Species composition of shoreline wolf spider communities vary with salinity but their diets vary with wrack inflow

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Abstract

Wolf spiders are typically the most common group of arthropod predators on both lake and marine shorelines, because of the high prey availability in these habitats. However, shores are also harsh environments due to flooding and, in proximity to marine waters, to toxic salinity levels. Here, we describe the spider community, prey availabilities and spider diets between shoreline sites with different salinities, albeit with comparatively small differences (5 vs. 7Despite the small environmental differences, spider communities between low and higher saline sites showed an almost complete species turnover. At the same time, differences in prey availability or spider gut contents did not match changes in spider species composition but rather changed with habitat characteristics within region, where spiders collected at sites with thick wrack beds had a different diet than sites with little wrack. These data suggest that shifts in spider communities are due to habitat characteristics rather than prey availabilities, and the most likely candidate restricting species in high salinity would be saline sensitivity. At the same time, species absences from low-saline habitats remain unresolved.

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Abstract

Wolf spiders are typically the most common group of arthropod predators on both lake and marine shorelines, because of the high prey availability in these habitats. However, shores are also harsh environments due to flooding and, in proximity to marine waters, to toxic salinity levels. Here, we describe the spider community, prey availabilities and spider diets between shoreline sites with different salinities, albeit with comparatively small differences (5 vs. 7Despite the small environmental differences, spider communities between low and higher saline sites showed an almost complete species turnover. At the same time, differences in prey availability or spider gut contents did not match changes in spider species composition but rather changed with habitat characteristics within a region, where spiders collected at sites with thick wrack beds had a different diet than sites with little wrack. These data suggest that shifts in spider communities are due to habitat characteristics rather than prey availabilities, and the most likely candidate restricting species in high salinity would be saline sensitivity. At the same time, species absences from low-saline habitats remain unresolved.

Key words : *Pardosa* , Molecular gut content analysis,*Fucus* , Shoreline fauna, *Alopecosa* , *Arctosa*

Introduction

Shorelines and other riparian habitats are often described as hotspots for arthropod predators, and spiders in particular seem to thrive in these habitats (Polis & Hurd 1995; Mellbrand & Hamback 2010; Batzer & Wu 2020). There are several reasons underlying these high spider densities, but an important factor seems to be the high prey density in these near-water habitats (Polis & Hurd 1995; Sanchez-Ruiz *et al.* 2018). Prey densities are high in these sites both because of a direct inflow of insects from the aquatic environment, such as midges with aquatic larvae and terrestrial adults, and because large inflows of organic material are deposited on shorelines providing food for detritivores and fertilizing plants (Colombini & Chelazzi 2003; Baxter, Fausch & Saunders 2005; Hyndes *et al.* 2022). At the same time, shorelines are often harsh environments due to flooding and wave disturbance, and on marine shorelines due to a high salinity and a high turnover of organic material (Defeo & McLachlan 2013; Barboza & Defeo 2015). Species diversity on shorelines may therefore be poor, particularly on marine shorelines where communities often consist of a range of habitat specialists that can endure high salinity levels (Cheng 1976; Irmler *et al.* 2002).

Despite these general patterns, there is a lack of understanding on how physical processes and prey availability interact in shaping coastal arthropod communities. In fact, the spatial variability of arthropod communities in these habitats is poorly documented compared to inland habitats. For instance, what differences in the species composition between limnic and marine shorelines are due to direct effects from a saline environment and what differences are rather due to differences in prey communities? Prey communities on limnic shorelines are often dominated by midges and a range of other taxa (Benke 1998; Delettre & Morvan 2000; Salvarina, Gravier & Rothhaupt 2017), whereas prey communities on marine shorelines are more dominated by species developing in rotting wrack beds (Schlacher *et al.* 2017; Hyndes*et al.* 2022). Similarly, what is the relative importance from the inflow of dead organic matter versus prey that developed in the water for shoreline predators? Previous studies suggest that the importance of these different resources for spiders and other shoreline predators may vary both between sites, between life stages and over time (Mellbrand*et al.* 2011; Verschut *et al.* 2019). The diet analysis of spiders across the season by Verschut et al. (2019) indicated that adult wolf spiders during early summer on marine shorelines feed largely on terrestrial dipterans such as dung flies, which have developed in wrack beds, whereas juvenile wolf spiders later in season had fed more on aquatic dipterans such as chironomids, where the larvae had fed on algae or detritus in the water.

To approach these questions, we studied prey communities, spider diets and spider community structure in a salinity gradient along the Swedish coast. Using this gradient allows us to explore effects from comparatively small salinity differences, as the salinity along the gradient changes continuously from freshwater (<1inner parts of the Bothnian Bay to oceanic conditions (>30included two coastal regions with 5 previous studies have indicated shifting dominance of spider species (Hamback *et al.* 2016; Verschut *et al.* 2019). We focus our attention on wolf spiders because these typically dominate the shoreline predator community in the area (Mellbrand & Hamback 2010). To account for the role of marine inflow, we aimed to include sites with and without thick wrack beds in each region. We also needed to control for climatic effects because the salinity gradient for our study is also a latitudinal gradient. For this reason, we used a similarly collected data set of spider communities on shores by inland waters along the same latitudinal gradient. Finally, to examine the role of a changing prey community and spider diet, we estimate prey densities using SLAM traps and collected spiders for gut metabarcoding in the same sites. Prey densities and spider diets were estimated two times, to cover seasonal changes in prey availability and diet differences between adult and juvenile spiders (cf. Verschut *et al.* 2019).

Methods

Study sites : The coastal regions included in the study were (a) Uppland north of Stockholm with the lowest salinity ([?]5region) and (b) Kalmar and Oland in southeastern Sweden with somewhat higher salinity ([?]7Information Table 1). The numbers of coastal sites were 13 (Uppland) and 7 (Kalmar). Among these, two sites respectively had thick wrack beds, and the other sites were similar but without thick wrack beds and often with short-cut grass due to grazing. The thick wrack beds had a thickness of more than 20cm with a considerable extension (several 10s of meters). The non-wrack sites either lacked wrack almost completely (as in the Uppland region) or that wrack occurred in scattered patches and never so thick as to provide a suitable habitat for detritivores (as in the Kalmar region). The inland regions included 15 and 23 shoreline sites in Uppland and southern Halland (same latitude as Kalmar) respectively (Fig. 1, SI Table 1), as part of a broader study focusing on both insect and spider communities in wetlands.

Field sampling : Coastal wolf spider communities were sampled using 10 pitfall traps per site placed in the wrack (wrack sites) or in open ground (non-wrack sites) for three nights in early May 2022 (Kalmar) or early-mid June 2021 and late May 2022 (Uppland). Inland wolf spider communities were sampled during June 2020. These times were chosen because wolf spiders are then adults or subadults, which simplifies species identification. Spiders were placed in 70% ethanol and brought to the laboratory for identification. Spiders from the inland sites were identified by R. Vicente and those from coastal sites by M. Langbak and A. Hoffmann, with assistance from R. Vicente for complicated cases (mainly involving *Pardosa agrestis/agricola/monticola*).

Spiders used for diet analyses were only collected from 13 sites, six from Uppland and seven from Kalmar, including all wrack sites. Spiders were individually collected by hand (30 per site), to reduce contamination risk, at two times (June and August 2019) and directly transferred to 95% ethanol. In the lab, samples were placed in a freezer (-20°C) until DNA extraction and further processing. Finally, prey densities were estimated by placing one SLAM (Sea Land Air Malaise) trap for two nights at the same time when collecting spiders for diet analyses. SLAM trap catches were placed in 70% ethanol, and brought to the laboratory for sorting to a family level.

Diet analyses : To metabarcode prey content of the hand-collected spiders, DNA was extracted from either a dissected abdomen (larger spiders) or the whole specimen (small spiders). To reduce the DNA yield of the focal spiders, we used a forward primer designed not to amplify wolf spider DNA (NoSpi2, Lafage *et al.* 2020) in combination with a general reverse primer (fwhR2n, Vamos, Elbrecht & Leese 2017) to amplify a section within the Folmer region of COI (Folmer *et al.*1994). Procedures for PCR amplification and library building follow Hamback et al. (2021), and sequencing of the spider samples was performed in one batch on the Illumina MiSeq3 platform at SciLifeLab in Stockholm. To detect individual samples after sequencing, a dual tagging approach was used where the 5'-end of both primers included an 8 base-pair tag (Binladen *et al.* 2007). Illumina-adaptors bearing unique indices were then ligated to the phosphorylated amplicons without a PCR step to preclude tag jumping errors (Bohmann *et al.* 2021). Due to problems with low DNA content, we had to change strategy and add a second PCR step with a low cycle number (6). Because this additional step increases the risk of tag jumping errors, we built libraries separately for each site, using SMARTer ThruPLEX DNA-seq library preparation kit excluding fragmentation of DNA (Takara Bio), as tag jumps between spiders within site do not affect the results due to pooling at this level before analysis. In each library, we also included at least 25% empty combinations to estimate tag jumping errors (which was about 6%). After sequencing, we used ObiTools (Boyer *et al.*2016) within the Galaxy Platform (Jalili *et al.* 2020) to assemble paired end sequences of high quality (score > 40), trim primers, clean sequences using 'obiclean', and demultiplex resulting sequences to individual samples using 'NGSFILTER' after filtering for size. These procedures resulted in a data set of 367 spider individuals and about 384,600 prey sequences that were grouped based on 97% similarity and where representative sequences were taxonomically assigned using BoLD (Ratnasingham & Hebert 2007) before further analyses.

Statistical analyses : Spider communities were modelled as the abundance of each spider species per site in a multivariate analysis with region, inland/coast, wrack and the region-by-inland/coast interactions as independent variables using the command manyglm (package: mvabund, Wang *et al.* 2012) with a negative binomial error distribution. Prey communities were similarly modelled as the abundance of major groups in a multivariate analysis with manyglm between regions with wrack as an independent variable and a negative binomial error distribution, but these tests additionally included season (June and August) as independent variable. Finally, the proportional number of prey sequences (logit-transformed) of major groups were pooled for each species within site and season, and was modelled using adonis2 (package: vegan, Oksanen *et al.* 2019). To compare diet composition between spider species, we also compared gut contents while controlling for effects of region. To examine model assumptions, we used plot.manyglm and all tests showed no pattern in errors which confirm the model appropriateness. Significant relationships were further explored using anova with adjusted p-values, to identify which groups that explained the variation. In all these tests, prey communities and spider diets were included at the level of family or higher taxonomic unit and not at a species level.

To study prey diversity and diet consistency within and among species, we first calculated individual diets using the dynamic threshold model in Cirtwill and Hamback (2021). We then compared species accumulation curves in spider guts using specaccum with spider individual as sampling unit (package: vegan, Oksanen *et al.* 2019), and then estimated diet consistency by calculating the Jaccard similarity index between diets of individual spiders' prey species and prey families, first between pairs of all spider individuals and then between individual pairs of the same species. Diet similarity was compared between region, wrack, and their interaction, firstly, depending on if pairs included all spider individuals or where restricted to within species comparison, and secondly, depending on if diets were based on prey species or prey family. If the interaction terms did not contribute, models were re-fit without the interaction. We then tested for pairwise differences between region-wrack combinations using a Tukey's HSD test applied to the analysis of variance of the above linear models, including the interaction term between region and wrack. All tests were performed using R 3.6.3 (R Core Team 2020).

Results

The analysis on spider communities included 3931 spider individuals separated into 16 taxa (Fig. 2). The variation in community composition was explained by a region-by-inland/coast interaction (Wald statistics=8.3, $p<0.001$) and not by the presence or absence of a thick wrack bed (Wald statistics=4.7, $p>0.1$). The region-by-inland/coast interaction arose because of a larger difference between southern and northern coastal sites compared with southern and northern inland sites (Fig. 2). When comparing abundances at the species level (Table 1), four species (*Pardosa agrestis* , *P. agricola, Arctosa leopardus* and *Alopecosa cuneata*) were found almost exclusively at southern coastal sites and three taxa (*Pardosa prativaga, P. amentata* and *Pirata* spp. [mainly*P. piraticus*]) almost never occurred in these sites but were abundant elsewhere (Fig. 2). In addition, one species (*P. monticola*) was mainly coastal whereas another species (*Pardosa palustris*) occurred mainly inland, irrespective of region.

The variation in the prey community was explained by a region-by-wrack interaction (Wald statistics=11.4, $p<0.001$) and by season (Wald statistics=11.6, $p<0.002$) (Fig. 3). The region-by-wrack interaction occurred because Coleoptera (Deviance=14.1, $p<0.02$) and Sciaridae (Deviance=20.3, $p<0.003$) were positively affected by wrack availability only in northern sites, whereas Dolichopodidae (Deviance=11.5, $p<0.05$) was negatively affected by wrack availability only in southern sites (Fig. 3). The seasonal effect occurred because Empididae (Deviance=12.4, $p<0.04$) and Homoptera (Deviance=12.8, $p<0.03$) were more abundant during early season in June, whereas Chironomidae (Deviance=14.7, $p<0.03$) and Trichoptera (Deviance=12.5, $p<0.04$) were more abundant during August.

The number of prey species encountered in the gut of spider individuals varied between one and 15, with an average of 3.9 prey species. The dominant order in the guts was Diptera, both Brachycera (60%) and Nematocera (18%), with minor amounts of other groups; Homoptera (10%, mainly Cicadellidae and Delphacidae), Collembola (4%), other flying prey (3%, Hymenoptera and Lepidoptera), Formicidae (2%), Acari (2%) and Heteroptera (1%) (Fig. 4, SI Table 2). The diet contents varied considerably among sites and were mainly explained by wrack (Lawley-Hotelling trace statistics=6.1, $p<0.001$) and season (Lawley-Hotelling trace statistics=2.6, $p<0.003$), with an almost significant effect from a region-by-wrack interaction (Lawley-Hotelling trace statistics=1.7, $p<0.07$) (Fig. 4). However, there was no effect of spider species either when including this variable alone or in combination with other variables, or when run separately for region. Because of the almost significant region-by-wrack interaction on gut contents, we repeated the analysis for sites with or without wrack separately. In this analysis, region was significant for sites without wrack ($p<0.03$)

but not for sites with wrack ($p>0.2$). The prey groups explaining the region difference for sites without wrack were Sphaeroceridae ($F_{1,6}=141$, $p<0.003$) and Enchytraeidae ($F_{1,6}=111$, $p<0.05$), that both had a higher frequency in spider guts from southern sites (Fig. 4). Finally, the comparison between sites with or without wrack suggested that mainly Sphaeroceridae ($F_{1,11}=17.2$, $p<0.06$) and Heteroptera ($F_{1,11}=19.9$, $p<0.05$) were more abundant in spider guts from site with wrack.

The species accumulation curves indicated that prey diversity was higher in southern sites and in sites with no wrack compared with northern sites and wrack sites (Fig. 5). When comparing diet consistency, we found that individual spiders had, on average, a Jaccard similarity of diets = 0.056 (sharing approximately 5.6% of the prey species consumed by two individuals). Diet consistency between any pair of individual spiders varied with region ($\beta=0.025$, $p<0.001$), wrack ($\beta=0.080$, $p<0.001$), and their interaction ($\beta=-0.042$, $p<0.001$). The interaction arose because spider from northern wrack sites had higher diet consistency than spiders from southern wrack sites, whereas spiders from northern non-wrack sites had lower consistency than those from southern non-wrack sites (Fig. 6). These diet similarities were larger when performed for pairs of the same spider species (Fig. 6) but patterns were otherwise similar (region: $\beta=0.062$, $p<0.001$; wrack: $\beta=0.108$, $p<0.001$; interaction: $\beta=-0.099$, $p<0.001$) and when diets were estimated at the prey family level both for all spider individuals (region: $\beta=0.038$, $p<0.001$; wrack: $\beta=0.094$, $p<0.001$; interaction: $\beta=-0.059$, $p<0.001$) and for pairs of the same spider species (region: $\beta=0.070$, $p<0.001$; wrack: $\beta=0.136$, $p<0.001$; interaction: $\beta=-0.124$, $p<0.001$).

Discussion

The spider community showed large regional changes along the Baltic Sea seashore despite comparatively small salinity differences (5 vs. 7Several spider species (*Pardosa agrestis* , *P. agricola, Arctosa leopardus* and *Alopecosa cuneata*) were almost exclusively located on the higher salinity sites compared to lower salinity sites by the Baltic Sea shore and by inland lakeshores. At the same time, other taxa (*Pardosa prativaga, P. amentata* and *Pirata* spp.) had the opposite distribution pattern, and this pattern was seemingly not explained by either prey availability or actual spider diets. In fact, there were no detectable diet differences between spider species or between spiders captured on shores with different salinity levels. Instead, spider diets varied between shores with or without thick beds of stranded wrack, a gradient that did not affect spider community structure. Consequently, and because the species shift only occurred on coastal sites and not on corresponding inland sites, it seems that coastal spider communities are directly affected by the saline conditions.

High salinity has several negative impacts on spiders and other arthropods, by reducing both survival and reproduction (Pétillon*et al.* 2011; Puzin *et al.* 2011; Foucreau *et al.*2012). Even though none of the species found on the Baltic shorelines can be considered true halophilic and are usually not found on more marine seashores (Pétillon *et al.* 2008), it seems reasonable to assume that species vary in their sensitivity to saline conditions. However, please note that previous studies on wolf spiders tested the responses of individuals at a much higher salinity (>30gradient, and it is unclear to what extent that their conclusions could be extrapolated to our study. Irrespective of the mechanisms, our data in combination with previous studies suggest a gradient in salinity thresholds of the dominant wolf spider species on marine shorelines in northwestern Europe where *P. prativaga*typically dominates low salinity sites, *P. agricola* dominates intermediate salinity sites and *P. purbeckensis* dominates high salinity sites. The species abundance distributions of wolf spider communities are often highly skewed with one dominant species having more than 60% of all individuals and a tail of rare species. Even though low salinity sites are not always dominated by *P. prativaga* , two-thirds are dominated by this species and then more rarely by *P. amentata* , *P. palustris* and some other species (see also Meriste, Helm & Ivask 2016).

Whereas the restriction to low salinity sites can likely be explained by salt sensitivity, the corresponding absence of other species at the same low salinity sites seems more puzzling. First, it is evident that the absence from low salinity sites is not absolute as both *Pardosa agrestis* and *P. agricola* are frequently reported also from inland habitats in central Europe and more rarely inland also from northern Europe (GBIF.org). Moreover, studies on *P. purbeckensis* , perhaps the most halophilic species, suggest that fitness is not reduced on low salinity sites (Petillon *et al.* 2011). It is possible that some other habitat characteristics restrict the occurrence in low salinity sites or that distributions are restricted by species interactions. Several wolf spider species are known for intraguild predation of other wolf spider species, at least in the laboratory, and dominance is mainly governed by size differences (Buddle, Walker & Rypstra 2003; Rypstra & Samu 2005; Rickers, Langel & Scheu 2006; Rypstra *et al.* 2007; Turney & Buddle 2019), but no study this far has evaluated the role of intraguild predation on the spatial distribution of wolf spiders.

Whatever the reason is for the difference in wolf spider community composition, the patterns are not likely explained by different dietary niches among spider species or by differences in prey availability. Both this, and previous studies using either molecular gut content analysis or other methods, indicate large overlaps in the diet of wolf spider species (Mellbrand & Hamback 2010; Verschut *et al.* 2019). Diet differences observed in this study instead seem to depend on whether spiders were collected on sites with or without accumulated wrack, but these diet shifts did not coincide with shifts in the wolf spider community. By far the most abundant prey group in the wolf spider guts on sites with either wrack or no wrack were dipterans (typically taxa with smaller individuals) and to some extent homopterans. This general prey composition of wolf spiders is of course well-known from non-molecular studies (e.g., Nyffeler 1999), but the relative importance of small dipterans is perhaps larger in our study habitats. Some differences between molecular and non-molecular studies may occur because the former provide an improved representation of small prey items, which are easily overlooked in non-molecular studies due to more rapid consumption. In either case, wolf spiders are likely quite opportunistic predators where prey choice perhaps depend more on encounter probabilities and catchability of prey in their selected habitat than on prey qualities. This opportunistic behavior is perhaps also reflected in the different number of prey species, where the number is higher in southern sites, as expected, and in sites with no wrack. Similarly, diet consistency was also higher on wrack sites, and both patterns observed for wrack sites may reflect that wrack beds are dominated by a small set of detritivorous species. More surprising was the higher diet consistency of spiders on southern non-wrack sites compared with northern non-wrack sites, despite the lower total prey diversity observed for the spiders in the southern region.

Even though opportunism seems to be a dominant pattern, particularly dark-winged fungus gnats (Sciaridae) are underrepresented in wolf spider guts despite their comparatively high occurrence at these sites, similar to what was found previously (Verschut *et al.* 2019). The reason for spiders to avoid fungus gnats may be that they represent low quality food (as suggested by Toft & Wise 1999b; Toft & Wise 1999a). Diet differences between sites with or without accumulated wrack otherwise reflect availability, even though we refrained from testing the availability-use relationship due to the bias in SLAM traps. Many small flies often occurring on wrack beds, such as Drosophilidae, Ephydridae, Sepsidae and Sphaeroceridae are underrepresented in Malaise type traps on shore lines because these flies tend not to stick to the ground. In either case, these small detritivorous flies that likely developed in or close to the decomposing wrack made up more than 75% of all prey in spider guts when collected from sites with heavy wrack beds and the diet composition was surprisingly similar for spiders collected on northern and southern wrack beds. More unexpected was perhaps the low frequency of chironomids in the spider gut contents, particularly in the non-wrack sites. In a previous study (Verschut *et al.* 2019), not far from the sites included in this paper, chironomids dominated the spider gut contents and particularly late in the season. In this study, there were no seasonal differences and spiders on non-wrack sites instead consumed a range of terrestrial prey groups, such as Homoptera and various terrestrial Diptera (Chloropidae, Empididae, Dolichopodidae etc.), and it seems that spiders were less strongly connected to the nearby marine environment than previously assumed. In either case, this variability among studies indicate how dynamic food choice of spiders may be.

To summarize, our study indicates that quite a small difference in salinity caused the species composition of wolf spider communities to change almost completely. The mechanism underlying this community shift is less obvious, both why species disappear in the high salinity and in the low salinity ends, but we can conclude that prey availability or differences in the trophic niche between species is likely not involved.

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Data accessibility

The data that support the findings of this study are openly available in Dryad at http://doi.org/[to be added] (Reference to be added)

Competing interest statement

The authors have no competing financial or personal interests that would conflict with the content of this paper

References

Barboza, F.R. & Defeo, O. (2015) Global diversity patterns in sandy beach macrofauna: a biogeographic analysis. *Scientific Reports,***5,** e14515.

Batzer, D.P. & Wu, H. (2020) Ecology of terrestrial arthropods in freshwater wetlands. *Annual Review of Entomology,* **65,**101-119.

Baxter, C.V., Fausch, K.D. & Saunders, W.C. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones.*Freshwater Biology,* **50,** 201-220.

Benke, A.C. (1998) Production dynamics of riverine chironomids: Extremely high biomass turnover rates of primary consumers.*Ecology,* **79,** 899-910.

Binladen, J., Gilbert, M.T.P., Bollback, J.P., Panitz, F., Bendixen, C., Nielsen, R. & Willerslev, E. (2007) The use of coded PCR primers enables high-throughput sequencing of multiple homolog amplification products by 454 parallel sequencing. *PLoS ONE,* **2,** e197.

Bohmann, K., Elbrecht, V., Caroe, C., Bista, I., Leese, F., Bunce, M., Yu, D.W., Seymour, M., Dumbrell, A.J. & Creer, S. (2021) Strategies for sample labelling and library preparation in DNA metabarcoding studies.*Molecular Ecology Resources* .

Boyer, F., Mercier, C., Bonin, A., Le Bras, Y., Taberlet, P. & Coissac, E. (2016) OBITOOLS: a UNIX-inspired software package for DNA metabarcoding. *Molecular Ecology Resources,* **16,** 176-182.

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.

Cheng, L. (1976) *Marine insects* . North Holland Publishing Company, Amsterdam.

Cirtwill, A.R. & Hamback, P. (2021) Building food networks from molecular data: Bayesian or fixed-number thresholds for including links.*Basic and Applied Ecology,* **50,** 67-76.

Colombini, I. & Chelazzi, L. (2003) Influence of marine allochthonous input on sandy beach communities. *Oceanography and Marine Biology, Vol 41,* **41,** 115-159.

Defeo, O. & McLachlan, A. (2013) Global patterns in sandy beach macrofauna: Species richness, abundance, biomass and body size.*Geomorphology,* **199,** 106-114.

Delettre, Y.R. & Morvan, N. (2000) Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. *Freshwater Biology,* **44,** 399-411.

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology,* **3,** 294-297.

Foucreau, N., Renault, D., Hidalgo, K., Lugan, R. & Petillon, J. (2012) Effects of diet and salinity on the survival, egg laying and metabolic fingerprints of the ground-dwelling spider Arctosa fulvolineata (Araneae, Lycosidae). *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology,* **163,** 388-395.

Hamback, P.A., Cirtwill, A.R., Garcia, D., Grudzinska-Sterno, M., Minarro, M., Tasin, M., Yang, X. & Samnegard, U. (2021) More intraguild prey than pest species in arachnid diets may compromise biological control in apple orchards. *Basic and Applied Ecology,***57,** 1-13.

Hamback, P.A., Weingartner, E., Dalen, L., Wirta, H. & Roslin, T. (2016) Spatial subsidies in spider diets vary with shoreline structure: Complementary evidence from molecular diet analysis and stable isotopes.*Ecology and Evolution,* **6,** 8431-8439.

Hyndes, G.A., Berdan, E.L., Duarte, C., Dugan, J.E., Emery, K.A., Hamback, P.A., Henderson, C.J., Hubbard, D.M., Lastra, M., Mateo, M.A., Olds, A. & Schlacher, T.A. (2022) The role of inputs of marine wrack and carrion in sandy-beach ecosystems: a global review. *Biological Reviews,* **97,** 2127-2161.

Irmler, U., Heller, K., Meyer, H. & Reinke, H.D. (2002) Zonation of ground beetles (Coleoptera : Carabidae) and spiders (Araneida) in salt marshes at the North and the Baltic Sea and the impact of the predicted sea level increase. *Biodiversity and Conservation,* **11,**1129-1147.

Jalili, V., Afgan, E., Gu, Q., Clements, D., Blankenberg, D., Goecks, J., Taylor, J. & Nekrutenko, A. (2020) The Galaxy platform for accessible, reproducible and collaborative biomedical analyses: 2020 update. *Nucleic Acids Research,* **48,** W395-W402.

Lafage, D., Elbrecht, V., Cuff, J.P., Steinke, D., Hamback, P.A. & Erlandsson, A. (2020) A new primer for metabarcoding of spider gut contents. *Environmental DNA,* **2,** 234-243.

Mellbrand, K. & Hamback, P.A. (2010) Coastal niches for terrestrial predators: a stable isotope study. *Canadian Journal of Zoology,***88,** 1077-1085.

Mellbrand, K., Lavery, P.S., Hyndes, G. & Hamback, P.A. (2011) Linking Land and Sea: Different Pathways for Marine Subsidies.*Ecosystems,* **14,** 732-744.

Meriste, M., Helm, A. & Ivask, M. (2016) Ground-Dwelling Spider Fauna of Flooded Meadows in Matsalu, Estonia. *Wetlands,* **36,**525-537.

Nyffeler, M. (1999) Prey selection of spiders in the field.*Journal of Arachnology,* **27,** 317-324.

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. & Wagner, H. (2019) *vegan: Community Ecology package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan* .

Petillon, J., Georges, A., Canard, A., Lefeuvre, J.C., Bakker, J.P. & Ysnel, F. (2008) Influence of abiotic factors on spider and ground beetle communities in different salt-marsh systems. *Basic and Applied Ecology,* **9,** 743-751.

Petillon, J., Lambeets, K., Ract-Madoux, B., Vernon, P. & Renault, D. (2011) Saline stress tolerance partly matches with habitat preference in ground-living wolf spiders. *Physiological Entomology,***36,** 165-172.

Polis, G.A. & Hurd, S.D. (1995) Extraordinarily high spider densities on islands - flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences of the United States of America,* **92,** 4382-4386.

Puzin, C., Acou, A., Bonte, D. & Petillon, J. (2011) Comparison of reproductive traits between two salt-marsh wolf spiders (Araneae, Lycosidae) under different habitat suitability conditions. *Animal Biology,* **61,** 127-138.

R Core Team, t. (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ratnasingham, S. & Hebert, P.D.N. (2007) BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Molecular Ecology Notes,***7,** 355-364.

Rickers, S., Langel, R. & Scheu, S. (2006) Stable isotope analyses document intraguild predation in wolf spiders (Araneae : Lycosidae) and underline beneficial effects of alternative prey and microhabitat structure on intraguild prey survival. *Oikos,* **114,**471-478.

Rypstra, A.L. & Samu, F. (2005) Size dependent intraguild predation and cannibalism in coexisting wolf spiders (Araneae, Lycosidae).*Journal of Arachnology,* **33,** 390-397.

Rypstra, A.L., Schmidt, J.M., Reif, B.D., DeVito, J. & Persons, M.H. (2007) Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk. *Oikos,***116,** 853-863.

Salvarina, I., Gravier, D. & Rothhaupt, K.O. (2017) Seasonal insect emergence from three different temperate lakes. *Limnologica,***62,** 47-56.

Sanchez-Ruiz, J.A., Phillips, J.S., Ives, A.R. & Gratton, C. (2018) Responses of orb-weaving spider aggregations to spatiotemporal variation in lake-to-land subsidies at Lake Myvatn, Iceland. *Polar Biology,***41,** 1547-1554.

Schlacher, T.A., Hutton, B.M., Gilby, B.L., Porch, N., Maguire, G.S., Maslo, B., Connolly, R.M., Olds, A.D. & Weston, M.A. (2017) Algal subsidies enhance invertebrate prey for threatened shorebirds: A novel conservation tool on ocean beaches? *Estuarine Coastal and Shelf Science,* **191,** 28-38.

Toft, S. & Wise, D.H. (1999a) Behavioral and ecophysiological responses of a generalist predator to single- and mixed-species diets of different quality. *Oecologia,* **119,** 198-207.

Toft, S. & Wise, D.H. (1999b) Growth, development, and survival of a generalist predator fed single- and mixed-species diets of different quality. *Oecologia,* **119,** 191-197.

Turney, S. & Buddle, C.M. (2019) Body size mediates the relationship between spider (Arachnida: Araneae) assemblage composition and prey consumption rate: results of a mesocosm experiment in the Yukon, Canada.*Oecologia,* **189,** 757-768.

Vamos, E.E., Elbrecht, V. & Leese, F. (2017) Short COI markers for freshwater macroinvertebrate metabarcoding. . *Metabarcoding and Metagenomics,* **1,** e14625.

Verschut, V., Strandmark, A., Esparza-Salas, R. & Hamback, P.A. (2019) Seasonally varying marine influences on the coastal ecosystem detected through molecular gut analysis. *Molecular Ecology,* **28,**307-317.

Wang, Y., Naumann, U., Wright, S.T. & Warton, D.I. (2012) mvabund- an R package for model-based analysis of multivariate abundance data.*Methods in ecology and evolution,* **3,** 471-474.

Table 1. Marginal deviance and adjusted significances for the abundance of wolf spider species relative to coast/inland (CI), region (R, north [Uppland]/south [Kalmar/Halland]) and the CI-by-R interaction (ns = non-significant [p>0.1]).

Species	CI	R	CI*R
Alopecosa cuneata	1.4 ns	0.3 ns	10.4 (p<0.02)
A. pulverulenta	0.1 ns	2.9 ns	0.8 ns
Arctosa leopardus	24.5 (p<0.001)	2.9 ns	8.1 (p<0.05)
Pardosa agrestis	11.8 (p<0.02)	25.8 (p<0.001)	0.2 ns
P. agricola	25.9 (p<0.001)	16.1 (p<0.005)	0.0 ns
P. amentata	1.5 ns	1.0 ns	10.6 (p<0.05)
P. fulvata	6.8 ns	3.5 ns	5.0 ns
P. monticola	42.7 (p<0.001)	0.7 ns	0.0 ns
P. palustris	13.5 (p<0.005)	0.8 ns	5.6 ns

Species	CI	R	CI*R
P. prativaga	0.4 ns	14.6 ($p<0.006$)	36.6 ($p<0.001$)
P. pullata	2.1 ns	0.7 ns	3.2 ns
Pirata spp.	1.1 ns	4.6 ns	13.1 ($p<0.007$)
Trochosa ruricola	3.0 ns	1.7 ns	1.7 ns
T. terricola	2.1 ns	19.7 ($p<0.001$)	0.0 ns

Figure legends

Fig. 1. Map showing the location of regions (Northern sites = Uppland, Southern coastal sites = Kalmar, Southern inland sites = Halland). For site information see SI Table 1.

Fig. 2. Relative abundance of wolf spider species in inland and coastal sites in Halland/Kalmar (S) and in Uppland (N).

Fig. 3. Relative abundances of prey catches in SLAM-traps, separated by wrack occurrence, region (south = Kalmar, north = Uppland) and season (A = August, S = July). Detritivore flies include Sepsidae, Sphaeroceridae and Coelopidae. Other flying prey include Hymenoptera and Lepidoptera but also a range of terrestrial Diptera.

Fig. 4. Relative contents of spider guts from sites with or without wrack, and in the northern (Uppland) or southern (Kalmar) region. Other detritivore flies include those connected to wrack, such as Anthomyiidae, Coelopidae, Ephydridae and Sepsidae. Other large flies include Dolichopodidae, Dryomyzidae, Empididae, Fannidae, Heleomyzidae, Hybotidae, Muscidae, Rhinophoridae, Scatophagidae, Sciomyzidae, Syrphidae, Tabanidae and Tachinidae. Other small flies include Acroceridae, Agromyzidae, Asteiidae, Canacidae, Carnidae, Chamaemyiidae, Chloropidae, Lonchopteridae, Opomyzidae, Phoridae, and Pipunculidae. Other Nematocera include Cecidomyiidae, Ceratopogonidae, Keroplatidae, Limoniidae, Mycetophilidae, Psychodidae, Scatopsidae and Sciaridae.

Fig. 5. Species accumulation curves (±S.D.) relative to the number of sampled spiders for northern sites (Uppland) and southern sites (Kalmar), with or without wrack accumulation.

Fig. 6. Individual diet similarity estimated as Jaccards similarity index (±S.E.) separated for region (N=Uppland, S=Kalmar) and wrack presence. The diet similarity was estimated between all pairs of individuals (red) or between pairs of the same species (white) and when prey where included at the species (circles) or family (squares) level. N-values refer to the number of pairs of individuals.

Figure 1

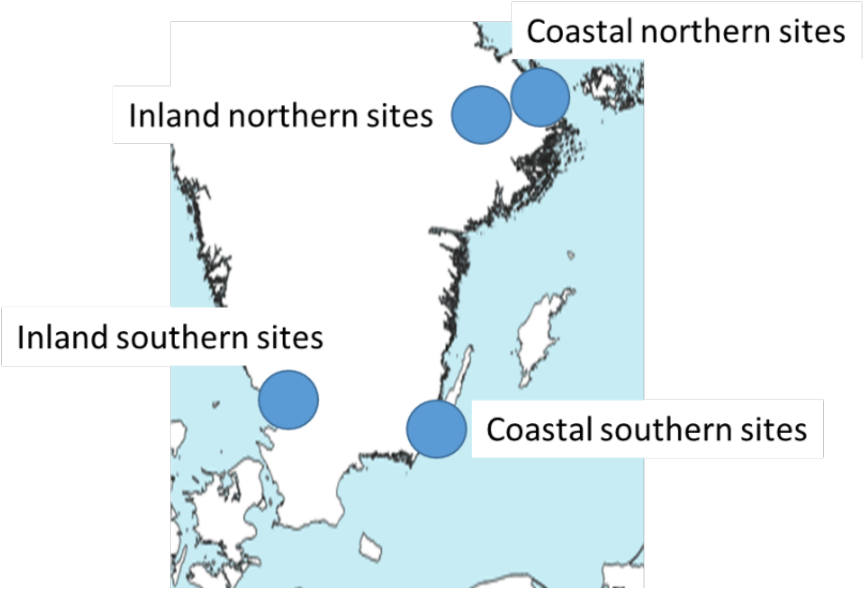


Figure 2

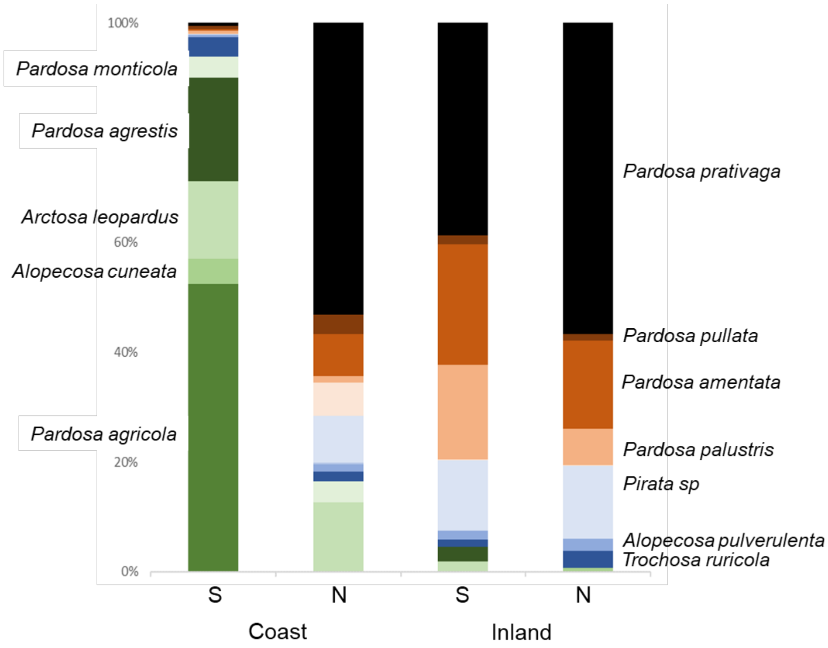


Figure 3

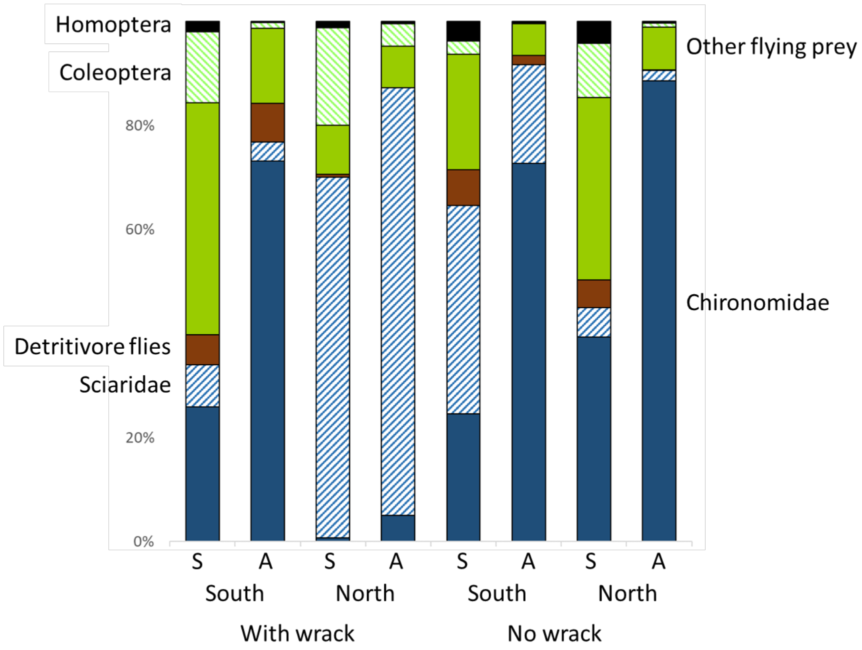


Figure 4

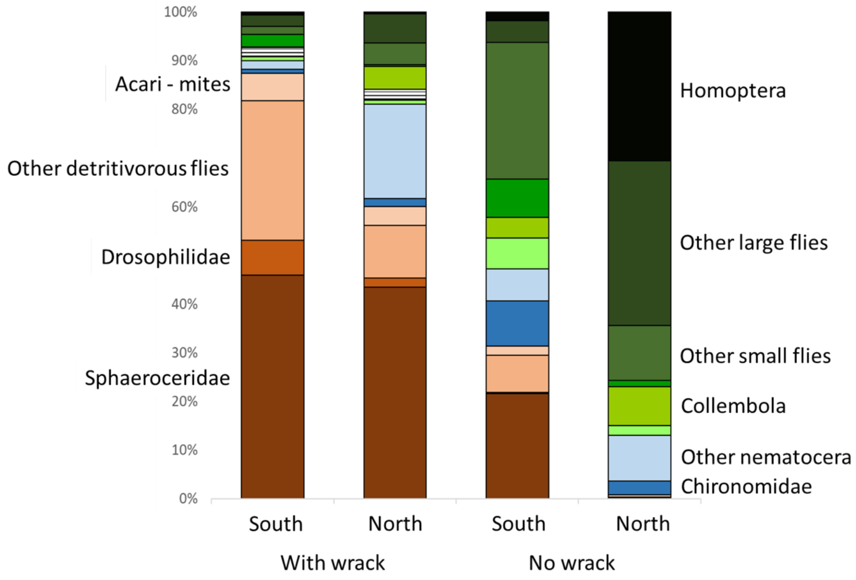


Figure 5

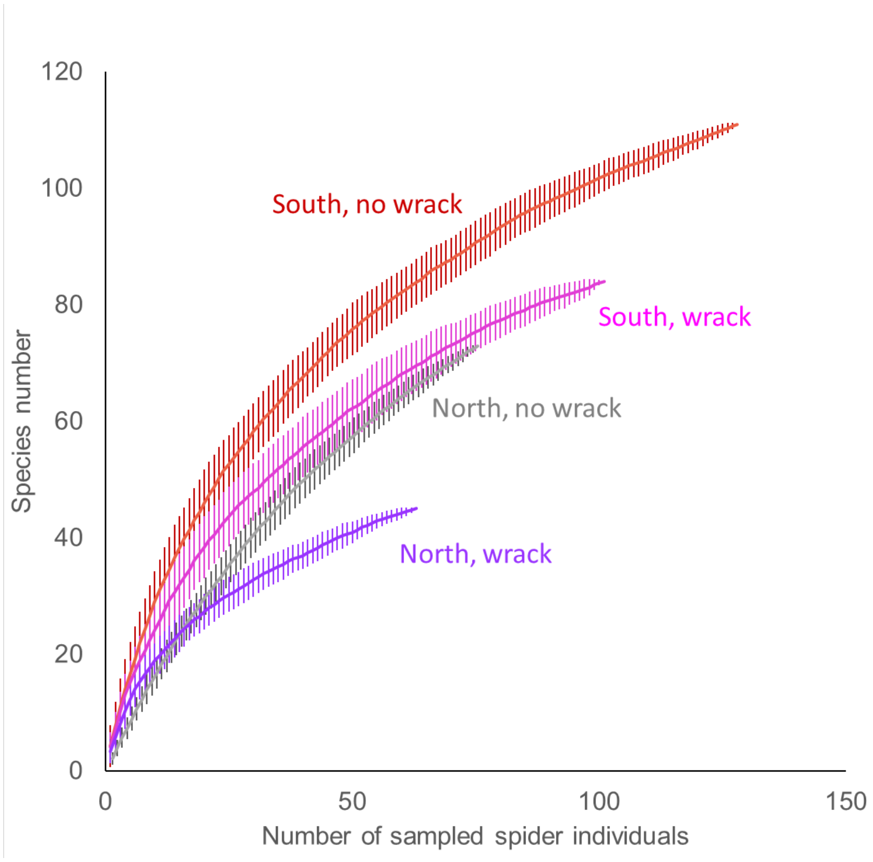
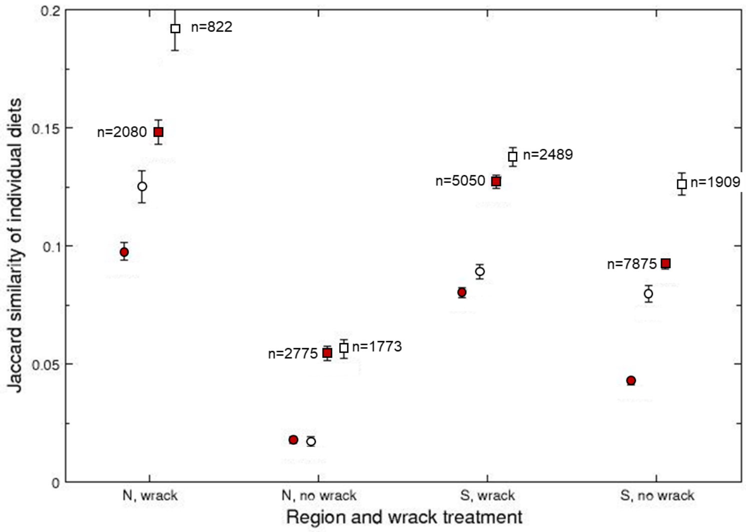

120
100
80
60
40
20
0
Species number
0
50
100
150
Number of sampled spider individuals
South, no wrack
South, wrack
North, no wrack
North, wrack

Fig. 6


0.2
0.15
0.1
0.05
0
Jaccard similarity of individual diets
n=822
n=2080
n=2489
n=5050
n=1909
n=7875
n=2775
n=1773
N, wrack
N, no wrack
S, wrack
S, no wrack
Region and wrack treatment

Appendix 1. Site information, where spider communities were quantified in all sites and where diet data and prey availabilities were collected from a subset of sites.

Site	Coast/Inland	Region	Wrack	Diet data	Latitude	Longitude
Barnens Ö	Coast	Uppland	Y	Y	59°55’38”N	18°56’29”E
Forsmark	Coast	Uppland	N	Y	60°23’41”N	18°13’12”E
Gudinge	Coast	Uppland	N		60°30’31”N	17°59’46”E
Klungsten	Coast	Uppland	N	Y	60°32’44”N	18° 1’10”E
Raggarön	Coast	Uppland	N		60°12’18”N	18°33’55”E
Rådmansholmen	Coast	Uppland	N		59°37’18”N	18°56’52”E
Senneby Hake	Coast	Uppland	Y	Y	59°58’23”N	18°54’21”E
Skedvik	Coast	Uppland	N		58°58’15”N	17°45’ 1”E
Storsten	Coast	Uppland	N	Y	60°31’16”N	18° 0’23”E
Sveden	Coast	Uppland	N		59°35’12”N	18°39’58”E
Tranviken	Coast	Uppland	N		60° 9’52”N	18°46’43”E
Tullgarn	Coast	Uppland	N		58°57’22”N	17°35’10”E
Tvärnö	Coast	Uppland	N	Y	60°12’ 9”N	18°32’42”E
Bergianska	Inland	Uppland	N		59°22’ 3”N	18° 2’46”E
Frötuna	Inland	Uppland	N		59°54’45”N	17°51’52”E
Jönsbolsjön	Inland	Uppland	N		59°51’21”N	18° 1’52”E
Kromsta	Inland	Uppland	N		59°40’38”N	17°15’13”E
Kärven	Inland	Uppland	N		59°54’54”N	18° 9’10”E
Ludden	Inland	Uppland	N		59°46’18”N	18°40’23”E
Ribbingebäck	Inland	Uppland	N		59°50’17”N	17°10’54”E
Segersta viltvatten	Inland	Uppland	N		59°38’12”N	17°24’27”E
Senneby	Inland	Uppland	N		59°57’47”N	18°51’13”E
Örsundsbro	Inland	Uppland	N		59°44’47”N	17°20’47”E
U27	Inland	Uppland	N		60°12’59”N	18°12’38”E
U28	Inland	Uppland	N		60°12’39”N	18°15’41”E
U46	Inland	Uppland	N		59°54’46”N	17°23’45”E
U113	Inland	Uppland	N		59°41’11”N	17°54’19”E
U132	Inland	Uppland	N		59°27’41”N	17°41’56”E
Dösjön	Coast	Kalmar	N	Y	56°28’35”N	16° 8’39”E
Enetri	Coast	Kalmar	N	Y	56°15’ 7”N	16°29’ 8”E
Enudden	Coast	Kalmar	N	Y	56°30’59”N	16°11’13”E
Fågelmara	Coast	Kalmar	N	Y	56°13’28”N	16° 0’53”E
Grisbäck	Coast	Kalmar	N	Y	56°19’59”N	16° 4’10”E
Sandvik	Coast	Kalmar	Y	Y	56°22’22”N	16°24’14”E
Ventlinge	Coast	Kalmar	Y	Y	56°17’ 2”N	16°23’49”E
BA6	Inland	Halland	N		56°34’60”N	13° 4’ 5”E
BA700	Inland	Halland	N		56°34’52”N	13° 5’27”E
D2	Inland	Halland	N		56°38’25”N	12°59’49”E
D3	Inland	Halland	N		56°37’58”N	13° 0’15”E
D7	Inland	Halland	N		56°36’34”N	12°55’28”E
D12	Inland	Halland	N		56°26’ 7”N	12°56’30”E
D15	Inland	Halland	N		56°26’52”N	13° 0’37”E
D16	Inland	Halland	N		56°27’ 0”N	13° 3’41”E
D17	Inland	Halland	N		56°40’ 5”N	12°46’46”E
D18	Inland	Halland	N		56°38’40”N	12°47’19”E
D19	Inland	Halland	N		56°45’28”N	12°39’43”E
D20	Inland	Halland	N		56°44’15”N	12°46’ 4”E

Site	Coast/Inland	Region	Wrack	Diet data	Latitude	Longitude
D22	Inland	Halland	N		56°45' 3"N	12°52'52"E
D23	Inland	Halland	N		56°49'47"N	12°53'28"E
D25	Inland	Halland	N		56°52'13"N	12°45'31"E
D28	Inland	Halland	N		56°52'44"N	12°44'57"E
D29	Inland	Halland	N		56°57'55"N	12°24'15"E
EA16	Inland	Halland	N		56°27'44"N	13° 4'27"E
EA18	Inland	Halland	N		56°27'40"N	13° 5'13"E
EA60	Inland	Halland	N		56°27'44"N	13° 8'43"E
KA7	Inland	Halland	N		56°49'23"N	12°39'51"E
MA18	Inland	Halland	N		56°25'38"N	13° 5'24"E
VA4	Inland	Halland	N		56°33'45"N	13° 6'26"E

Appendix 2. Total list of prey species with DNA in spider guts, and the number of spiders where the prey DNA was detected. Species id is provided as multiple species or genus level when the identity cannot be resolved (i.e., multiple species with sequence similarity > 97%).

Prey order	Family	Species	No of spiders
Annelidae	Enchytraeidae	Enchytraeus albidus	6
Annelidae	Enchytraeidae	Enchytraeus buchholzi	1
Annelidae	Enchytraeidae	Enchytraeus moebii/albidus	4
Annelidae	Enchytraeidae	Lumbricillus pagenstecheri	3
Aranae	Clubionidae	Clubiona phragmitis	3
Aranae	Clubionidae	Clubiona reclusa/norwegica	2
Aranae	Linyphiidae	Erigone arctica	17
Aranae	Linyphiidae	Erigone longipalpis	7
Aranae	Theridiidae	Anelosimus vittatus	1
Aranae	Theridiidae	Theridion varians	1
Coleoptera	Anthicidae	Anthicus flavipes	2
Coleoptera	Carabidae	Bembidion pallidipenne	2
Coleoptera	Carabidae	Elaphrus uliginosus	1
Coleoptera	Carabidae	Pterostichus rhaeticus/nigrita	1
Coleoptera	Carabidae	Trechus secalis	2
Coleoptera	Chrysomelidae	Chrysolina staphylaea	2
Coleoptera	Curculionidae	Pelenomus quadrituberculatus	6
Coleoptera	Dermestidae	Dermestes szekessyi	5
Coleoptera	Hydraenidae	Ochthebius marinus/minimus	1
Coleoptera	Hydrophilidae	Cercyon depressus	3
Coleoptera	Scarabaeidae	Melolontha melolontha	1
Coleoptera	Scarabaeidae	Serica brunnea	1
Coleoptera	Silphidae	Oiceoptoma thoracicum	2
Coleoptera	Staphylinidae	Acrolocha sulcula	1
Coleoptera	Staphylinidae	Aleochara bipustulata/verna	2
Coleoptera	Staphylinidae	Atheta fungi	1
Coleoptera	Staphylinidae	Atheta vestita	3
Coleoptera	Staphylinidae	Cafius xantholoma	1
Coleoptera	Staphylinidae	Carpelimus rivularis	18
Coleoptera	Staphylinidae	Cordalia obscura	1
Coleoptera	Staphylinidae	Gnypeta carbonaria	4
Coleoptera	Staphylinidae	Omalium riparium	9

Prey order	Family	Species	No of spiders
Coleoptera	Staphylinidae	Tachyporus nitidulus	1
Collembola	Entomobryidae	Desoria grisea	8
Collembola	Entomobryidae	Entomobrya lanuginosa	2
Collembola	Entomobryidae	Entomobrya multifasciata	3
Collembola	Entomobryidae	Lepidocyrtus lignorum	1
Collembola	Entomobryidae	Orchesella cincta/villosa	5
Collembola	Entomobryidae	Orchesella flavescens	2
Collembola	Hypogastruridae	Hypogastrura viatica	2
Collembola	Isotomidae	Halisotoma maritima	9
Collembola	Isotomidae	Isotoma anglicana	3
Collembola	Isotomidae	Isotoma riparia	31
Collembola	Isotomidae	Isotoma viridis(coerulea	8
Collembola	Isotomidae	Isotomurus fucicolus	3
Collembola	Katiannidae	Sminthurinus signatus	1
Collembola	Sminthuridae	Sminthurinus aureus	2
Collembola	Sminthuridae	unid	2
Collembola	Tomoceridae	Pogonognathellus spp	2
Diptera	Acroceridae	Acrocera orbicula	16
Diptera	Acroceridae	Ogcodes pallipes	3
Diptera	Agromyzidae	Agromyza albipennis	1
Diptera	Agromyzidae	Agromyza filipendulae	1
Diptera	Agromyzidae	Phytomyza horticola	6
Diptera	Anthomyiidae	Delia florilega	1
Diptera	Anthomyiidae	Delia platura	10
Diptera	Anthomyiidae	Fucellia fucorum	31
Diptera	Anthomyiidae	Fucellia tergina/maritima	36
Diptera	Asteiidae	Asteia amoena	1
Diptera	Carnidae	Meoneura sp	1
Diptera	Cecidomyiidae	Rhopalomyia sp.	4
Diptera	Cecidomyiidae	unid	26
Diptera	Ceratopogonidae	Atrichopogon fusculus	4
Diptera	Ceratopogonidae	Bezzia annulipes	4
Diptera	Ceratopogonidae	Culicoides newsteadi	1
Diptera	Ceratopogonidae	Dasyhelea turficola	12
Diptera	Ceratopogonidae	Forcipomyia hygrophila	1
Diptera	Ceratopogonidae	Palpomyia lineata	2
Diptera	Ceratopogonidae	unid	2
Diptera	Chamaemyiidae	Chamaemyia geniculata	2
Diptera	Chironomidae	Arctopelopia griseipennis	1
Diptera	Chironomidae	Chironomus aprilinus/pseudothummi	6
Diptera	Chironomidae	Cladopelma virescens	1
Diptera	Chironomidae	Cladotanytarsus difficilis	1
Diptera	Chironomidae	Cladotanytarsus gedanicus	4
Diptera	Chironomidae	Cladotanytarsus mancus	20
Diptera	Chironomidae	Cladotanytarsus nigrovittatus	2
Diptera	Chironomidae	Cladotanytarsus wexionensis/bicornutus	1
Diptera	Chironomidae	Cricotopus caducus/patens/flavocinctus	11
Diptera	Chironomidae	Cricotopus ornatus	1
Diptera	Chironomidae	Halocladius variabilis	2
Diptera	Chironomidae	Limnophyes sp.	1

Prey order	Family	Species	No of spiders
Diptera	Chironomidae	Metriocnemus atriclava	1
Diptera	Chironomidae	Paratanytarsus inopertus/Chironomus plumosus	16
Diptera	Chironomidae	Paratanytarsus natvigi	8
Diptera	Chironomidae	Psectrocladius limbatellus	4
Diptera	Chironomidae	Psectrocladius oxyura	10
Diptera	Chironomidae	Pseudosmittia trilobata	3
Diptera	Chironomidae	Smittia leucopogon	1
Diptera	Chironomidae	Smittia sp.	1
Diptera	Chironomidae	Tanytarsus gracilentus	1
Diptera	Chironomidae	Tanytarsus usmaensis	5
Diptera	Chironomidae	unid	1
Diptera	Chloropidae	Chlorops pumilionis	1
Diptera	Chloropidae	Eutropha fulvifrons	4
Diptera	Chloropidae	Incertella sp./Rhopalopterum sp.	3
Diptera	Chloropidae	Meromyza nigriventrix/saltatrix	1
Diptera	Chloropidae	Oscinella sp.	56
Diptera	Chloropidae	Thaumatomyia notata	2
Diptera	Coelopidae	Coelopa frigida	17
Diptera	Dolichopodidae	Dolichopus nitidus	1
Diptera	Dolichopodidae	Dolichopus nubilus	20
Diptera	Dolichopodidae	Dolichopus pumilus mfl	4
Diptera	Dolichopodidae	Gymnopternus aerosus	3
Diptera	Dolichopodidae	Medetera truncorum/petrophiloides	1
Diptera	Dolichopodidae	Syntormon pallipes	1
Diptera	Dolichopodidae	Xanthochlorus ornatus	1
Diptera	Drosophilidae	Cacoxenus argyreator	4
Diptera	Drosophilidae	Scaptomyza flava/pallida	36
Diptera	Dryomyzidae	Heterocheila buccata	8
Diptera	Empididae	Rhamphomyia geniculata	3
Diptera	Empididae	unid	2
Diptera	Ephydridae	Discocerina obscurella	5
Diptera	Ephydridae	Hydrellia griseola	1
Diptera	Ephydridae	Lamproscatella sibilans	3
Diptera	Ephydridae	Limnellia quadrata	1
Diptera	Ephydridae	Paracoenia fumosa	6
Diptera	Ephydridae	Philotelma alaskense/defectum	2
Diptera	Ephydridae	Psilopa nigritella	1
Diptera	Ephydridae	Scatella paludum	7
Diptera	Ephydridae	Scatella stagnalis mfl	23
Diptera	Ephydridae	Scatella subguttata	3
Diptera	Ephydridae	Scatophila despecta	2
Diptera	Heleomyzidae	Trixoscelis obscurella	3
Diptera	Keroplatidae	Pyratula zonata	1
Diptera	Limoniidae	Symplecta stictica	5
Diptera	Limoniidae	unid	1
Diptera	Lonchopteridae	Lonchoptera bifurcata	3
Diptera	Muscidae	Coenosia lacteipennis	1
Diptera	Muscidae	Coenosia pedella/testacea	6
Diptera	Muscidae	Coenosia pumila	1
Diptera	Muscidae	Coenosia testacea	1

Prey order	Family	Species	No of spiders
Diptera	Muscidae	Lispocephala erythrocera	1
Diptera	Muscidae	Morellia sinensis/tempestiva	1
Diptera	Muscidae	Schoenomyza litorella	1
Diptera	Muscidae	Spilogona aerea	1
Diptera	Opomyzidae	Geomyza sp.	1
Diptera	Opomyzidae	Opomyza germinationis/florum	2
Diptera	Phoridae	Megaselia albicans	2
Diptera	Phoridae	Megaselia brevicostalis	14
Diptera	Phoridae	Megaselia manicata	4
Diptera	Phoridae	Megaselia pleuralis	5
Diptera	Phoridae	Megaselia pusilla/ignobilis	1
Diptera	Phoridae	Megaselia sp.	1
Diptera	Phoridae	Metopina sp.	3
Diptera	Phoridae	unid	5
Diptera	Pipunculidae	Eudorylas fuscipes	2
Diptera	Psychodidae	Psychoda lativentris	2
Diptera	Rhinophoridae	Tricogena rubricosa	2
Diptera	Scathophagidae	Spaziphora hydromyzina	1
Diptera	Scathophagidae	Trichopalpus fraternus	2
Diptera	Scatopsidae	Coboldia fuscipes	21
Diptera	Scatopsidae	Scatopse notata	10
Diptera	Sciaridae	Corynoptera inundata	1
Diptera	Sciaridae	Lycoriella sativae	13
Diptera	Sciomyzidae	Ditaeniella grisescens	1
Diptera	Sepsidae	Themira putris	43
Diptera	Sphaeroceridae	Coproica hirtula	2
Diptera	Sphaeroceridae	Coproica lugubris	9
Diptera	Sphaeroceridae	Leptocera curvinervis	73
Diptera	Sphaeroceridae	Opacifrons coxata	5
Diptera	Sphaeroceridae	Opalimosina mirabilis	4
Diptera	Sphaeroceridae	Pullimosina heteroneura	6
Diptera	Sphaeroceridae	Pullimosina pullula	2
Diptera	Sphaeroceridae	Rachispoda intermedia/fuscipennis	34
Diptera	Sphaeroceridae	Rachispoda limosa	10
Diptera	Sphaeroceridae	Rachispoda lutosa/breviceps	10
Diptera	Sphaeroceridae	Thoracochaeta seticosta	58
Diptera	Sphaeroceridae	Thoracochaeta zosterae	51
Diptera	Syrphidae	Eristalis sp	1
Diptera	Syrphidae	Eupeodes corollae	1
Diptera	Syrphidae	Platycheirus sp.	1
Diptera	Tabanidae	Chrysops relictus/viduatus/rufipes	2
Diptera	Tabanidae	Tabanus cordiger/unifasciatus	1
Diptera	Tachinidae	Siphona sp.	3
Hemiptera	Anthocoridae	Orius majusculus/minutus	2
Hemiptera	Anthocoridae	Orius niger/horvathi	3
Hemiptera	Aphididae	Euceraphis betulae	1
Hemiptera	Cicadellidae	Arthaldeus striifrons	3
Hemiptera	Cicadellidae	Euscelis sordida	3
Hemiptera	Cicadellidae	Limotettix striola	3
Hemiptera	Cicadellidae	Paralimnus phragmitis	2

Prey order	Family	Species	No of spiders
Hemiptera	Cicadellidae	Planaphrodes bifasciatus	1
Hemiptera	Cicadellidae	Psammotettix confinis/alienus	14
Hemiptera	Cicadellidae	Psammotettix nodosus/dubius	1
Hemiptera	Cicadellidae	Sarhoanus sp.	2
Hemiptera	Delphacidae	Delphax crassicornis	2
Hemiptera	Delphacidae	Euconomelus lepidus	3
Hemiptera	Delphacidae	Evacanthus interruptus	1
Hemiptera	Delphacidae	Javesella dubia/pellucida/forcipata	12
Hemiptera	Delphacidae	Unkanodes sp.	13
Hemiptera	Gerridae	Gerris thoracicus	2
Hemiptera	Miridae	Atractotomus mali/Phytocoris pini	1
Hemiptera	Miridae	Closterotomus norwegicus	2
Hemiptera	Miridae	Orthotylus sp.	19
Hemiptera	Nepidae	Nepa cinerea/rubra	1
Hemiptera	Piesmatidae	Parapiesma quadratum	3
Hemiptera	Saldidae	Saldula sp.	5
Hymenoptera	Aphelinidae	Aphelinus asychis	2
Hymenoptera	Aphelinidae	Aphelinus sp	1
Hymenoptera	Braconidae	Aphaereta minuta	1
Hymenoptera	Braconidae	Dolichogenida sp.	2
Hymenoptera	Braconidae	Praon flavinode	1
Hymenoptera	Braconidae	unid	1
Hymenoptera	Encyrtidae	Copidosoma floridanum	1
Hymenoptera	Eulophidae	Diglyphus isaea	1
Hymenoptera	Eulophidae	Pediobius sp.	2
Hymenoptera	Eulophidae	Tamarixia pronomus	1
Hymenoptera	Eulophidae	unid	1
Hymenoptera	Formicidae	Lasius niger	14
Hymenoptera	Formicidae	Lasius sp.	3
Hymenoptera	Formicidae	Myrmica rubra	9
Hymenoptera	Formicidae	Myrmica ruginodis	12
Hymenoptera	Ichneumonidae	Cotesia vestalis	1
Hymenoptera	Ichneumonidae	Diadegma armillatum	1
Hymenoptera	Ichneumonidae	Diadegma fenestrale/nanus	2
Hymenoptera	Ichneumonidae	Homotropus signatus	1
Hymenoptera	Mymaridae	Anaphes sp.	2
Hymenoptera	Pteromalidae	Halticoptera aenea	1
Hymenoptera	Pteromalidae	Psilonotus adamas	2
Hymenoptera	Pteromalidae	Pteromalus semotus	1
Hymenoptera	Pteromalidae	Trichomalopsis sp.	3
Hymenoptera	Pteromalidae	Trichomalus sp.	6
Hymenoptera	Pteromalidae	unid	5
Lepidoptera	Gelechiidae	Monochroa tetragonella	1
Lepidoptera	Gelechiidae	Scrobipalpa obsoletella	6
Lepidoptera	Glyphypterigidae	Glyphipterix thrasonella	1
Lepidoptera	Noctuidae	Autographa gamma	1
Lepidoptera	Plutellidae	Plutella xylostella	14
Lepidoptera	Psychidae	Narycia duplicella	1
Lepidoptera	Psychidae	Psyche casta	1
Mesostigmata	Ascidae	unid	1

Prey order	Family	Species	No of spiders
Mesostigmata	Blattiscociidae	Cheiroseius sp.	9
Mesostigmata	Eviphipidae	unid	14
Mesostigmata	Macrocheliidae	unid	11
Mesostigmata	Parasitidae	Pergamasus crassipes	2
Mesostigmata	Parasitidae	unid	39
Opiliones	Phalangiidae	Mitopus morio	1
Orthoptera	Acrididae	Chorthippus spp.	5
Orthoptera	Acrididae	Stethophyma grossum	2
Orthoptera	Tetrigidae	Tetrix subulata	1
Sarcoptiformes	Ameronothridae	Ameronothrus	1
Sarcoptiformes	Ceratozetidae	Trichoribates novus	1
Sarcoptiformes	Crotoniidae	Platynothrus thori	1
Thysanoptera	Thripidae	unid	6
Trichoptera	Leptoceridae	Oecetis ochracea	1
Trombidiformes	Erythraeidae	Balaustium	6
Trombidiformes	Eupodidae	unid	3
Trombidiformes	Hydryphantidae	Hydryphantes crassipalpis	1