence cannibalism propensity, but the best documented examples deal with proximate triggers, such as food availability and hunger (Fox, 1975; Dong & Polis, 1992; Wagner & Wise, 1996, 1997; Samu *et al.* 1999; Nishimura & Isoda, 2004), crowding and population density (Fox, 1975; Dong & Polis, 1992; Wagner & Wise, 1996; Buddle *et al.*, 2003; Nishimura & Isoda, 2004), and individual size differences (Samu *et al.*, 1999; Buddle *et al.*, 2003). As a result, it can be expected that cannibalism rates will vary between natural populations in response to the local prevailing conditions. This has, however, been studied very poorly. Only Baur (1994) reported significant interdemographic variation in cannibalism rates between four completely isolated natural populations of a terrestrial gastropod, suggesting an adaptive response to the prevailing conditions (e.g. juvenile mortality rate, predation risk, maternal investment in egg size or number, length of growth season, overall relatedness in the population).

Avoidance of cannibalism may also cause adaptive shifts in microhabitat use by different age- and size groups within a population, leading to microhabitat segregation (Fox, 1975; Dong & Polis, 1992). Besides vertebrates (e.g. Foster *et al.*, 1988; Byström *et al.*, 2003),

adaptive microhabitat segregation as a means of cannibalism avoidance has also been reported in isopods (Leonardsson, 1991; Jormalainen & Shuster, 1997) and insects (Sih, 1982). In wolf spiders of different age classes, differential microhabitat use has been observed (Hallander, 1970; Edgar, 1971), but there is no convincing evidence yet that this pattern really emerged in response to cannibalism. Nevertheless, it is clear that the segregation of different size classes of spiders in different microhabitats will have an impact on cannibalism rate in the population.

As mentioned above, most studies have focused on proximate factors influencing cannibalism by manipulating hunger level and/or densities in the laboratory or field. These studies aim to determine the importance of cannibalism for population regulation (e.g. Wagner & Wise, 1996; Samu *et al.*, 1999; Buddle *et al.*, 2003), by studying variation within one population. In this paper, possible interdemographic variation of cannibalism rates within a metapopulation of the wolf spider *Pardosa monticola* (Clerck), according to expectations of prey availability and population density in the field, is explored. Because of intrinsic difficulties of measuring cannibalism rates directly in the field, a ‘semi-field’ approach was adopted, in which the cannibalistic propensity of spiders, originating from four well-chosen subpopulations, was assessed in a laboratory setup, while preserving the field hunger level of the spider. Additionally, differential microhabitat use by the spiders depending on their size was investigated, because this could affect the occurrence of cannibalism differentially among populations in different habitat types.

Materials and methods

Study species

Pardosa monticola (Clerck) (Araneae: Lycosidae) is a widespread species in Europe and Asia, typically occurring in short-grazed, oligo- and mesotrophic pastures and heathlands

(Alderweireldt & Maelfait, 1990). In the Flemish coastal dunes, the spider is an indicator species for mesotrophic grasslands of two types: rabbit-grazed dry dune grasslands and young humid dune slacks (Bonte *et al.*, 2002a). Being ground-dwelling predators, the food of the early instars consists primarily of larger epigeic springtails of the genera *Entomobrya* (Collembola: Entomobryidae) and *Isotoma* (Collembola: Isotomidae) (Bonte & Maelfait, 2001), the most abundant arthropleone springtails in the grasslands of the Flemish coastal dunes (Bonte *et al.*, 2002b). An important fraction of the prey items of older instars and adults are ground-living *Medetera* spp. (Diptera: Dolichopodidae) and both con- and heterospecific spiders (D. Bonte, unpubl. data). *P. monticola* females can produce up to two or possibly even three cocoons from June to September (Vlijm & Kessler-Geschiere, 1967; D. Bonte & J.-P. Maelfait, unpubl. data). This results in a mixed annual-biennial life cycle, with different cohorts reaching adulthood after one or after two hibernations (Bonte & Maelfait, 2001).

Study area

This study was carried out in the Flemish coastal sand dunes of the communities of De Panne (Belgium, 51°05'N, 2°34'E) and Ghyvelde (Northern France, 51°03'50"N, 2°33'E). The vegetation of these dunes is dominated by scrub (mainly sea buckthorn *Hippophae rhamnoides* L.) and blond dunes (with European beachgrass *Ammophila arenaria* (L.)). Within this matrix, suitable habitat occurs very patchily, leading *P. monticola* to live within a metapopulation, with habitat quality (as measured by vegetation height) and patch size being of primary importance in the spatial structuring of the population (Bonte *et al.*, 2003). As *P. monticola* prefers short grasslands, habitat quality for this species varies inversely with vegetation height. Four patches with populations of *P. monticola*, within a short range (< 3 km) from each other, were selected for this study: two dry grasslands and two humid dune slacks, with contrasting population densities (high: > 1 m⁻²; low: < 1 m⁻²). According to their

characteristics, the four populations were abbreviated as GH (grassland, high density), GL (grassland, low density), SH (slack, high density) and SL (slack, low density) (see Table 1). Both habitat types have a rather low vegetation coverage and a low structural complexity. Dune grasslands (GH and GL) are year-round dry habitats, characterized by an explicit microrelief causing a small scaled variability in microclimate and edaphic factors. Although the soil organic matter content is in general low, the vegetation responds to the varying thickness of the organic Ah soil horizon, creating patches with short vegetation (mainly grasses, sedges, mosses, and lichens, with a few typical herbs) on places with a thicker Ah-horizon, interspersed with patches of bare sand and no Ah-horizon. Drought stress can be severe, especially during summer. The young dune slacks (SH and SL) are humid throughout the year because of the permanent influence of ground water. Soil organic matter content is much higher, and the vegetation is dominated by creeping willow (*Salix repens* L.) and low sedges (*Carex* spp.), but patches of wet bare sand are also abundant. In winter, inundation of these slacks is frequent (Provoost *et al.*, 2002; Provoost, 2004).

Collecting and microhabitat characterization

During the late summers of two consecutive years (August and September 2001 and 2002), juvenile as well as adult female *P. monticola* were caught by hand in the four study sites. In total, 409 specimens were collected for the whole of this study, approximately evenly distributed over the sites and years (Table 1). In 2001, the microhabitat of every collected spider (n = 223) was characterized. In a square of 40 by 40 cm around the exact finding spot of the spider, an estimation was made of the coverage of the soil by the following structural layers: moss, low herbs, taller herbs (defined as dwarf shrubs and tall grasses), litter, and also the percentage of bare sand. For the dune slacks, the heights of the two herb layers (low and tall herbs) were measured at ten random points in the observed square. For the grasslands, this

was only carried out for the low herb layer, since taller herbs are very sparse in this habitat type. In GH, the coverage of the structurally different burnet rose (*Rosa pimpinellifolia* L.) was also recorded.

Cannibalism experiments

Cannibalism experiments were carried out on the day of collecting of the spider, in order to assure that the hunger level of the spiders was solely a result of the success of a given spider in catching prey in the field. 189 replications were carried out (using 378 specimens). The spiders caught on one day were randomly assigned to one another in pairs, and put together per pair in a Petri dish (diameter: 87 mm) with a moistened plaster bottom. They were kept together for a minimum of 11 hours to a maximum of 17 hours (including one night) while being checked regularly for the prevalence of cannibalism. Afterwards, the cephalothorax size of the spiders was measured under a binocular with a magnification of 2.5×20 . For the separation of different size classes, both length and width of the cephalothorax were measured in the 2001-survey. In 2002, only cephalothorax width was measured. Due to various circumstances (moulting, escapes, extreme damage to the cannibalized spider), the size of some spiders could not be soundly determined. These cases were excluded from further analyses, except for the first part of the microhabitat analysis (DCA; see below).

Data analysis

Detrended Correspondence Analysis (PC-ORD 4.21; McCune & Mefford, 1999) was used to draw up an ordination of the finding spots ($n = 223$) of the spiders based on the following microhabitat characterizing parameters: percentage of bare sand; coverage of litter, moss, low and tall herb layer; and average height, standard deviation and standard error of heights of both low and tall herb layer (only low herb layer for grasslands). Because microhabitat-

characteristics differed between populations, ordinations of each study site were created separately. Consecutively, a multiple linear regression of the microhabitat parameters was carried out on the scores of each finding spot along the first and second axes of the ordination, in order to determine the main parameters reflected in each of the axes. Axis 3 always had very low eigenvalues, and was therefore not retained in further analyses. Based on the cephalothorax size (length \times width), each measured spider of 2001 ($n = 201$) was assigned to one of nine size classes, related to the different instar stages (cf Bonte & Maelfait, 2001). A Kruskal-Wallis test was used to find out whether the scores along one of the axes differed significantly between size classes.

Data on individual cannibalistic performance ($n = 177$ replications) were analysed by generalized linear mixed models (GLMM) with logit link function and binomial error structure. Calculations were performed with the SAS procedure Glimmix (SAS statistical package version 9.1; SAS Institute, 2003). The degrees of freedom were approximated using Satterthwaite's procedure. A backwards elimination of the non-significant parameters was performed in the multiple models.

Habitat type (grassland versus dune slack) as well as population density (high versus low) of the largest individual of a pair were included as fixed class factors, the sizes (cephalothorax widths) of both individuals of a pair as continuous variables. The effect of size and size ratio on cannibalistic propensity was assumed to be independent of environmental factors; therefore interactions between class and continuous variables were excluded from the analysis to avoid unnecessary complication of the model. Sampling year (2001 versus 2002) as well as population of origin of the smaller spider of a pair were included as random factors, to account for any effects caused by year-to-year fluctuations or by various differences (e.g. behavioural) between populations respectively.

Results

Microhabitat

The percentage of bare sand and the coverage by moss, litter, and tall herbs proved to be important factors that differed between microhabitat spots within a study site. Variation in the height of the herb layers was of lesser importance. In none of the studied populations, a difference in microhabitat use was found between specimens of different size classes (Table 2), indicating the absence of microhabitat segregation between different instar stages (size classes) of this dune wolf spider species.

Cannibalism

Cannibalism occurred in 38 cases out of 189 replications (20.1%; 32 out of 177 (18.1%) retained in further analyses). The results of the logistic regression model on the data of cannibalism are shown in Table 3. The prevalence of cannibalistic interactions depended significantly on the size of both the smaller and the larger individual. Here, only smaller individuals became cannibalized, by only larger individuals. Spiders with smaller cephalothorax widths had more chance of becoming a victim of cannibalism, while spiders with larger cephalothorax widths were more often cannibalistic (Fig. 1). The habitat type of the largest individual additionally explained a large amount of the observed variation: when controlling for the sizes of both spiders, the probability of cannibalizing in grasslands was estimated to be 36.5% (± 20.1 , SE), while it was only 3.0% (± 10.5 , SE) in dune slacks. The probability of cannibalizing was not significantly different in spiders from high-density populations compared to low-density populations. The random variance of the sampling year was substantial ($s^2 = 0.14$, SE 0.96), while the random variance caused by the population of origin of the smaller spider equalled zero ($s^2 < 1.08 \text{ E-}18$).

Discussion

Although an effective way of minimizing the risk of cannibalism, microhabitat segregation between size classes was not detected in this study species. Smaller and larger juveniles, as well as adult females, use the same microhabitat during the summer period, making it probable that they encounter, a prerequisite for cannibalistic interactions to occur. This finding is in contrast with Edgar (1971), who observed microhabitat segregation in juveniles of related *Pardosa* species with similar degrees of cannibalistic behaviour as *P. monticola*. Unlike *P. monticola* however, these species live in structurally complex habitats (forest litter floors). Therefore, the lack of differential microhabitat use in *P. monticola* seems to be a result of the low structural complexity of the studied habitats (leaving little refuges for smaller individuals), rather than to be a result of a lower selection pressure for differential microhabitat use (because of lower cannibalistic mortality). However, both possibilities may be hard to tell apart: simply structured habitats may allow spiders to detect the presence of conspecifics from larger distances, resulting in lower cannibalism success rates in simple compared to complex habitats (Wagner & Wise, 1996).

In this study, an overall cannibalism rate of 20.8% was observed, which is comparable to cannibalism rates reported in other laboratory studies with *Pardosa* spp. (26% in Samu *et al.*, 1999; 11% in Buddle *et al.*, 2003). Hallander (1970) found conspecific prey to account for approximately 20% and 28% of all prey items observed in the field in *P. lugubris* (Walckenaer) and *P. pullata* (Clerck) respectively. Due to the applied experimental setup (increased possibility of repeated encounters between spiders), the relation of the cannibalism rates observed in this study and the field cannibalism rates remains difficult to assess, but field cannibalism rates are probably lower than the rates observed here. However, an appreciable part of conspecific encounter events in the field may very well result in cannibalism, especially if one keeps in mind the virtual absence of complex microhabitat

features.

When cannibalism occurred, the larger spider was always the cannibal, as also observed by Samu *et al.* (1999) and Buddle *et al.* (2003). The size of both the larger spider, the potential cannibal, and the smaller spider, the potential victim, had a significant influence on the outcome of the interaction. This means that in this study, like in Buddle *et al.* (2003), large size differences between paired individuals enhanced the probability of cannibalism. These observations are consistent with the predictions derived from general theory on cannibalism: The risk of retaliation by conspecifics is one of the major potential costs of cannibalism (Polis, 1981; Elgar & Crespi, 1992). Cannibalistic individuals will try to minimize this potential cost of self-injury and increase the chance of a successful attack, by choosing more vulnerable prey. The vulnerability of a prey is a function of its size and of the size ratio of predator to prey (Dong & Polis, 1992): smaller individuals are more vulnerable for predation, especially by larger conspecifics. In *P. monticola*, as a result of the extended female reproductive season, larger (from first broods) and smaller (from second broods) juveniles coexist over a long time of the year (Bonte & Maelfait, 2001), creating ample chance for two spiders unequal in size to meet.

The habitat type of the largest spider of a pair accounts for a large part of the variation in cannibalistic behaviour found in this study. Spiders originating from grasslands were more apt to cannibalize than spiders from dune slacks. Interdemic variation in cannibalism is only documented for a snail (*Arianta arbustorum* (L.) (Pulmonata: Helicidae)) (Baur, 1994), where considerable differences in propensity for sibling egg cannibalism were found between isolated populations. In *Pardosa monticola*, the interdemic variation coincides with the variation in habitat types sampled. In contrast to the study of Baur (1994), the studied *P. monticola* populations are part of the same metapopulation (Bonte *et al.*, 2003), so adaptive mechanisms are not to be expected, but cannot be ruled out as an explanation without further

investigations. In the present study however, interdemographic variation is much more probable to be the result of the behavioural plasticity of *P. monticola* to respond to differing prey availability. As spiders in general are thought to be food-limited (Wise, 1993), hunger level is a major factor affecting the probability of cannibalism. It can enhance cannibalism by (i) increasing foraging activity of individuals, thus increasing encounter and interaction rates among conspecifics; (ii) weakening at least some individuals, which then become more vulnerable to cannibalism; and (iii) increasing the proneness of an individual to cannibalize, by expanding its range of acceptable prey beyond its normal limits (Polis, 1981; Dong & Polis, 1992).

Humid dune slacks, by their permanent influence of groundwater and their fairly high soil organic matter content, can harbour high abundances of epigeic springtails (Berbiers & Mertens, 1989; J. Vanden Borre, pers. obs.). Bonte *et al.* (2002b) investigated the epigeic arthropod springtails of coastal dune grasslands by means of pitfall-trapping, and found *Entomobrya nivalis* (L.) and *Isotoma viridis* Bourlet to be the two most abundant species. Although hygrophilous, they are able to survive in the dry environment of the dune grasslands because of the high aerial humidity (close to the seashore) (Bonte *et al.*, 2002b), and their ability to retreat in the moist organic soil layer in periods of extreme drought (Bonte *et al.*, 2004; J. Mertens, pers. comm.). Both *E. nivalis* and *I. viridis* peaked in abundance in early summer, but rapidly declined in numbers in late summer as a result of drought stress, leading to an aggregative distribution pattern: they disappeared completely from patches with bare sand, while patches with some soil development still harboured some individuals, probably as a result of the waterholding capacity of the organic soil matter (Bonte *et al.*, 2002b). With large springtails constituting the main food supply for the smaller juveniles of *P. monticola* (Bonte & Maelfait, 2001), this pattern results in very contrasting conditions for juvenile wolf spiders in late summer in grasslands as opposed to dune slacks. While springtails are more

abundant, more evenly distributed and available to the spiders throughout the season in dune slacks, they become a limited and aggregated food source in dune grasslands. As a consequence, spiders of dune grasslands probably experience higher levels of food deprivation, and are more prone to cannibalize, resulting in the higher cannibalism rates in spiders from dune grasslands found in this study. The aggregative distribution of springtails in late summer may also attract the spiders to the same patches, resulting in more intraspecific encounters, and thus more opportunities to cannibalize. However, this possibility remains to be investigated. Another possibility that would merit further study is an indirect effect of food shortage on cannibalism rates: as opposed to dune slacks where growth is expected to be more synchronized, lower food availability in the grasslands will slow down growth rate of the juvenile instars, resulting in a broader range of size classes during the summer because of a larger proportion of individuals with a biennial year cycle (cohort IIb; see Bonte & Maelfait, 2001). This cohort will hibernate twice and survive their first summer as subadult instars which coexist with the new generation of first instar spiderlings. The larger size differences within grassland habitats resulting from this pattern, may enhance cannibalism. A partial support for this possible effect is found in the fact that the variance in cephalothorax width was higher in spiders from dune grasslands (median = 1.36 mm; interquartile range = 0.56) than in spiders from dune slacks (median = 1.39 mm; interquartile range = 0.40).

Population density is also often recognized as a determinant of cannibalism levels in a population, although its effects are often confounded with those of food shortage (Fox, 1975). Density may affect cannibalism in two ways (Polis, 1981; Dong & Polis, 1992). Firstly, an increasing density results in higher encounter rates with conspecifics. Secondly, potential cannibals can show a density-dependent response to more conspecific prey being present, e.g. by altering their searching behaviour to hunt more effectively on this type of prey (type III (sigmoid) functional response; Holling, 1959). The impact of density on cannibalism levels in

wolf spiders was illustrated by Buddle *et al.* (2003), who found higher cannibalism rates of *P. milvina* in experimental treatments with density levels up to four times the natural density, and by Wagner and Wise (1996), who showed cannibalism to act as a strong density-dependent mortality factor in *Schizocosa ocreata* (Hentz) instars. In the present experiment however, cannibalism rates were not significantly different in spiders originating from high-density compared to low-density populations. The applied experimental setup, in which all pairs were put in arenas of the same size and encounter rates were very high for a long period, standardized the encounter rates and therefore may have eliminated any density effect. Additionally, these results also suggest that *P. monticola* probably exhibits a type II (cyrtoid) functional response instead of a type III, as otherwise one would expect spiders from dense populations to recognize conspecifics more easily as a prey item than spiders from sparse populations, even in this experimental setup. This finding is in accordance with other studies on wolf spiders which revealed type II functional responses to heterospecific prey (e.g. Walker & Rypstra, 2002).

Although the approach adopted in the present study is limited in that it cannot directly measure and compare cannibalism rates in field conditions, the obtained results give strong indications that cannibalism is a realistic part of the life history of *P. monticola*. Absolute spider sizes significantly affected the occurrence of cannibalism, and various populations of this species exhibited different cannibalism rates. This could be explained by differences in prey availability between distinct habitat types, with potentially both direct and indirect influences. Additionally, a microhabitat assay revealed that smaller and larger spiders occupy similar microhabitats, resulting in ample opportunity for encounters. A challenge for future studies will be to investigate whether dissimilar cannibalism rates in populations may result in different dynamics, even within the same metapopulation, both in *P. monticola* as in other organisms, as this may shed new lights on our understanding of the dynamics of natural

populations and metapopulations.

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References

- Alderweireldt, M. & Maelfait, J.P. (1990) Catalogus van de spinnen van België. Deel VII. Lycosidae. *Studiedocumenten van het KBIN*, **61**, 1-92.
- Andrade, M.C.B. (1996) Sexual selection for male sacrifice in the Australian redback spider. *Science*, **271**, 70-72.
- Baur, B. (1994) Inter-population differences in propensity for egg cannibalism in hatchlings of the land snail *Arianta arbustorum*. *Animal Behaviour*, **48**, 851-860.
- Berbiere, P. & Mertens, J. (1989) Collembola (Insecta) collected in Belgium by the Laboratory of Ecology R.U.G. *Verhandelingen van het symposium "Invertebraten van België"* (ed. by K. Wouters and L. Baert), pp. 233-238. Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, Belgium.
- Bonte, D., Baert, L. & Maelfait, J.P. (2002a) Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *Journal of Arachnology*, **30**, 331-343.
- Bonte, D., Lens, L., Maelfait, J.P., Hoffmann, M. & Kuijken, E. (2003) Patch quality and connectivity influence spatial dynamics in a dune wolfspider. *Oecologia*, **135**, 227-233.
- Bonte, D. & Maelfait, J.P. (2001) Life history, habitat use and dispersal of a dune wolf spider

- (*Pardosa monticola* [Clerck, 1757] Lycosidae, Araneae) in the Flemish coastal dunes (Belgium). *Belgian Journal of Zoology*, **131**, 145-157.
- Bonte, D., Van Heuverswyn, F. & Mertens, J. (2002b) Temporal and spatial distribution of epigeic Arthropleona springtails (Collembola : Hexapoda) in coastal grey dunes. *Belgian Journal of Entomology*, **4**, 17-26.
- Bonte, D., Van Heuverswyn, F. & Mertens, J. (2004) Springstaarten. *Levende duinen: een overzicht van de biodiversiteit aan de Vlaamse kust* (ed. by S. Provoost and D. Bonte), pp. 312-319. Instituut voor Natuurbehoud, Brussels, Belgium.
- Buddle, C.M., Walker, S.E. & Rypstra, A.L. (2003) Cannibalism and density-dependent mortality in the wolf spider *Pardosa milvina* (Araneae : Lycosidae). *Canadian Journal of Zoology*, **81**, 1293-1297.
- Byström, P., Persson, L., Wahlström, E. & Westman, E. (2003) Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. *Journal of Animal Ecology*, **72**, 156-168.
- Claessen, D., De Roos, A.M. & Persson, L. (2004) Population dynamic theory of size-dependent cannibalism. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 333-340.
- Dong, Q. & Polis, G.A. (1992) The dynamics of cannibalistic populations: a foraging perspective. *Cannibalism: ecology and evolution among diverse taxa* (ed. by M. A. Elgar and B. J. Crespi), pp. 13-37. Oxford University Press, New York.
- Edgar, W.D. (1971) The life-cycle, abundance and seasonal movement of the wolf spider, *Lycosa (Pardosa) lugubris*, in central Scotland. *Journal of Animal Ecology*, **40**, 303-322.
- Elgar, M.A. (1991) Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders (Araneidae). *Evolution*, **45**, 444-448.
- Elgar, M.A. (1992) Sexual cannibalism in spiders and other invertebrates. *Cannibalism:*

ecology and evolution among diverse taxa (ed. by M. A. Elgar and B. J. Crespi), pp. 128-155. Oxford University Press, New York.

Elgar, M.A. & Crespi, B.J. (1992) Ecology and evolution of cannibalism. *Cannibalism: ecology and evolution among diverse taxa* (ed. by M. A. Elgar and B. J. Crespi), pp. 1-12. Oxford University Press, New York.

Fincke, O.M. (1994) Population regulation of a tropical damselfly in the larval stage by food limitation, cannibalism, intraguild predation and habitat drying. *Oecologia*, **100**, 118-127.

Foster, S.A., Garcia, V.B. & Town, M.Y. (1988) Cannibalism as the cause of an ontogenetic shift in habitat use by fry of the threespine stickleback. *Oecologia*, **74**, 577-585.

Fox, L.R. (1975) Cannibalism in natural populations. *Annual Review of Ecology and Systematics*, **6**, 87-106.

Fromhage, L., Uhl, G. & Schneider, J.M. (2003) Fitness consequences of sexual cannibalism in female *Argiope bruennichi*. *Behavioral Ecology and Sociobiology*, **55**, 60-64.

Hallander, H. (1970) Prey, cannibalism and microhabitat selection in the wolf spiders *Pardosa chelata* O. F. Müller and *P. pullata* Clerck. *Oikos*, **21**, 337-340.

Holling, C.S. (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist*, **91**, 293-320.

Jormalainen, V. & Shuster, S.M. (1997) Microhabitat segregation and cannibalism in an endangered freshwater isopod, *Thermosphaeroma thermophilum*. *Oecologia*, **111**, 271-279.

Leonardsson, K. (1991) Effects of cannibalism and alternative prey on population dynamics of *Saduria entomon* (Isopoda). *Ecology*, **72**, 1273-1285.

McCune, B. & Mefford, M.J. (1999) PC-ORD for Windows: Multivariate analysis of ecological data Version 4.21. MjM Software, Gleneden Beach, Oregon, U.S.A.

Morse, D.H. (2004) A test of sexual cannibalism models, using a sit-and-wait predator. *Biological Journal of the Linnean Society*, **81**, 427-437.

- Nishimura, K. & Isoda, Y. (2004) Evolution of cannibalism: referring to costs of cannibalism. *Journal of Theoretical Biology*, **226**, 293-302.
- Polis, G.A. (1981) The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics*, **12**, 225-251.
- Provoost, S. (2004) Het kustecosysteem. *Levende duinen: een overzicht van de biodiversiteit aan de Vlaamse kust* (ed. by S. Provoost and D. Bonte), pp. 10-45. Instituut voor Natuurbehoud, Brussels, Belgium.
- Provoost, S., Ampe, C., Bonte, D., Cosyns, E. & Hoffmann, M. (2002) Ecology, management and monitoring of dune grasslands in Flanders, Belgium. *Littoral 2002, The Changing Coast* (ed. by EUROCOAST), pp. 11-22. Eurocoast/EUCC, Porto, Portugal.
- Samu, F., Toft, S. & Kiss, B. (1999) Factors influencing cannibalism in the wolf spider *Pardosa agrestis* (Araneae, Lycosidae). *Behavioral Ecology and Sociobiology*, **45**, 349-354.
- SAS Institute (2003) SAS 9.1.3. SAS Institute Inc., Cary, North Carolina, U.S.A.
- Sih, A. (1982) Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology*, **63**, 786-796.
- Vlijm, L. & Kessler-Geschiere, A.M. (1967) The phenology and habitat of *Pardosa monticola*, *P. nigriceps* and *P. pullata* (Araneae, Lycosidae). *Journal of Animal Ecology*, **36**, 31-56.
- Wagner, J.D. & Wise, D.H. (1996) Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology*, **77**, 639-652.
- Wagner, J.D. & Wise, D.H. (1997) Influence of prey availability and conspecifics on patch quality for a cannibalistic forager: laboratory experiments with the wolf spider *Schizocosa*. *Oecologia*, **109**, 474-482.
- Walker, S.E. & Rypstra, A.L. (2002) Sexual dimorphism in trophic morphology and feeding behavior of wolf spiders (Araneae: Lycosidae) as a result of differences in reproductive roles.

Canadian Journal of Zoology, **80**, 679-688.

Wise, D.H. (1993) *Spiders in ecological webs*. Cambridge University Press, Cambridge.

Legends

Fig. 1. Scatterplot of cephalothorax widths (μm) of both spiders of a pair. CT = cephalothorax.

Table 1. Characteristics of the sampled populations, number of collected individuals and number of cannibalism tests.

Table 2. Kruskal-Wallis ANOVA of the scores of the spider finding spots along the axes of the DCA-ordination on nine size classes of spiders.

Table 3. Fixed effects of the logistic regression model explaining variation in cannibalistic behaviour.

Figure 1

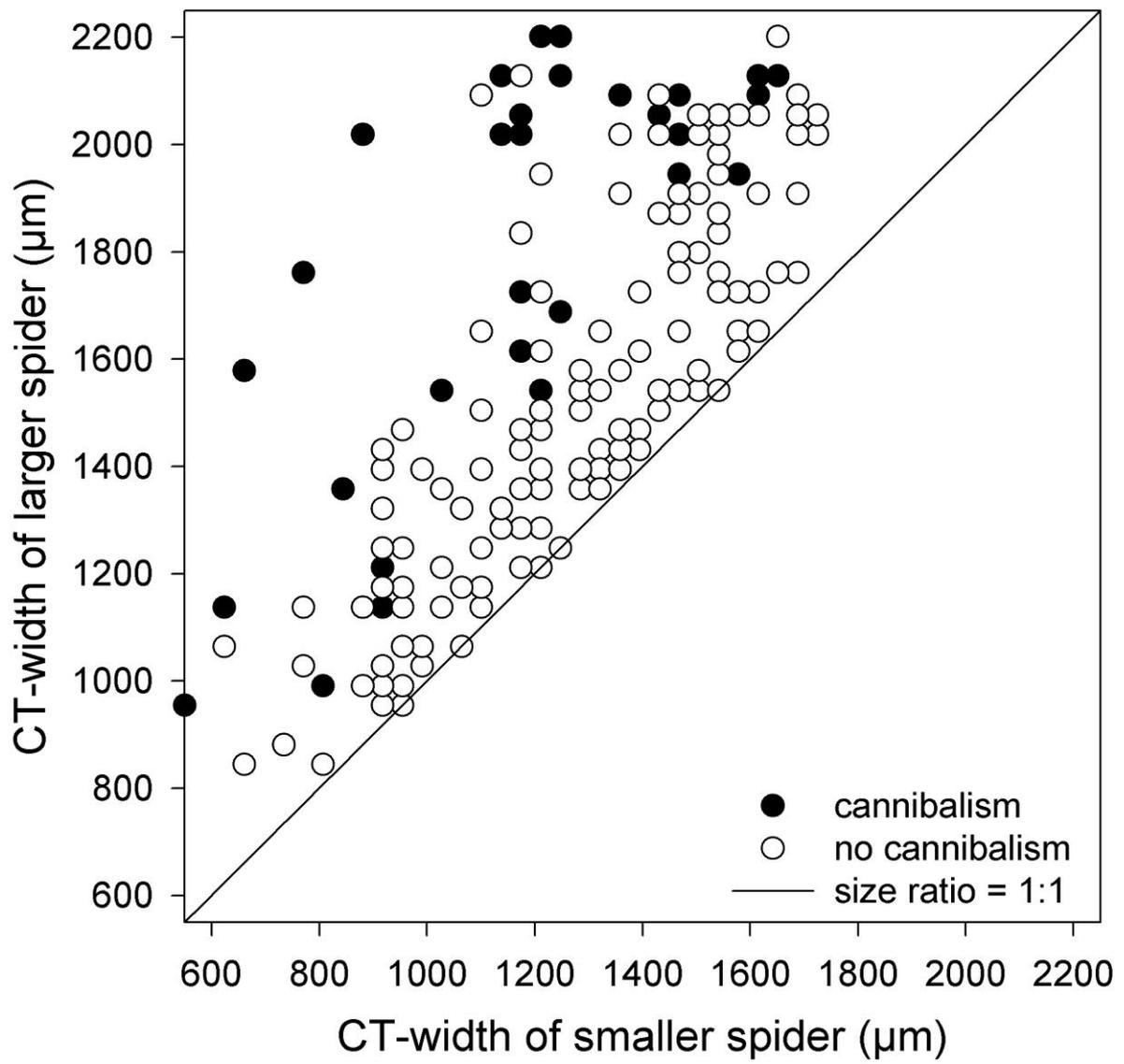


Table 1

Population		GH	GL	SH	SL
Habitat type		grassland	grassland	slack	slack
Population density (m ⁻²) (mean ± SD)		2.15 ± 0.92	0.35 ± 0.87	1.12 ± 1.38	0.85 ± 1.16
Patch size (ha) (D. Bonte, unpubl. data)		0.95	1.30	0.39	0.33
Number of collected individuals	2001	58	60	56	49
	2002	56	40	48	42
Number of pairs for cannibalism tests (grouped by population of origin of larger spider)	2001	14	19	27	24
	2002	25	21	27	20

Table 2

	GH		GL		SH		SL	
	axis 1	axis 2						
<i>H</i>	5.89	12.80	3.99	4.31	12.56	3.20	10.97	6.92
d.f.	8		5		8		8	
<i>N</i>	51		51		54		45	
<i>P</i>	NS							

Table 3

Factor	d.f. (numerator, denominator)	<i>F</i>	<i>P</i>
Size of largest spider of a pair	1, 44.89	22.04	<0.0001
Size of smallest spider of a pair	1, 173	20.54	<0.0001
Habitat type of larger spider of a pair (HAB)	1, 173	15.51	0.0001
Density of population of larger spider of a pair (DENS)	1,172	0.78	0.378
Size smallest * Size largest	1,171	2.26	0.134
HAB * DENS	1,170	0.00	0.997