Regulation of wolf spider populations: The role of habitat structure, autochthonous and allochthonous prey

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Veröffentlichungen aus der vorliegenden Dissertation

RICKERS S. & SCHEU S. (in press) Cannibalism in *Pardosa palustris* (Araneae, Lycosidae): effects of alternative prey, habitat structure, and density. Basic and Applied Ecology

RICKERS S., LANGEL R., SCHEU S. (submitted) Effects of food quality on survival and reproduction of a generalist predator (*Pardosa lugubris*; Araneae: Lycosidae). Functional Ecology

RICKERS S., LANGEL R., SCHEU S. (submitted) Effects of alternative prey and microhabitat structure on intraguild predation in wolf spiders (Araneae: Lycosidae). Oikos

If you wish to live and thrive
Let a spider run alive.
English Proverb

Der Beginn aller Wissenschaften ist das Erstaunen,
dass die Dinge so sind, wie sie sind.
Aristoteles

Summary

Aim of this study was to identify major regulatory mechanisms for wolf spider populations. Field and laboratory experiments focussed on the importance of prey availability (autochthonous & allochthonous), food quality and habitat heterogeneity on performance of individual wolf spiders or whole populations and on intra- (cannibalism) and interspecific (intraguild predation) relationships in wolf spiders.

Wolf spider populations on xeric grasslands near Darmstadt (Germany) are increased on grazed sites as compared to sites without sheep grazing. Since potential prey was also more abundant on grazed sites, I hypothesised that spiders were bottom-up controlled. Therefore, alternative prey (*Drosophila melanogaster*; Diptera) was added to fenced plots on grazed and non-grazed sites in the field and spider as well as prey densities (detritivores & herbivores) were compared to plots without prey addition. In order to document integration of *D. melanogaster* into the arthropod food web, stable isotopes in the most abundant animals were analysed.

Even though *D. melanogaster* was integrated into the diet of most predators as documented by stable isotope analysis, neither spiders nor ground beetles increased in densities when provided with additional alternative prey. Similarly, densities of potential prey, such as Collembola and Auchenorrhyncha, were not affected by prey addition, indicating that prey populations were not effectively controlled by predator populations. Stable isotope analysis documented the dependence of Lycosidae and Carabidae on prey from the detritivore food. Collembola were strongly increased on grazed sites, presumably being responsible for increased wolf spider densities indicating that wolf spider populations were bottom-up controlled. Probably, the amount of alternative prey added was not sufficient to significantly affect predator and prey densities in addition to the beneficial effect of grazing.

The importance of allochthonous resources in food webs has been documented and spider populations are often sustained by prey from the detritivore food web (see above). In coastal ecosystems, predators often benefit from allochthonous input from the marine ecosystem. Kelp and sea grass deposition is common on sandy beaches on the east coast of Tasmania (Australia) providing marine input for cursorial predators on the beach and foredunes. I hypothesised that the terrestrial predators benefit from these allochthonous resources. Animals from the beach and the foredune were collected and most abundant taxa were selected for stable isotope analysis in order to trace the importance of marine subsidies in animal diet. This is possible, because stable isotope ratios in algae differ strongly from those in terrestrial plants that determine the baseline of the terrestrial food web.

According to activity abundance of animals, arthropods could be separated into the beach and the foredune community that hardly overlapped. Stable isotope analysis documented that kelp deposits were used by amphipods and isopods that were the most abundant animals on the beach. Despite of their high abundance, only few predators, such as *Tetralycosa oraria* (Lycosidae), *Cafius* 2 (Staphylinidae) and *Tuoba laticeps* (Geophilomorpha) preyed on these isopods and amphipods. Stable isotope analyses revealed feeding niches of predators and documented that the marine subsidies were not incorporated into the foredune food web. Thus, the availability of allochthonous resources is not necessarily important for arthropod food webs in the vicinity of ecosystem borders. However, some predators specialize on prey depending on marine allochthonous resources.

Dietary mixing and food quality have become major issues in foraging theory. Both prey availability and prey quality play an important role in growth and reproduction of generalist predators. In general, food mixing is beneficial for predators, since it may optimise nutrient uptake and dilute toxins. The springtail *Folsomia candida* has been used in many laboratory experiments and was proven toxic for various predators. In contrast, *Drosophila melanogaster* and *Heteromurus nitidus* (Collembola) are considered to be intermediate to high quality prey. Performance and reproduction of female *Pardosa lugubris* (Lycosidae) fed with prey of different quality were investigated. Spiders were fed either a single diet of *D. melanogaster*, *H. nitidus* or *F. candida*, or a mixed diet of *D. melanogaster* and *H. nitidus*, or of *D. melanogaster* and *F. candida*.

Feeding on high quality prey (*D. melanogaster* only, *H. nitidus* only and both combined) resulted in similar growth and reproduction of female *P. lugubris* as well as in similar offspring number, size and survival. There was no positive effect of mixing high quality prey. In contrast, feeding on toxic prey (*F. candida*) in single and mixed diet was detrimental and none of the females survived. *P. lugubris* did not develop acquired aversion against *F. candida* and offering high quality prey (*D. melanogaster*) mixed with *F. candida* did not improve survival.

Nutrient flow from females into offspring during egg production was investigated using stable isotope analysis. *D. melanogaster* was enriched in ^{13}C and this allowed tracing the carbon flow from prey into females and into their offspring. Furthermore, both *D. melanogaster* and *H. nitidus* were enriched in ^{15}N compared to female spiders so that nitrogen flow from prey into offspring could be followed. The enrichment in ^{13}C and ^{15}N differed strongly between juveniles and their mothers. The analyses suggest that adult females invested dietary nutrients almost exclusively into egg production.

Mortality of juvenile *Pardosa palustris* (Lycosidae) is high on xeric grasslands near Darmstadt likely resulting from predation by conspecifics (cannibalism) or other predators (intraguild predation). Cannibalism is common among spiders and likely is a major mortality factor for juvenile wolf spiders in the field. Potential driving factors for intraspecific predation in *P. palustris* were investigated conducting two laboratory experiments to evaluate the role of availability of alternative prey, habitat structure and spider density for cannibalism between and within developmental stages.

Availability of alternative insect prey strongly reduced cannibalism between adult spiders and juveniles as well as among juveniles. For juvenile spiders habitat complexity reduced predation by adult females, whereas cannibalism among second instar spiderlings was not affected by habitat structure suggesting that complex habitat structure only provides shelter from cannibalism by large conspecifics. High density of juvenile spiders increased cannibalism only when alternative prey was available, suggesting that alternative prey increased aggression and interference at higher density. High mortality and low growth of spiders in treatments without alternative prey likely resulted from starvation indicating that intraspecific prey is of low food quality and does not allow spider development.

Intraguild predation is also common among generalist predators and an important issue for food web theory. Juveniles of *Alopecosa cuneata* (Lycosidae) are likely to be successful intraguild predators of the smaller *P. palustris*, adding to juvenile mortality on xeric grasslands near Darmstadt. Intraguild predation of third instar *A. cuneata* on second instar *P. palustris* was investigated in a laboratory experiment manipulating availability of alternative prey and microhabitat complexity.

Both, the presence of alternative prey and complex microhabitat structure reduced mortality of juvenile *P. palustris* during the first week. During the second week, mortality increased in complex structure without alternative prey presumably due to enhanced activity of starving *P. palustris* and cannibalism among second instar juveniles. Stable isotope analysis documented predation of *A. cuneata* on *P. palustris* and predation on alternative prey by both juveniles. Thus, using stable isotope analysis intraguild predation among arthropod predators was documented for the first time under semi-natural conditions in the laboratory. In conclusion, intraguild predation can be an important mortality factor for juvenile wolf spiders in the field, if resources are limited and shelter by a complex structured microhabitat is missing.

Since shelter is abundant on xeric grasslands near Darmstadt, intraguild predation by *A. cuneata* can be excluded as an important mortality factor for juvenile *P. palustris* in the field suggesting that rather cannibalism and/or intraguild predation by other spider species of similar size cause substantial mortality in *P. palustris*.

Results of this study document the importance of prey availability, food quality and habitat heterogeneity for wolf spider populations. Cannibalism and intraguild predation among wolf spiders depended on the availability of alternative prey and microhabitat structure and may be major factors regulating spider populations. When juveniles hatch in close proximity, cannibalism and intraguild predation can contribute to population regulation by imposing greater per capita mortality at high densities. Furthermore, cannibalism and intraguild predation increase population synchrony by exerting size-specific mortality on smaller individuals throughout development.

Zusammenfassung

Ziel dieser Arbeit war es, Regulationsmechanismen von Populationen von Wolfspinnen herauszuarbeiten. Experimente im Freiland und Labor fokussierten auf Beuteverfügbarkeit (autochthon und allochthon), Nahrungsqualität und Habitatheterogenität als wichtigste Faktoren für einzelne Spinnen oder Populationen und deren Einfluss auf intra- (Kannibalismus) und interspezifische Beziehungen (Intragilde-Prädation) von Wolfspinnen.

Populationen von Wolfspinnen auf Sandtrockenrasen bei Darmstadt (Deutschland) weisen auf beweideten Flächen größere Dichten auf, als auf Flächen ohne Schafbeweidung. Da potenzielle Beute auf den beweideten Flächen ebenfalls höhere Dichten erreicht, wurde die Hypothese abgeleitet, dass Spinnen bottom-up kontrolliert sind. Um dies zu untersuchen, wurde im Freiland auf abgegrenzten beweideten und nicht beweideten Flächen alternative Beute (*Drosophila melanogaster*; Diptera) ausgebracht. Abundanzen von Spinnen und deren potenzieller Beute (Detritivore und Herbivore) wurden zwischen Flächen mit und ohne Beutezugabe verglichen. Um die Integration von *D. melanogaster* in das Arthropoden-Nahrungsnetz nachzuweisen, wurden die stabilen Isotope der häufigsten Konsumenten analysiert.

D. melanogaster war Bestandteil in der Nahrung der meisten Prädatoren, wie die Analyse der stabilen Isotope belegte. Allerdings wurden weder Spinnen- noch Laufkäferdichten durch die Zugabe alternativer Beute erhöht. Auch die Dichten ihrer potenziellen Beute (Collembolen und Zikaden) wurden durch Zugabe alternativer Beute nicht beeinflusst. Dies weist darauf hin, dass die Beutepopulationen nicht von den Räuberpopulationen kontrolliert wurden. Die Analyse der stabilen Isotope zeigte, dass Spinnen und Laufkäfer sich vorwiegend aus dem Zersetzersystem ernähren. Da sowohl Springschwänze als auch Spinnen auf den beweideten Flächen am häufigsten waren, liegt der Schluss nahe, das Wolfspinnen bottom-up kontrolliert sind und in ihrer Dichten auf die erhöhte Verfügbarkeit von Beute aus dem Zersetzersystem auf den beweideten Flächen reagiert haben. Womöglich reichte die Menge der zugegebenen alternativen Beute nicht aus, um die Dichten der Räuber darüber hinaus signifikant zu beeinflussen.

Neben autochthonen spielen allochthone Ressourcen eine zentrale Rolle in Nahrungsnetzen. Wolfspinnenpopulationen hängen häufig vom Zersetzersystem ab (siehe oben), aber auch andere allochthone Ressourcen können von Bedeutung sein. Ökosysteme an Küsten erhalten oft einen hohen Eintrag an Ressourcen aus dem marinen Ökosystem, wovon terrestrische

Prädatoren profitieren. Tang und Seegras werden häufig an Sandstränden der Ostküste Tasmaniens angespült und liefern die Nahrungsgrundlage für Beute von vaganten Räubern auf dem Strand und den Vordünen. Ich untersuchte die Hypothese, dass terrestrische Arthropoden von diesem Ressourcenangebot profitieren. Tiere vom Strand und der Vordüne wurden gefangen und die häufigsten Taxa wurden zur Analyse der stabilen Isotope ausgewählt, um den Anteil der marinen Ressource an der Nahrung der Tiere zu untersuchen. Anhand der Aktivitätsdichten der Arthropoden konnten zwei in sich geschlossene Lebensgemeinschaften auf dem Strand und auf der Vordüne abgebildet werden; nur wenige Arten kamen sowohl auf dem Strand, als auch auf der Vordüne vor. Die Analyse stabiler Isotope zeigte, dass die häufigsten Arten, Amphipoden und Isopoden, den angeschwemmten Tang als Nahrungsressource nutzten. Allerdings existierten nur wenige Räuber, wie *Tetralycosa oraria* (Lycosidae), *Cafius* 2 (Staphylinidae) und *Tuoba laticeps* (Geophilomorpha), die diese Arthropoden erbeuteten. Die Analyse der stabilen Isotope verdeutlichte Nahrungspräferenzen dieser Räuber und zeigte insgesamt, dass der Eintrag mariner Ressourcen auf dem Strand für das Nahrungsnetz der Vordüne keine Rolle spielt. So beeinflusst die Verfügbarkeit von allochthonen Ressourcen nicht zwangsläufig Nahrungsnetze an der Grenze zweier Ökosysteme.

Nahrungsqualität und Mischkost sind entscheidend für Theorien über Nahrungswahl und -suche. Sowohl Beuteverfügbarkeit als auch Qualität der Beute spielen eine große Rolle für das Wachstum und die Reproduktion von generalistischen Prädatoren. Im Allgemeinen wirkt sich das Mischen verschiedener Beute positiv auf Räuber aus, da die Aufnahme von Nährstoffen optimiert wird und es zur Verdünnung von Toxinen kommt. Der Collembole *Folsomia candida* wird in vielen Labor-Experimenten als Beute eingesetzt und hat sich dabei als toxisch für verschiedene Räuber erwiesen. Im Gegensatz dazu sind *Drosophila melanogaster* und *Heteromurus nitidus* (Collembola) Beute von mittlerer bis hoher Qualität. Überleben und Reproduktion von Weibchen der Wolfspinne *Pardosa lugubris* (Lycosidae) bei Fütterung mit Beute verschiedener Qualität wurde im Labor untersucht. Den Spinnen wurde entweder Einzelkost von *D. melanogaster*, *H. nitidus* bzw. *F. candida*, oder Mischkost von *D. melanogaster* und *H. nitidus*, bzw. von *D. melanogaster* und *F. candida* angeboten.
Wachstum und Reproduktion (Anzahl und Größe der Juvenilen) sowie Überleben der Juvenilen waren bei Spinnen, die hoch qualitative Beute fraßen (Einzelkost *D. melanogaster* bzw. *H. nitidus* und deren Mischkost), einheitlich. Folglich gab es keinen positiven Effekt der Mischkost bei hoch qualitativer Beute. Toxische Beute (*F. candida*) führte in Einzel- und

Mischkost letztendlich zum Tod der Spinnen. *P. lugubris* entwickelte keine Aversion gegen *F. candida* und auch das Anbieten von zusätzlicher hoch qualitativer Beute in der Mischkost verbesserte das Überleben der Spinnen nicht.

Der Nährstofffluss von Weibchen zu den Nachkommen während der Eiproduktion wurde mit Hilfe von stabilen Isotopen untersucht. *D. melanogaster* war ^{13}C angereichert, was das Verfolgen des Kohlenstoffflusses aus der Beute in die Weibchen und deren Nachkommen ermöglichte. Außerdem waren sowohl *D. melanogaster* als auch *H. nitidus* ^{15}N angereichert im Vergleich zu den Weibchen, so dass der Stickstofffluss von der Beute in die Nachkommen ebenfalls verfolgt werden konnte. Die Anreicherung von ^{13}C und ^{15}N unterschied sich deutlich zwischen Juvenilen und Müttern. Die Analysen deuten darauf hin, dass adulte Weibchen Nährstoffe aus der aufgenommenen Nahrung fast ausschließlich in die Produktion von Eiern investieren.

Die Mortalität von juvenilen *Pardosa palustris* (Lycosidae) auf Sandtrockenrasen bei Darmstadt ist hoch und wird wahrscheinlich von Prädation von Artgenossen (Kannibalismus) oder anderen Räubern (Intragilde-Prädation) verursacht. Kannibalismus ist ein häufiges Phänomen bei Spinnen und wahrscheinlich ein bedeutender Mortalitätsfaktor für juvenile Wolfspinnen im Freiland. Faktoren, die das Auftreten von Kannibalismus beeinflussen, wurden in zwei Labor-Experimenten untersucht. Dabei wurde die Auswirkung von Beuteverfügbarkeit, Habitatstruktur und Spinnendichte auf Kannibalismus zwischen Juvenilen bzw. zwischen juvenilen und adulten Spinnen überprüft.

Die Verfügbarkeit von alternativer Beute verringerte Kannibalismus zwischen adulten und juvenilen Spinnen sowie zwischen Juvenilen deutlich. Komplexe Habitatstruktur reduzierte lediglich Prädation von adulten an juvenilen Spinnen; Kannibalismus zwischen Juvenilen blieb aber von der Struktur des Habitats unbeeinflusst. Diese Ergebnisse deuten darauf hin, dass komplexe Habitatstruktur nur gegenüber deutlich größeren Prädatoren als Refugium dient. Die hohe Dichte juveniler Spinnen erhöhte Kannibalismus nur, wenn alternative Beute verfügbar war, was nahe legt, dass alternative Beute Aggression und Interferenz bei hohen Dichten bedingt. Insgesamt beruhten die hohe Mortalität und das geringe Wachstum von Spinnen in Behandlungen ohne alternative Beute wahrscheinlich auf Verhungern der Tiere, was darauf hindeutet, dass intraspezifische Beute lediglich von geringer Nahrungsqualität ist und eine Entwicklung der Spinnen nicht zulässt.

Intragilde-Prädation ist ebenfalls häufig bei generalistischen Prädatoren und wichtig für Theorien über Nahrungsnetze. Juvenile *Alopecosa cuneata* (Lycosidae) sind wahrscheinlich erfolgreiche Intragilde-Prädatoren von den kleineren *P. palustris* und tragen somit zur Mortalität dieser Juvenilen im Freiland bei. Deshalb wurde Intragilde-Prädation von juvenilen *A. cuneata* (3. Entwicklungsstadium) an juvenilen *P. palustris* (2. Stadium) im Labor untersucht, wobei die Verfügbarkeit alternativer Beute und Habitatstruktur manipuliert wurden.

Sowohl die Verfügbarkeit alternativer Beute als auch die komplexe Habitatstruktur verringerten die Mortalität juveniler *P. palustris* während der ersten Woche. Während der zweiten Woche stieg die Mortalität in der komplexen Struktur ohne alternative Beute an. Vermutlich ist dies auf erhöhte Aktivität der hungernden Tiere und Kannibalismus zwischen den juvenilen *P. palustris* zurückzuführen. Die Analyse stabiler Isotope belegte Prädation von *A. cuneata* an *P. palustris* und die Prädation beider Spinnen an alternativer Beute. So konnte mit Hilfe der Analyse stabiler Isotope Intragilde-Prädation zum ersten Mal unter naturähnlichen Verhältnissen im Labor dokumentiert werden. Aus diesen Ergebnissen folgt, dass Intragilde-Prädation ein wichtiger Mortalitätsfaktor für juvenile Spinnen im Freiland sein kann, wenn Ressourcen limitiert sind und Refugien fehlen. Allerdings ist die Vegetationsstruktur auf den Sandtrockenrasen bei Darmstadt sehr komplex und liefert somit vermutlich ausreichend Refugialraum. Deshalb kann Intragilde-Prädation von *A. cuneata* an *P. palustris* als wichtiger Mortalitätsfaktor ausgeschlossen werden. Wichtiger sind wahrscheinlich Kannibalismus und/ oder Intragilde-Prädation von anderen Spinnenarten von vergleichbarer Größe.

Die Ergebnisse dieser Arbeit belegen die Bedeutung von Beuteverfügbarkeit, Nahrungsqualität und Habitatstruktur für Populationen von Wolfspinnen. Kannibalismus und Intragilde-Prädation zwischen Wolfspinnen hingen von der Verfügbarkeit alternativer Beute und Habitatkomplexität ab; sie sind zentrale Faktoren für die Regulation von Spinnenpopulationen. Wenn juvenile Wolfspinnen in enger räumlicher Nähe schlüpfen, können sowohl Kannibalismus als auch Intragilde-Prädation zur Regulation der Populationen beitragen, da bei hohen Dichten die Mortalität erhöht ist. Außerdem wird durch Kannibalismus und Intragilde-Prädation eine Synchronität der Population erreicht, da beide Prozesse eine größen-spezifische Mortalität verursachen, wobei vor allem kleinere Individuen betroffen sind.

I Introduction

I.1 Ecology of Spiders

Spiders compromise over 34,000 species (FOELIX 1996) and are among the most abundant macroinvertebrate predators in terrestrial ecosystems, which is why they are proposed to be model organisms for predators (WISE 1993). Most spiders live a solitary life, but intriguing details about socially living spiders such as *Agelena consociata* (Agelenidae) and spiders of the genus *Stegodyphys* (Eresidae) have been documented (RIECHERT et al. 1986; SALOMON et al. 2005). Spiders show different types of brood care ranging from the mere choice of oviposition sites to very sophisticated female behavior. Many females hide their eggsacs under stones (Gnaphosidae) or make camouflaged eggsacs suspended in vegetation (*Agroeca*, Clubionidae) and many females guard their eggsacs until hatching (e.g. Pisauridae) (BRISTOWE 1958). Wolf spiders (Lycosidae) attach their eggsacs to their spinnerets and actively choose sites with favourable microclimatic conditions for egg development. When eggs have developed into second instar spiderlings, females open the eggsac and juveniles are carried on the female's opisthosoma for a couple of days until spiderlings finally disperse (BRISTOWE 1958). *Theridion notatum* (Theridiidae) and some spiders of the genus *Stegodyphus* (Eresidae) feed hatched juveniles by regurgitating pre-digested food (FOELIX 1996) and matriphagy by juvenile *Amaurobius* (Amaurobiidae) is an extreme form of brood care found in spiders (BRISTOWE 1958).

Spiders are largely regarded as generalist invertebrate predators with limited dietary specialisation (WISE 1993) and only few spiders are known to prey on vertebrates (frogs: FORMANOWICZ et al. 1981; skinks: RUBBO et al. 2001; salamanders: RUBBO et al. 2003). The specialisation found in bolas spiders in South America that attract male moths mimicking moth pheromones (WISE 1993) is a famous exception to that rule. Yet, several studies document that spiders in general might be choosier concerning prey than assumed: Some spiders develop a search image for a specific prey type (JACKSON & LI 2004) and show the highest growth efficiency when fed their preferred prey (LI & JACKSON 1997), indicating adaptation to a certain prey type. Additionally, some spiders even feed on nectaries, supplementing their diet with a plant derived nitrogen source (TAYLOR & FOSTER 1996; RUHREN & HANDEL 1999; JACKSON et al. 2001). Furthermore, spiders can forage selectively for protein and lipids to redress specific nutritional imbalances (MAYNTZ et al. 2005).

Several types of foraging exist in spiders and the most obvious distinction is between web-builders and cursorial spiders hunting without a web (UETZ 1992; WISE 1993; NYFFELER et al. 1994). While web-builders rely almost exclusively on insects as prey, cursorial spiders additionally include other spiders into their diet (NYFFELER 1999). However, cursorial spiders also differ strongly in their foraging mode, as some employ a sit-and-wait strategy (e.g. most Thomisidae), while others actively hunt down their prey (e.g. most Salticidae) (WISE 1993). Wolf spiders are visually orienting predators that detect their prey by movement and vibrations (UETZ 1992; SAMU 1993; PERSONS & UETZ 1998) ranging from sit-and-wait predators that ambush prey (Lycosidae: *Hogna helluo*) to more active predators that hunt down their prey (Lycosidae: *Pardosa milvina*) (MARSHALL et al. 2002). Diptera, Hemiptera, Collembola, and Araneae represent the major groups in wolf spider diet (NYFFELER & BENZ 1988).

Most spiders use silk and/or venom to immobilize their prey and digest their prey extra intestinally (FOELIX 1996), which is why gut dissection of spiders cannot reveal the identity of the prey they were feeding on. Wolf spiders additionally masticate their prey (NYFFELER & BENZ 1988), so that remaining prey material is not recognizable. Consequently, data on prey of wolf spiders in the field is very limited and mostly relies on direct observation (EDGAR 1969; HALLANDER 1970; NYFFELER & BENZ 1988). Stable isotope analysis proved powerful in determining the trophic position of animals (PETERSON & FRY 1987; POST 2002), but the detection of direct feeding links in generalist predators is highly exceptional. Only recently matters seem to improve due to the progress in DNA based molecular gut analysis (SYMONDSON 2002; AGUSTI et al. 2003), that directly assesses the consumption of specific prey organisms in the field. Detailed knowledge about prey preference and diet breadth of spiders is crucial for the interpretation of diversity and density of spiders as well as for understanding the impact of spiders on prey populations and for determining their role in food webs.

I.2 Generalist Predators & Biological Control

For a long time it has been a matter of debate whether natural ecosystems are predominately top-down (e.g. Hairston et al. 1960) or bottom-up controlled (e.g. White 1978). In top-down controlled systems, predator populations limit herbivore populations and lessen the impact of herbivores on plants, while in bottom-up controlled systems, resource availability limits herbivore populations and thereby also predator populations. Over the last decade both theories have been integrated into food web theory realizing that both mechanisms can act simultaneously (Polis & Winemiller 1996; Chase 1996; Moran & Scheidler 2002). Consequently, predator-prey relationships are important ecosystem processes, while not only the act of predation itself is important for predator-prey interactions. Already the risk of predation (e.g. predator presence) affects behaviour and performance of prey organisms due to changes in habitat use, activity, foraging behaviour and group dynamics (Sih 1980; Lima & Dill 1990; Abrams & Schmitz 1997; Heithaus 2001; Relyea 2003). Chemical cues of wolf spiders decrease herbivory of beetle pests (Hlivko & Rypstra 2003) documenting that predators don’t even have to be present to affect prey organisms. Since animals in natural ecosystems face more than one predator (Sih et al. 1998; Sokol-Hessner & Schmitz 2002) prey organisms have to take complex behavioral decisions evaluating the importance of each risk (Sih 1992; Krupa & Sih 1998). Largely, species within the same trophic level in a food web have been assigned to one feeding guild studying the impact of predators on prey populations. However, animals within one feeding guild may exert species specific different direct and indirect effects (e.g. trait- or density-mediated) on species of lower trophic levels (Schmitz & Suttle 2001; Schmitz et al. 2004) emphasizing that investigations of predator-prey relationships need to be resolved to species level.

Generalist predators receive more and more attention in biological control as natural enemies of crop pests (Symondson et al. 2002). Increasing concern about contaminated food due to the broad use of pesticides in agriculture led to the development of organic farming and the use of natural enemies in pest control. Natural enemies may increase plant productivity and/or decrease plant damage by herbivores via trophic cascades. If predators limit densities of herbivores, plants indirectly benefit from predator presence (Fig. 2.1).

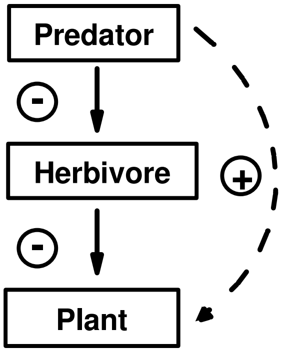

Fig. 2.1: Trophic cascade including three functional levels. Indirect interactions are indicated with hatched arrows. -: negative impact; +: positive impact.

Theoretically, biocontrol agents should be rather specialized on the target species (e.g. parasitoids) with short generation times to cause substantial mortality of the pest species within a short time (DEBACH & ROSEN 1991). Generalist predators, in contrast, have rather long generation times and do not achieve tight dynamical linkage with any single pest species due to prey switching (DEBACH & ROSEN 1991; ROSENHEIM et al. 1995). Consequently, the use of generalist feeders, like spiders and ground beetles, remained neglected for a long time despite of their high abundances in agricultural fields and natural ecosystems. Yet, they may indeed control herbivore populations in agricultural (RIECHERT & BISHOP 1990; CARTER & RYPSTRA 1995; LANG et al. 1999; SNYDER & WISE 2001; LANG 2003) and natural systems (FAGAN & HURD 1994; MORAN et al. 1996; SCHMITZ et al. 2000; HALAJ & WISE 2001; DENNO et al. 2003).

Wolf spiders are important generalist predators in both agricultural and natural systems that are known to limit the abundance of herbivores and detritivores (RIECHERT & BISHOP 1990; SNYDER & WISE 1999; CHEN & WISE 1999; WISE 2004) thereby influencing plant performance and decomposition processes (KAJAK 1995). Furthermore, an assembly of predators may control herbivore populations even better than a single species (LOSEY & DENNO 1998; RIECHERT et al. 1999; CARDINALE et al. 2003; SNYDER & IVES 2003).

However, the model of three trophic levels including generalist predators does not apply exclusively (POLIS et al. 2000; SCHMITZ et al. 2000), since positive top-down effects on herbivore pests may be restricted by intraguild predation (IGP) and cannibalism (ROSENHEIM et al 1993; SNYDER & IVES 2001; SNYDER & WISE 2001; DENNO et al. 2004; PRASAD & SNYDER 2004), and the effects of alternative prey on biocontrol are controversial (SETTLE et al. 1996; HARMON & ANDOW 2004; MADSEN et al. 2004; KOSS & SNYDER 2005).

Foraging behavior and ecology of both the predator and the prey are the major keys to understand the occurrence of trophic cascades (ROSENHEIM & CORBETT 2003; ROSENHEIM et al. 2004). If for example the herbivore is rather sedentary, its populations are unlikely to be controlled by predators with a sit-and-wait foraging mode. Rather, these predators may prey on the actively hunting intermediate predators, which could control herbivore populations.

In conclusion, generalist predators including wolf spiders play an important role in food webs (SCHEU 2001) and are promising agents for biological control (NYFFELER & BENZ 1987; GREENSTONE 1999; HODGE 1999; RIECHERT 1999), if foraging behavior and relation to other species in higher/lower trophic levels are considered. Consequently, phenology and factors influencing population size and structure of these predators need to be understood in detail.

I.3 Phenology & Regulatory Mechanisms of Spider Populations

Populations of spiders, and animals in general, are affected by abiotic (e.g. humidity, temperature, habitat structure) and biotic factors (e.g. resource availability and quality, competition/ interference) resulting in species specific distribution and phenology of animals.

Temperature is one of the most important abiotic factors for spiders (DONDALE & BINNS 1977) influencing reproduction, juvenile survival and development, and determining body size of adults (LI & JACKSON 1996; LI 1998; THORBEK et al. 2003). Spiders are very sensitive to desiccation (FOELIX 1996; DEVITO & FORMANOWICZ 2003) and web-site selection can depend on humidity, too (GILLESPIE 1987; SAMU et al. 1996).

Since microclimate is often closely related to microhabitat (BOSSENBROEK et al. 1977b; WORKMAN 1978; CADY 1984), density and diversity of spiders is also related to habitat structure (UETZ 1991; BALFOUR & RYPSTRA 1998; MARSHALL & RYPSTRA 1999; WAGNER et al. 2003). Vegetation structure is important for web-building (reviewed in RIECHERT & GILLESPIE 1986), sexual signalling (UETZ & STRATTON 1982; KOTIAHO et al. 2000), oviposition (DUFFEY 1962) and overwintering (BOESSENBROEK et al. 1977a; BAYRAM & LUFF 1993). Furthermore, spiders find refuge from predators in spatially complex habitats (GUNNARSSON 1996); however, habitat selection in general is also affected by additional biotic and abiotic factors (HAMPTON 2004). Spiders and their ability to control herbivores in arable fields benefit from the selection of appropriate farming practices, such as organic farming, intercropped polycultures and mulching due to the diversification of the habitat (FEBER et al. 1998; RYPSTRA et al. 1999; SAMU et al. 1999). Despite its apparent importance, effects of microhabitat structure on strong biotic interactions, such as cannibalism and IGP among spiders, have been largely neglected.

The availability of autochthonous and allochthonous resources is a major biotic regulatory factor influencing performance of individual spiders and spider populations. Starvation is proposed to be common for spiders in the field (reviewed in WISE 1993) and spiders have evolved several behavioral and physiological adaptations to deal with long periods of food shortage (ANDERSON 1974; COLLATZ & MOMMSEN 1975; NAKAMURA 1987). Emigration rate and web-replacement strongly depend on resource availability and patch quality (SHEAR 1986; WEYMAN & JEPSON 1994; WAGNER & WISE 1997; SCHMALHOFER 2001), as hunger may enhance locomotory activity of spiders (WALKER et al. 1999; KREITER & WISE 2001). Predator foraging and microhabitat selection also respond to changes in prey behaviour and morphology (LIMA 2002). Wolf spiders assess patch quality and patch residence primarily on present sensory (visual) information delivered by prey organisms (PERSONS & UETZ 1998), even though also chemical cues left behind from prey seem to be important (PERSONS & RYPSTRA 2000; HOEFLER et al. 2002). Furthermore, resource availability during juvenile development affects body size at maturity (UETZ 1992), mating success (UETZ et al. 2002; MOYA-LARAÑO et al. 2003a), and foraging behavior of adults (MOYA-LARAÑO et al. 2003b). Reproduction in spiders is also coupled with prey availability (KESSLER 1971; KREITER & WISE 2001) and quality (BILDE & TOFT 2001), allowing a numerical response to prey abundance, which is important in biological control of crop pests, if spiders are given a “head start” through alternative or allochthonous resources (GUO et al. 1995; SETTLE et al. 1996). Apart from resource availability also prey quality is important for predators since many phytophagous insects accumulate toxins affecting predator performance (KEITH & BROWN 1984; PARADISE & STAMP 1990; STROHMEYER et al. 1998), and thus prey organisms differ strongly in their quality for predators.

Finally, spiders are not only predators, but also prey (HURD & EISENBERG 1990; WISE & CHEN 1999; LANG 2003) and nitrogen deprivation at higher trophic levels may favour intraguild predation (DENNO & FAGAN 2003). Spiders represent 24 % of the prey of *Pardosa lugubris* (EDGAR 1969), 34 % and 38 % of the prey of *P. chelata* and *P. pullata*, respectively (HALLANDER 1970). Accordingly, spiders exhibit different types of anti-predator behaviour as they may emigrate from patches with high predator load (MORAN et al. 1996; BALDRIDGE & MORAN 2001), reduce activity and foraging in response to the presence of a top predator (PERSONS et al. 2001; OKUYAMA 2002; LEHMANN et al. 2004; WILDER & RYPSTRA 2004), or change temporal and spatial use of the habitat (BALDRIDGE & MORAN 2001). Interestingly, chemical cues from predators may even influence the incubation time of spider eggs (LI & JACKSON 2005). Consequently, cannibalism and IGP may be important population structuring factors in the field (WISE, in review), reducing competition and/or providing additional food resources.

The following field and laboratory experiments focus on the question how resource availability (CHAPTERS I.3.2, I.3.3; I.3.5 & I.3.6), food quality (CHAPTER I.3.4), cannibalism (CHAPTER I.3.5), IGP (CHAPTER I.3.6), and microhabitat structure affect (CHAPTERS I.3.5 & I.3.6) spider populations and/or individuals.

I.3.1 Phenology

Investigating the influence of sheep grazing and the invasion of the Bermuda grass (*Cynodon dactylon*; Poaceae) on predatory arthropods on sand dry grasslands near Darmstadt, the spider community was analysed (RICKERS 2002). Wolf spiders were the most abundant cursorial predators and comprised ten different species. The most abundant species, *Alopecosa cuneata* and *Pardosa palustris*, reached densities of four and six adults per square meter, respectively, during May, when densities were highest (RICKERS 2002). I was interested to know whether development and reproduction time of these wolf spiders differed in the field to get an idea about how these two species coexist. Therefore, spiders were sampled monthly with pitfall traps in order to gain data on the phenology of both spider species. Detailed phenological data is essential for the interpretation of population density and dispersal in the field and invaluable for the design of field and laboratory experiments dealing with the regulation of spider populations.

I.3.2 Prey Availability

One of the major issues in food web ecology is whether natural ecosystems are predominately top-down (e.g. HAIRSTON et al. 1960) or bottom-up controlled (e.g. WHITE 1978). Eventually, both theories have been integrated into food web theory as both mechanisms may act simultaneously (POLIS & WINEMILLER 1996; CHASE 1996; MORAN & SCHEIDLER 2002). The importance of top-down control via trophic cascades in the field is investigated by manipulating predator density (HURD & EISENBERG 1990; HALAJ & WISE 2001; DENNO et al. 2002; PREISSER 2003), prey density (MORAN & HURD 1997; MIYASHITA et al. 2003), abiotic conditions (CHASE 1996; BOYER et al. 2003) or a combination of these factors (OVADIA & SCHMITZ 2004).

Spiders and ground beetles often encounter periods of food shortage in the field (Araneae: reviewed in WISE 1993; Carabidae: JULIANO 1986; BILDE & TOFT 1998) and reproduction of spiders and beetles is strongly depending on resource availability and quality (BILDE & TOFT 1994; BILDE et al. 2000; KREITER & WISE 2001; MAYNTZ et al. 2003; CHAPTER I.3.4). Furthermore, cannibalism (WAGNER & WISE 1996; CHAPTER I.3.5) and intraguild predation (MEYHÖFER & HINDAYAMA 2000; CHAPTER I.3.6) decrease in presence of alternative prey. Consequently, top-down or bottom-up control of communities with high abundances of spiders and ground beetles may be investigated with prey addition experiments, since alternative prey may relax predation pressure within the guild of predators and on prey populations.

Predatory arthropods, such as wolf spiders (Lycosidae) and ground beetles (Carabidae) on grasslands near Darmstadt benefit from sheep grazing (RICKERS 2002). In general, effects of grazing on arthropods are controversial. Trampling and enhanced exposure to natural enemies due to grazing may increase mortality of arthropods (EAST & POTTINGER 1975, 1983). Grazing also alters plant diversity and vegetation structure affecting insect herbivore populations (MORRIS 1967; HUNTLY 1991; TSCHARNTKE & GREILER 1995; KRUESS & TSCHARNTKE 2002). Consequently, availability of insect prey may be reduced due to grazing, affecting predator populations (DENNIS et al. 1998). In general, densities of spiders and ground beetles are often negatively affected by grazing (GIBSON et al. 1992; RUSHTON & EYRE 1992; DENNIS et al. 1997; GARDNER et al. 1997; DENNIS et al. 2001), since habitat structure creates optimal microclimatic and foraging conditions for spiders and beetles (UETZ 1991; WEEKS & HOLTZER 2000; BROSE 2003). However, the impact of grazing on arthropods differs between grazers and grazing intensity (DENNIS et al. 1998; MORRIS 2000) and certain species may even benefit from extensive grazing (EAST & POTTINGER 1983; TSCHARNTKE & GREILER 1995; KRUESS & TSCHARNTKE 2002).

Potential prey for generalist predators, such as Collembola and insect herbivores, is more abundant on grazed sites of the above mentioned grasslands (RICKERS 2002; WALLUS 2002). Since both, wolf spiders and ground beetles reached higher densities on grazed sites, I hypothesised that populations of spiders and beetles were bottom-up controlled. To test this hypothesis, I established fenced plots with and without prey addition in the field. Vestigal winged mutants of *Drosophila melanogaster* (Diptera) that are of intermediate to high quality for spiders and beetles (BILDE et al. 2000; MAYNTZ & TOFT 2001), were used as additional prey. Arthropods were sampled twice to evaluate reproduction and development of wolf spiders. In order to detect changes in food web structure stable isotope signatures of predators and prey were analysed. Stable nitrogen ($^{15}N/^{14}N$) and carbon ($^{13}C/^{12}C$) ratios reflect trophic position and food resource of animals due to differential fractionation processes in consumers (PETERSON & FRY 1987; POST 2002; MCCUTCHAN et al. 2003).

I.3.3 Allochthonous Resources

Resource availability is regarded as one of the major factors affecting animal abundance and distribution (WHITE 1978; HUNTER & PRICE 1992; see CHAPTER I.3.2) and the transfer of energy between ecosystems is an important feature of food webs (POLIS & WINEMILLER 1996; POLIS et al. 1997a; STAPP et al. 1999) influencing food web stability (HUXEL & MCCANN 1998; HUXEL et al. 2002). Cross-habitat transport of allochthonous resources has been documented crucial for vertebrates (ROSE & POLIS 1998; MARKWELL & DAUGHERTY 2002; CARLTON & HODDER 2003; STAPP & POLIS 2003a), arthropods (POLIS & HURD 1995; HENSCHEL et al. 2001; BASTOW et al. 2002) and plants (ANDERSON & POLIS 1999). The relative importance of allochthonous input depends on the extent of the productivity of the focal community (POLIS & HURD 1996 a,b; POLIS et al. 1997b; NAKANO & MURAKAMI 2001) and its distance from the source of allochthonous resources (POLIS & HURD 1996b, HENSCHEL et al. 2001; MURAKAMI & NAKANO 2002; STAPP & POLIS 2003b).

Sandy beaches represent the functional link between sea and land, where nutrients are transferred in both directions (SCAPINI 2003). Algae and carrion are washed ashore providing resources for the terrestrial ecosystem (MARSDEN 1991; POLIS & HURD 1995, 1996a; ANDERSON & POLIS 1999). Since sandy beaches generally lack higher plants, i.e. in situ primary production (MCLACHLAN 1990), macro-consumers depend on the input of marine angiosperms and macroalgae (MARSDEN 1991; POLIS & HURD 1995; ADIN & RIERA 2003). Sandy beaches have been differentiated into two to three separate zones, according to the distribution of animals that form discrete communities (DAHL 1952; SALVAT 1964; BROWN 1983). MCLACHLAN & BROWN (1990) suggest that there is a general trend on sandy beaches for insects to become less abundant downshore, while crustaceans become less abundant upshore where the dunes begin that often back sandy beaches. Beaches and dunes form the “littoral active zone“, a system that is linked by sand exchange via wave-action and wind (MCLACHLAN & BROWN 1990). Consequently, animals from the terrestrial food web and from the marine food web overlap in the transitional zone of the beach fostering energy transfer between both food webs.

A mixture of kelp and sea grass is periodically washed ashore at Marion Bay, a beach at the south-east coast of Tasmania (Australia) (personal observation). I hypothesised that the allochthonous input of energy resources on the beach via wrack deposition propagates through the arthropod community onto the adjacent dunes. Stable isotope analysis has proven a powerful tool to investigate allochthonous input into terrestrial (BASTOW et al. 2002; STAPP & POLIS 2003a, b; BARRETT et al. 2005) and marine ecosystems (RUESINK et al. 2003) and was therefore applied to document the importance of kelp deposits for arthropods along a transect from the shoreline to the foredune at Marion Bay. Animals were collected at 5 stations from the shoreline across the foredune to obtain specimen for stable isotope analysis and to determine activity-densities along the transect.

I.3.4 Food Quality

Generalist predators play an important role in food webs as they forage on a broad variety of prey types on different trophic levels (SCHEU 2001). Even though a generalist mode of feeding bears the dilemma that taking decisions slows down speed of hunting and reduces attention to danger (BERNAYS 1999), it may optimise nutrient uptake (i.e. amino and fatty acids) and dilute toxins (GREENSTONE 1979; SLANSKY & RODRIGUEZ 1987). Over the last decades more attention has been drawn to dietary mixing in generalist feeders (TOFT 1999; SINGER & BERNAYS 2003). In general, food mixing was demonstrated to be beneficial for consumers (UETZ et al. 1992; WALLIN et al. 1992; BERNAYS et al. 1994; ACHARYA et al. 2004) and even positive effects of mixing high- and low-quality prey have been documented (TOFT 1995; EVANS et al. 1999; SCHEU & FOLGER 2004; SCHEU & SIMMERLING 2004). Nevertheless, predators should evolve mechanisms to recognize and exclude unfavourable prey from their diet. Even though avoidance of unpalatable prey is regularly reported (PARADISE & STAMP 1993; BILDE & TOFT 1994; MAYNTZ & TOFT 2000), several studies document that invertebrate predators do not necessarily acquire food aversion (TOFT 2000; FISKER & TOFT 2004; STAMP & MEYERHOFER 2004).

In this study I focus on the effect of different prey quality on performance and reproduction of *Pardosa lugubris*, a wolf spider that is common in forests throughout Europe. Female *P. lugubris* produce two eggsacs per year and increase feeding rates prior to eggsac production (EDGAR 1971). It is widely accepted that resource availability influences offspring number in spiders (KESSLER 1971; HEAD 1995). However, only little is known on the effect of food quality on offspring numbers, size and fitness, and how females invest energy into their offspring. To investigate energy flow in gravid females I employed stable isotope analysis of $^{13}C/^{12}C$ and $^{15}N/^{14}N$. This method is widely used in food web studies to detect and describe trophic relationships and metabolic pathways (e.g. PETERSON & FRY 1987). The fruit fly *Drosophila melanogaster* (Diptera: Drosophilidae) has been used in numerous feeding experiments with spiders and is regarded as prey of intermediate quality (MIYASHITA 1968; TOFT 1999; MAYNTZ & TOFT 2001). *D. melanogaster* cultures in our study were reared on resources enriched in ^{13}C in order to trace carbon flow from prey into females and consequently into offspring. Furthermore, two springtail species (Collembola) were selected as prey that are known to differ strongly in food quality for lycosid spiders: *Folsomia candida* (Isotomidae) which is toxic for juvenile *Schizocosa* (TOFT AND WISE 1999a), *P. lugubris* (OELBERMANN & SCHEU 2002a), and *P. prativaga* (FISKER & TOFT 2004) and *Heteromurus nitidus* (Entomobryidae) which is high quality prey for juvenile *P. lugubris* (OELBERMANN &

SCHEU 2002a). Diptera and Collembola form a substantial part of the diet of forest dwelling wolf spiders (EDGAR 1969; CHEN & WISE 1999). Single diets (*D. melanogaster*; *H. nitidus*; *F. candida*) as well as two mixed diets (*D. melanogaster* + *H. nitidus*; *D. melanogaster* + *F. candida*) were established in the laboratory.

I hypothesised that fecundity of female wolf spiders and offspring fitness (number, size, weight, survival) differ with diet quality and that females are able to compensate negative effects of *F. candida* when fed a mixed diet with beneficial prey. Also, I hypothesised that females use most of the nutrients ingested directly for egg production.

I.3.5 Cannibalism

Cannibalism is common in generalist arthropod predators, and this is particularly true for spiders (Riechert & Lockley 1984; Wise 1993). Above all sexual cannibalism has been studied (e.g. Elgar 1992), but several authors stress the importance of cannibalism that is not related to reproduction (e.g. Riechert & Lockley 1984). For wolf spiders of the genera *Schizocosa* (Wagner & Wise 1996) and *Pardosa* (Edgar 1969; Hallander 1970; Yeargan 1975) intraspecific predation has been suggested to be an important mortality factor in the field.

Cannibalism is prevalent when food resources are limited and reduces competition for these resources (Dong & Polis 1992; Wagner & Wise 1996, 1997; Samu et al. 1999). Accordingly, starvation can enhance cannibalism (Polis 1981 for a review; Wagner & Wise 1996, 1997; Samu et al. 1999). Consequently, cannibalistic interactions depend on the availability of food resources and therefore the nutritional condition of predators.

Habitat structure is an important factor for both the distribution of spider populations and the foraging behaviour of individual spiders (Uetz 1991) and appears to affect the intensity of cannibalism (Edgar 1969). Complex habitat structure may reduce interference due to lower encounter rates (Crowley et al. 1987; Thompson 1987; Convey 1988). Hallander (1970) suggested that microhabitat selection reduces cannibalism in lycosid spiders since different stages use different habitats. While Wagner & Wise (1996) could not prove that habitat complexity reduced rates of cannibalism, they confirmed density-dependence of cannibalism in laboratory studies.

Density-dependent cannibalism has also been shown for other taxa (Polis 1988), and field studies indicate that cannibalism among lycosid spiderlings is density-dependent and enhanced at high densities (Oraze & Grigarick 1989; Wise & Wagner 1992).

The foraging behaviour of female lycosid spiders during reproduction has been investigated in detail (Vljim & Richter 1966; Higashi & Rovner 1975; Moring & Stewart 1992; Wagner 1995). However, little is known on cannibalistic interactions between females and juveniles after dispersal of spiderlings and on cannibalism between juvenile stages.

Adult females of *P. palustris* produce on average 30 ± 7 (n = 104) spiderlings during the first reproduction period on xeric grasslands in southern Germany, yet, only 6 individuals per m² reach adulthood suggesting high mortality of spiderlings. I was interested to know whether or not cannibalism could be a significant factor contributing to the mortality observed in the field. Therefore, I set up two laboratory experiments to evaluate factors influencing cannibalism between and among developmental stages of *P. palustris*. I expected decreased spider mortality with availability of alternative prey and complex habitat structure, and increased mortality at high density of individuals. Thus, in a first experiment I investigated, if cannibalism between juveniles of the same developmental stage is affected by starvation, habitat structure and/or density. In a second experiment I tested whether starved females that had previously produced offspring prey upon second instar juveniles. Since females were not related to juveniles and off-spring dispersal had taken place four weeks previously, I expected high rates of filial cannibalism even if alternative prey was present.

I.3.6 Intra Guild Predation (IGP)

Intraguild predation (IGP) is common in food webs and predatory species often coexist in stable natural communities (POLIS & MCCORMICK 1986; ARIM & MARQUET 2004) despite of theoretically destabilising effects of strong IGP on communities due to species exclusion (HOLT & POLIS 1997; MCCANN & HASTINGS 1997; MCCANN et al. 1998). Age-/stage-restricted predation, interactions with other species, and spatial heterogeneity are promising mechanisms favouring the coexistence of predator species (HOLT & POLIS 1997). The vulnerability to predation can change during development of animals due to size-refugia (CHASE 1999) which is why IGP is often restricted to particular ages or stages (EBENMAN & PEARSON 1988; WISSINGER 1992). Since IGP systems are part of complex food webs, the tritrophic cascades are linked to other species, fostering the existence of IG prey populations through alternative resources (HOLT & POLIS 1997). Cannibalism being a special case of IGP is strongly reduced when alternative prey is available (DONG & POLIS 1992; WAGNER & WISE 1996, 1997; CHAPTER I.3.5). Accordingly, IGP decreases in presence of alternative prey (HODGE 1999; CHEN & WISE 1999; MEYHÖFER & HINDAYAMA 2000). Furthermore, IG prey escapes predation in spatial refuges counteracting species exclusion (DIEHL 1993; FINKE & DENNO 2002; LEWIS & EBY 2002; LANGELLOTTO & DENNO 2004). In general, IGP is strongly asymmetric and determined by relative body-size of IG predator and IG prey (SNYDER & HURD 1995; LUCAS et al. 1998; WOODWARD & HILDREW 2002; BALFOUR et al. 2003). Consequently, smaller individuals of wolf spiders are more sensitive to starvation (TANAKA 1992; WALKER et al. 2003) and more vulnerable to predation (TANAKA 1992).

Alopecosa cuneata (Clerck) and *Pardosa palustris* (L.) are common wolf spiders on grasslands differing strongly in size, with female *A. cuneata* being almost twice the size of *P. palustris* (ROBERTS 1995). Both species reach abundances of four (*A. cuneata*) to six (*P. palustris*) adults per square meter and belong to the most common cursorial predators on xeric grasslands near Darmstadt (S. Rickers, unpublished data). In July, third instar *A. cuneata* co-occur with second instar *P. palustris* and mortality of juvenile wolf spiders is high in the field (CHAPTER IV.1). I focussed on IGP as important mortality factor and hypothesised that the larger instars of *A. cuneata* prey on the smaller *P. palustris* when alternative prey is rare and habitat structure serving as shelter is limited. Therefore, I established four treatments in the laboratory manipulating prey availability (with, without *Drosophila melanogaster*) and microhabitat structure (simple, complex). Each one individual of *A. cuneata* was placed together with six juveniles of *P. palustris*. In order to compare weight gain without intraguild prey and/ or alternative prey, four more treatments without *P. palustris* were established.

Finally, *D. melanogaster* provided during the experiment was enriched in the heavier carbon isotope to document differential predation of *A. cuneata* on *P. palustris* and alternative prey, using stable isotope analysis.

II Materials and Methods

II.1 Phenology

The study site ‘Ehemaliger August-Euler-Flugplatz’ is located west of Darmstadt in Hesse, Germany (49°51’ N; 8°35’ E). Pleistocene sand deposits are abundant between the rivers Rhine and Main and formed the geological bases for the soils at the study site. In 1993 the site was declared nature reserve to protect the endangered inland sand dune plant community. Key species include *Armeria maritima* ssp. *elongata* Bonnier (Plumbaginaceae), *Koeleria macrantha* Schult. (Poaceae), *Potentilla argentea* L. (Rosaceae) and *Trifolium arvense* L. (Fabaceae). Since 1997 the site is managed by sheep grazing to counteract colonization by neophytic plants and to prevent regrowth of shrubs and trees (for more details see RICKERS 2002).

From May 2001 until April 2002 spiders were sampled monthly with pitfall traps that operated for two weeks. Sampling ceased during winter (November – February) due to the low temperatures and accordingly low activity of animals. Pitfall traps were installed within fenced plots of 5 m² to gain semi-quantitative data. Detailed data on wolf spider density during summer (May – August) is documented elsewhere (RICKERS 2002) and presentation of data is restricted to phenology of the two most abundant wolf spiders *Pardosa palustris* and *Alopecosa cuneata*. Since the instar stage of field captured spiderlings cannot be determined accurately, juveniles were ascribed either to second instar juveniles that were caught with their mothers (Juv. II) or to a collection of spiderlings from the third instar on (Juv. III/+).

II.2 Prey Availability

Sampling

Field sites were located in the nature reserve “Ehemaliger August-Euler-Flugplatz” close to Darmstadt, Hesse (49°51’ N; 8°35’ E). The plant community is endangered by the invasion of *Cynodon dactylon* (Poaceae) that reaches up to 60 % of ground cover (for further details see CHAPTER II.1). To counteract succession and further dispersal of this neophyte, the nature reserve is managed by extensive sheep grazing. The study was conducted on three grazed sites and on three permanent field sites that had been excluded from grazing 5 years previously. In April 2002, four circular plots of 5 m² were fenced within each of the grazed and ungrazed sites and ascribed either to the prey addition treatment or the control. Fences made of PVC were 40 cm high and dug ca. 5 cm into the soil to prevent immigration and emigration of cursorial animals. In each plot of the prey addition treatment vestigal winged *D. melanogaster* (ca. 5,000 individuals) (b.t.b.e Insektenzucht GmbH, Schnürpflingen, Germany) was added every two weeks. After 6 weeks (early June) half of the plots were sampled and the remaining plots were sampled 10 weeks later (mid August) with five pitfall-traps per plot. Traps contained an oversaturated saltwater solution and were operated for four weeks within each plot. Selected arthropods (Araneae; Carabidae, Heteroptera, Auchenorrhyncha, Collembola) were determined to species level whenever possible and counted. Animals were stored in oversaturated saltwater solution at -10°C until they were processed for stable isotope analysis.

Stable Isotope Analysis

Whenever possible, three replicates of each species per treatment were selected and dried at 60°C for 6 days. Either homogenized animal tissue or whole animals (240 - 1300 µg) were weighed into tin capsules, which had been cleaned with acetone previously. Capsules were closed and analysed in a system consisting of an elemental analyser (NA 1500, Carlo Erba, Milan) coupled with a mass spectrometer (MAT 251, Finnigan; REINEKING et al. 1993). Acetanilide (C_8H_9NO: C 71.1 %; H 6.7 %; N 10.4 %; O 11.8 %; Merck, Darmstadt) was used for internal calibration. The ratio between ^{13}C and ^{12}C was expressed relative to that in Pee Dee Belemnite and that between ^{15}N and ^{14}N relative to that in air. Ratios [‰] were calculated according to the following formula (PETERSON & FRY 1987):

$\delta X = (R_{sample} - R_{standard})/(R_{standard}) \times 1000$ with X representing the heavier isotope (^{15}N or ^{13}C), and R the ratio between the heavy and the light isotope ($^{15}N/^{14}N$ respectively $^{13}C/^{12}C$).

Statistical Analysis

Repeated measures ANOVA were used to calculate differences of animal densities and occurrence of eggsacs in *P. palustris* between treatments (with/without grazing; with/without prey addition) and between June and August. To calculate differences in clutch size of *Pardosa palustris* in June GLM (general linear model) was applied. Since densities of the first replicate differed from replicates two and three, a block was included in the analysis to extract variation due to the block design. Stable isotope signatures (δ^{13}C, $\delta\ ^{15}$N) of single species were analysed using repeated measures ANOVA or repeated GLM, if cell size was not equal. Regression of number of juvenile Auchenorrhyncha and juvenile Araneae in June was performed in Statistica 6.0 (Stat Soft). Outliers in numbers of juvenile Auchenorrhyncha at the second sampling were determined after ROUSSEEUW et al. (1999) and excluded from the multiple regression analysis. All other statistical analyses were calculated using SAS 8.02 (SAS Institute Inc., Cary, USA).

II.3 Allochthonous Resources

Experimental set-up

The study was carried out at Marion Bay (147°52' S, 42°49' E) on the south east coast of Tasmania (Australia). At the end of December 2004, each five pitfall traps were established along 6 transects that were set 75 m apart (Fig. 3.1). The first trap (a) was installed well above the high tide mark to prevent flooding of the traps. The second trap (b) was established half way from the first trap to the base of the foredune, where the third trap (c) was installed. The fourth trap (d) was installed right on top of the foredune and the last trap (e) was installed on even ground behind the top.

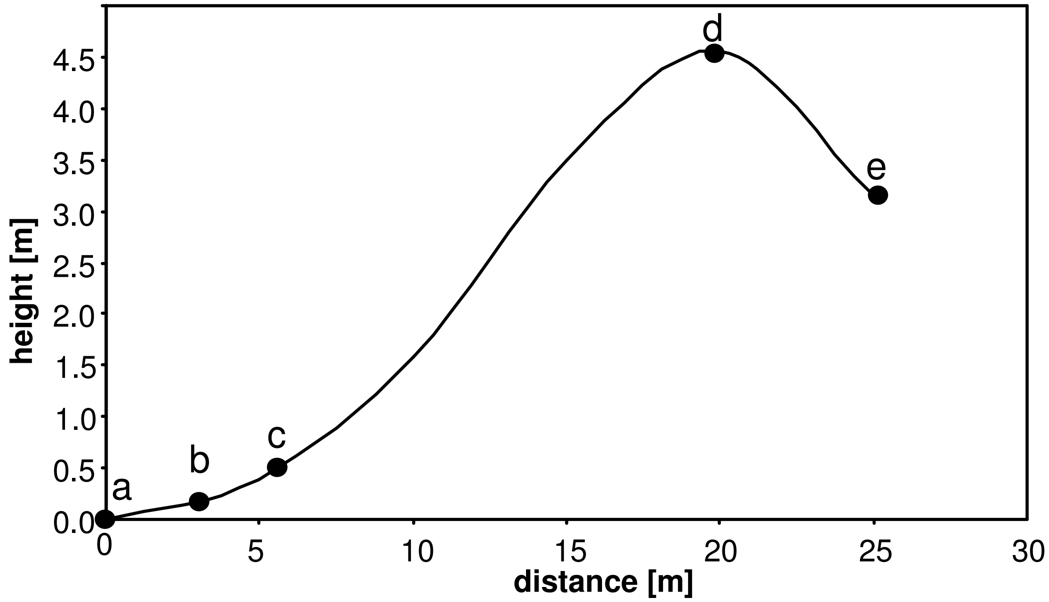

Fig. 3.1: Sketch of the foredune profile including a transect across the foredune at Marion Bay with the locations of the pitfall traps (a-e).

The traps consisted of plastic drinking cups (Ø 7.5 cm) and contained an oversaturated saltwater solution. All traps were sheltered with a 10 x 10 cm square of plywood on wire supports to prevent spill over from rain and sand. Traps were operated for 9 days and checked every two to three days. Lost traps as well as those filled with sand were exchanged, while traps buried with sand were emptied into a hand sieve to retrieve animals. At the end of the sampling, plant biomass of the most abundant herbs, grasses and shrubs on the foredune were collected. Additionally, samples of kelp and sea grass that had been washed ashore were taken. Arthropods were counted and determined to species level whenever possible (amphipod nomenclature after an unpublished key of A.A.M. RICHARDSON) and morphospecies were established for unidentified taxa. Animals were stored in oversaturated saltwater at -10°C until they were processed for stable isotope analysis.

Stable isotope analysis

Only the most abundant taxa were selected for stable isotope analysis. Animals and plants were dried at 60°C for 6 days and either whole animals or mechanically homogenized animal (22 – 1030 µg) and plant tissue (1950 – 3010 µg) were weighed into tin capsules. Samples were analysed as described in CHAPTER II.2. The proportion of carbon from kelp and sea grass in animal tissue was calculated using a two source mixing model (NEWMAN GEARING 1991):

$$F = (\delta^{13}C_{\text{animal}} - \delta^{13}C_{\text{foredune vegetation}})/(\delta^{13}C_{\text{kelp/ sea grass}} - \delta^{13}C_{\text{foredune vegetation}}) \text{ x } 100$$

with F the percentages of carbon derived from kelp and sea grass, $\delta^{13}C_{\text{animal}}$ the carbon isotope ratio of animals, $\delta^{13}C_{\text{fordune vegetation}}$ the average carbon isotope ratio of the foredune vegetation, and $\delta^{13}C_{\text{kelp/ sea grass}}$ the carbon isotope ratio of kelp and sea grass.

Contribution of prey to predator diet was examined in IsoSource (PHILIPPS & GREGG 2003) and feasible solutions for linear mixing models containing multiple sources were calculated. Source increment was set to 1 % and mass balance tolerance was set to ± 0.1 %. Trophic level fractionation in carbon ($\Delta^{13}C = 0$ ‰) and nitrogen ($\Delta^{15}N = 3.4$ ‰) was adopted from PETERSON & FRY (1987). Stable isotope signatures of amphipods and isopods were chosen as sources for predators (*T. oraria*, *T. laticeps*, *Cafius* 2 and Scatophagidae 1). For the antlion, mass balance tolerance was set to ± 0.5 % and the ants Myrmecinae and *Iridomymex* were additionally included as food sources, while *Talorchestia* 2 and *A. bipleura* were excluded from the analysis due to strong enrichment in ^{15}N and ^{13}C, respectively, as compared to the $\delta^{15}N$ and $\delta^{13}C$ signature of the antlion. The calculated 1-99th percentile range was used as an indicator for the importance of a food source in predator diet.

Statistical analysis

Differences in stable isotope signatures ($\delta^{15}N$, $\delta^{13}C$) among plant species were calculated in a one-way ANOVA (analysis of variance) in Statistica 6.0 (StatSoft). In order to investigate the distribution of animals along the transect, mean log-transformed abundance of animals was analysed in a DCA (detrended correspondence analysis) that was performed in Canoco 4.0 (TER BRAAK & SMILAUER 1998). Only taxa with more than four individuals were included in the analysis.

II.4 Food Quality

Experimental procedures

At the end of May 2004, a total of 103 female *P. lugubris* were collected from the Kranichsteiner Forest, a deciduous forest, near Darmstadt, Germany. Only females that carried eggsacs were selected and all females were weighed in the laboratory. Spiders were kept separately in covered plastic containers (Ø 6.5 cm x 4.5 cm) in a climate controlled greenhouse at constant temperature of 21°C. Plastic containers contained a small amount of moss that was collected in the field, frozen for 48 h at -20°C and dried at 60°C for 48 h to exclude possible prey. After four days of starvation, 15 females were ascribed to each of 5 different feeding treatments (Table 4.1). Three females were frozen to obtain the initial stable isotope signature. Weight of gravid females ranged between 34.70 and 64.40 mg and averaged 46.93 ± 5.22 mg; it did not differ between treatments ($F_{4,71} = 0.17$, $p = 0.9541$).

Cultures of vestigal winged mutants of the fruit fly *Drosophila melanogaster* (b.t.b.e Insektenzucht GmbH, Schnürpflingen, Germany) were established in the laboratory on an agar-sugarcane-maize-semolina medium (agar: Acros Organics Geel, Belgium; sugarcane & maize-semolina: Alnatura GmbH, Bickenbach, Germany) to obtain cultures with a distinct C_4 isotopic signature ($\delta^{13}C = -12.36 \pm 0.36$ ‰). Both Collembola species were reared on brewer's yeast (Heirler Cenovis GmbH, Radolfzell, Germany) to obtain a distinct C_3 isotopic signature ($\delta^{13}C = -22.06 \pm 0.27$‰). Females were maintained on three single-species and two mixed-species diets (Table 4.1) spanning from very low to high quality in the following order: single diet *F. candida* (F) < mixed diet *D. melanogaster* + *F. candida* (DF) < single diet *D. melanogaster* (D) < single diet *H. nitidus* (H) < mixed diet *D. melanogaster* + *H. nitidus* (DH). Prey biomass was kept constant between the different treatments in order to compare prey quality.

Table 4.1: Expected food quality, prey species and culture medium of the different diets in the feeding experiment with female *Pardosa lugubris*.

diet code	prey	average fresh weight [mg]	culture medium	no. of prey items per 2 days	expected quality
D	*Drosophila melanogaster*	0.57 ± 0.09	agar-sugarcane-maize-semolina	5	intermediate
H	*Heteromurus nitidus*	0.12 ± 0.02	brewer's yeast	24	high
F	*Folsomia candida*	0.16 ± 0.03	brewer's yeast	17	lowest
DH	*D. melanogaster* + *H. nitidus*	see above	see above	2 D + 13 H	highest
DF	*D. melanogaster* + *F. candida*	see above	see above	2 D + 9 H	low

Moss was moistened daily and survival of spiders was checked analogously. The amount of prey fed daily resembled ca. 5 % of the females' body weight and remained constant during the experiment (Table 4.1); yet, they were not fed again as long as more than half of the prey previously introduced was still alive. EDGAR (1970) proposed an average of 14 % of the body weight as daily average of food for females in the field, but as spiders experience optimal temperature and humidity conditions in the laboratory and interference is excluded, I restricted the amount of prey to ensure a sufficient period of egg production. When fed 10 % of body weight per day in the laboratory females of *P. palustris* produced subsequent eggsacs already 5 days after spiderling dispersal (personal observation). This period of feeding is probably too short to detect a change in stable isotope composition, as a period of three weeks was needed to establish the $^{13/12}C$ ratio of the diet in juveniles of *P. lugubris* (OELBERMANN & SCHEU 2002b). Feeding ceased at hatching of the second eggsac to prevent juveniles from feeding. Directly after spiderling dispersal, females were frozen at -80 °C for at least 24 h and width of prosoma was determined. Spiders were then stored in oversaturated NaCl solution until they were processed for stable isotope analyses.

Juveniles of the first and second eggsac were counted and 10 spiderlings of each eggsac were randomly selected for stable isotope measurements, determination of prosoma width, and dry weight. Furthermore, survival of remaining spiderlings of the second eggsac was examined. Directly after dispersal, spiderlings were kept separately in covered transparent plastic containers (Ø 3.5 cm x 2.5 cm) without food. Moistened moss was provided to ensure sufficient humidity and survival was checked daily. Finally, also starved spiderlings were selected for stable isotope analysis.

Stable isotope analysis

Springtails, fruit flies and spiders were dried at 60 °C for 6 days. Dry weight of all females and of a maximum of 10 juveniles per eggsac was measured. From each feeding treatment, three females and their juveniles (1st eggsac, 2nd eggsac, 2nd eggsac starved) were chosen for stable isotope analysis. Either homogenized animal tissue or whole animals (280 - 1000 µg) were weighed into tin capsules, which had been cleaned with acetone previously. Samples were analysed as described in CHAPTER II.2.

The proportion of carbon from *Drosophila melanogaster* in animal tissue was calculated using a two source mixing model (NEWMAN GEARING 1991):

$$F = (\delta^{13}C_{\text{P. lugubris}} - \delta^{13}C_{\text{P. lugubris initial}})/(\delta^{13}C_{\text{D. melanogaster}} - \delta^{13}C_{\text{P. lugubris initial}}) \times 100$$

with F the percentages of carbon derived from *D. melanogaster*, $\delta^{13}C_{P.\ lugubris}$ the carbon isotope ratio of *P. lugubris* after feeding on ^{13}C enriched *D. melanogaster*, $\delta^{13}C_{P.\ lugubris\ initial}$ the carbon isotope ratio of *P. lugubris* before the experiment and $\delta^{13}C_{D.\ melanogaster}$ the carbon isotope ratio of *D. melanogaster*. The calculation was not corrected for trophic level fractionation of ^{13}C, since fractionation in *P. lugubris* is negligible (OELBERMANN & SCHEU 2002b).

Statistical analyses

Data on time until production of the second eggsac, carrying periods of the eggsacs and survival of juveniles were analysed by GLM (general linear model). For differences in weight before the experiment and dry weight of females at the end of the experiment ANOVA (analysis of variance) was applied. ANOVA was used to analyse C:N ratios, $\delta^{13}C$ and $\delta^{15}N$ of females and juveniles (1st eggsacs). Also, ANOVA was used to analyse differences in C:N ratio and isotopic enrichment of juveniles (2nd eggsacs) and their mothers. Repeated measures GLM was used to analyse number, dry weight, and prosoma width of juveniles from the first and the second eggsac. To analyse the effect of starvation on C:N ratio, $\delta^{13}C$ and $\delta^{15}N$ of juveniles (2nd eggsacs) repeated measures GLM was applied, too. Outliers in number and survival of juveniles, as well as time until production of the second eggsac, were determined after ROUSSEEUW et al. (1999) and excluded from statistical analysis. Regressions of body size of females and offspring number as well as average offspring size were performed in Statistica 6.0 (Stat Soft). All other statistical analyses were calculated using SAS 8.02 (SAS Institute Inc., Cary, USA).

II.5 Cannibalism

P. palustris (L.) is common on grasslands of northern Europe (BAYRAM 1996). Adult females were collected from xeric grasslands in May and June 2003 at the "Ehemaliger August-Euler-Flugplatz" (for further details on the field site see CHAPTER II.1). Spiders were kept separately in covered plastic containers (Ø 6.5 cm x 4.5 cm). The experiments were carried out in a climate-controlled green house at natural light conditions and constant temperature of 23°C. Plastic containers were filled with *Hypnum cupressiforme* (L.), a moss that covers large areas of the ground at the study site. Plants were collected in the field, frozen for 48 h at -20°C and dried at 60°C for 48 h to exclude possible prey. Females were fed four living individuals of the dipteran *Drosophila melanogaster* (curly; b.t.b.e Insektenzucht GmbH, Schnürpflingen, Germany) each day. Moss in the plastic containers was moistened daily. Spiders were either carrying eggsacs when captured or produced eggsacs during captivity. After two to three weeks spiderlings hatched and left their mothers three to four days later. Dispersing juveniles of the same eggsac were kept in a moistened plastic container (Ø 8.5 cm x 4.5 cm) for 10 to 17 days without adding prey before the experiments started. Spiderlings in these containers easily cannibalised each other (personal observation), and only the biggest spiderlings, being the most successful cannibals, were selected for the experiments.

The experiments were set up in transparent plastic containers (Ø 8.5 cm x 4.5 cm) which were filled with either 0.3 g (simple habitat structure treatment) or 1.0 g (complex habitat structure treatment) of moss (*H. cupressiforme*). The amount of moss resembled that of microsites with low and high cover of moss in the field. In May 2004 nine gravid females of *P. palustris* were collected to determine the average survival of starving second instar juveniles. Females were maintained at the same conditions as the year before until the eggsacs hatched. After dispersal, between 5 and 12 spiderlings of each eggsac (n = 86) were kept separately in small plastic containers (Ø 3.3 cm x 1.2 cm) containing a small amount of moistened moss. Containers were checked daily for sufficient humidity and survival of spiderlings.

Cannibalism among second instar juveniles

The influence of habitat structure, density and alternative prey availability on cannibalistic interactions between second instar spiderlings of *P. palustris* was investigated in a three factorial design resulting in 8 treatments. Factors were 'density' (low, high), 'alternative prey' (with, without) and 'habitat structure' (simple, complex; see above); ten replicates were set up in each treatment. Five (low density) or 15 (high density) spiderlings were placed per container and 15 individuals of the collembolan *Heteromurus nitidus* (Tempelton) taken from laboratory cultures were added every third day in the alternative prey treatments. Prey was added in excess to exclude resource competition. Spiderlings having hatched from different eggsacs were randomly distributed among treatments; initial weight (± SD) of second instar juveniles was 0.32 ± 0.07 mg. Spiderlings were counted every third day for 18 days. Per capita mortality was determined and spiderlings surviving until the end of the experiment were weighed.

Cannibalism between adult females and juveniles

The influence of availability of alternative prey and habitat structure on the cannibalistic interactions between female *P. palustris* and second instar spiderlings was investigated in a two factorial design with the factors 'habitat structure' (simple, complex) and 'alternative prey' (with, without). Habitat structure treatments were set up as above with ten replicates per treatment. Eight spiderlings were placed together with one adult female which was introduced 12 hours later to allow spiderlings to accommodate to the new environment. Second instar juveniles were randomly distributed among treatments; average weight (± SD) of spiderlings was 0.33 ± 0.05 mg. In order to control for possible kin-recognition, the spiderlings added to a certain container were neither related to each other nor to the females. Since the foraging behaviour of virgin lycosid spiders may differ strongly from those that reproduced previously (ANTHONY 2003), only females that had successfully produced offspring were used in the experiment. Females were starved for 30 days and only very active individuals were used in the experiment as evaluated by observing agility and behaviour during capture of *D. melanogaster* the day before the experiment. This long period of starvation was necessary to keep females from producing subsequent offspring and to ensure homogenous predation rates. At the beginning of the experiment average weight (± SD) of females used was 18.17 ± 2.12 mg and did not differ between treatments ($F_{3,36} < 0.0001$, $p = 1.000$).

In treatments with alternative prey, four individuals of *D. melanogaster* were added as prey for adult spiders daily and once before females were placed together with spiderlings. The amount of alternative prey represented 14 % of the females' body weight and is the amount that spiders feed on in the field (EDGAR 1971). Due to their small size second instar spiderlings of *P. palustris* were not able to prey on *D. melanogaster*.

Starting at day three, juveniles were counted every other day for 11 days and the per capita mortality of spiderlings was calculated. In the treatment with complex habitat structure without additional prey 50 %, of the females were dead after 7 days. Therefore, the statistical analysis of the mortality of juveniles was restricted to data of days 3 and 5.

Statistical analysis

Data on per capita mortality of juveniles were analysed by repeated measures ANOVA (analysis of variance). Differences in weight of juveniles (log-transformed data) between treatments at the end of the experiment were analysed using GLM (general linear model). Repeated measures ANOVA was used to analyse whether effects of habitat structure and alternative prey on mortality of spiderlings changed with time. Differences between initial and final weight of females (log-transformed data) were compared between treatments using GLM. To calculate differences of female mortality between treatments G-tests of independence with Williams' correction were used (SOKAL & ROHLF 2001). Homogeneity of variances were inspected using the Levene test implemented in Statistica 6.0 (StatSoft). All other statistical analyses were calculated using SAS 8.02 (SAS Institute Inc., Cary, USA).

II.6 IGP

The experiment was carried out in a climate controlled green house at natural light conditions and constant temperature of 21°C. Adult females were collected from xeric grasslands in May and June 2004 at the "Ehemaliger August-Euler-Flugplatz" close to Darmstadt, Hesse (49°51' N, 8°35' E) (for further details on the field site see CHAPTER II.1). Spiders were kept separately in covered plastic containers (Ø 6.5 cm x 4.5 cm) that were filled with *Hypnum cupressiforme* (L.), a moss that covers large areas of the ground at the study site (RICKERS 2002). Plants were collected in the field, frozen at -20°C for 48 h and dried at 60°C for another 48 h to exclude possible prey. Females of *A. cuneata* weighed 55.78 ± 21.57 mg and those of *P. palustris* 23.83 ± 7.68 mg. Spiders either carried eggsacs or produced eggsacs during captivity. According to their body size, females of *A. cuneata* were fed 10 living individuals of the dipteran *Drosophila melanogaster* (curly; b.t.b.e Insektenzucht GmbH, Schnürpflingen, Germany) daily, while for *P. palustris* only 5 fruit flies per day were provided. Moss in plastic containers was moistened daily to ensure sufficient humidity. After production of eggsacs, females of *A. cuneata* retreated to a web burrow and stopped feeding, while females of *P. palustris* actively exposed the eggsacs to the light and continued feeding. The eggsacs of *A. cuneata* hatched after 20.00 ± 2.79 (n = 10) days, while eggsacs of *P. palustris* hatched already after 18.13 ± 1.69 (n = 31) days. *A. cuneata* produced 40.80 ± 13.48 juveniles, while eggsacs of *P. palustris* contained only 33.28 ± 10.10 spiderlings. Subsequent to dispersal from their mothers after three to four days, spiderlings were kept separately in small transparent plastic containers (Ø 3.5 cm x 2.5 cm). Juveniles of *A. cuneata* were fed fruit flies *D. melanogaster* and the springtail *Heteromurus nitidus* (laboratory culture) ad libitum until they reached the third instar. Since second instar juveniles of *P. palustris* were too small to prey on fruit flies, they were fed only *H. nitidus* ad libitum to exclude starvation and to minimize cannibalism during the experiment. All spiderlings were weighed shortly before the experiment started: weight of *A. cuneata* ranged from 0.92 to 2.02 mg and weight of *P. palustris* ranged from 0.35 to 0.80 mg.

Intraguild predation was investigated in a two factorial design including four treatments. Factors were availability of alternative prey (without, with *D. melanogaster*) and habitat structure (simple, complex). Each one specimen of *A. cuneata* was grouped together with 6 juveniles of *P. palustris.* Neither weight of *A. cuneata* ($F_{7,72} = 0.01$, $p = 1.000$) nor average weight of *P. palustris* per container ($F_{3,36} < 0.01$, $p = 1.000$) differed between treatments. Furthermore, each 6 *P. palustris* were virtually of the same size (standard deviation: 0.00-0.02 mg). Juveniles of *A. cuneata* were on average 2.53 ± 0.02 times heavier than the selected juveniles of *P. palustris* to exclude differential predation probability due to different size ratios of predator and prey. To ensure uniform predation rates, juvenile *A. cuneata* were starved for four days before the experiment started. In treatments with alternative prey a constant prey level of three individuals of *D. melanogaster* was established, resembling prey in excess. Plastic containers (Ø 6.5 cm x 4.5 cm) contained either 0.1 g (simple habitat structure) or 0.3 g (complex habitat structure) of moss (*H. cupressiforme*; see above). The amount of moss resembled that of microsites with low and high cover of moss in the field.

Since I could not exclude predation on *D. melanogaster* or conspecifics by juvenile *P. palustris* during the experiment, I established four more treatments without *P. palustris* in order to compare weight gain and isotopic signature of *A. cuneata* with and without IGP prey. Thus, the experiment was designed orthogonally and consisted of three factors (alternative prey, habitat structure and IGP) including 8 treatments. Each treatment was replicated 10 times and survival of spiderlings and fruit flies was checked every other day; missing fruit flies were replaced accordingly. After two weeks all juveniles of *P. palustris* in the treatment without alternative prey at simple habitat structure had died and the experiment ended: surviving spiders were frozen at -80°C for 24 h, weighed and dried for stable isotope analysis. Since an average of three weeks is needed to detect changes in isotopic composition in juvenile spiders (OELBERMANN & SCHEU 2002b), drastic differences in carbon stable isotope ratio of IG prey and alternative prey are necessary to allow earlier detection. Consequently, *D. melanogaster* used during the experiment was reared on an agar-sugarcane-maize-semolina medium with D-glucose-1-^{13}C (Campro Scientific GmbH, Berlin, Germany) that was highly enriched in ^{13}C (min. 99 atom%). The calculated proportion of ^{13}C was 1.275 atom%, representing an enrichment of 188 ‰ as compared to the isotopic signature of *D. melanogaster* raised on a C_3 resource (1.087 atom%).

Stable isotope analysis

Animals (spiders, fruit flies, springtails) were dried at 60°C for 6 days. At least three measurements per treatment were done. For *P. palustris* two sets of samples were generated to document possible differences in feeding during the experiment; the heaviest juveniles per treatment were selected and analysed separately, while the lightest juveniles per treatment had to be combined to ensure sufficient biomass for stable isotope measurements. Thus, whole animals (9 – 1200 µg) were weighed into tin capsules, which had been cleaned with acetone previously. Samples were analysed as described in CHAPTER II.2.

Statistical analyses

Data on survival of *P. palustris* was analysed using repeated measures GLM (general linear model). For differences in weight of *A. cuneata* and *P. palustris* GLM was applied. GLM was also used to detect differences in C:N ratio, $\delta^{13}C$ and $\delta^{15}N$ of spiderlings. In order to explain high standard deviations in $\delta^{13}C$ ratios of *P. palustris*, single measurements of ^{13}C were correlated to final biomass of juveniles. Regressions were performed in Statistica 6.0 (Stat Soft). All other statistical analyses were calculated using SAS 8.02 (SAS Institute Inc., Cary, USA). To calculate differences in mortality of *A. cuneata* between treatments G-tests of independence with Williams' correction were used (SOKAL & ROHLF 2001).

III Results

III.1 Phenology

With 6 adults per square meter in May *P. palustris* was the most abundant wolf spider of the grasslands at the ‘Ehemaliger August-Euler-Flugplatz’. Subadult individuals occurred only in April and moulted to adult animals in May when mating occurred immediately (Fig. 1.1a). First eggsacs occurred in June and could be found as long as July. Analogously, females carrying second instar juveniles were captured in June and July, while males were captured only from May until June. Older instars of *P. palustris* occurred from August until the end of the season and were caught after the winter in March of the next year until they moulted to subadult spiders in April.

With four adults per square meter *A. cuneata* was the second most abundant wolf spider. Subadult spiders occurred already in March and moulted to adult spiders in April when mating took place (Fig. 1.1b). While males occurred only from April until June, females were captured from April until July carrying second instar juveniles from June until July. In July also older instars of *A. cuneata* occurred and were captured until September. In September some of the older instars already moulted into subadult spiders, which were also caught after the winter in March of the next year. At the end of March subadults mature and the life cycle is completed. Interestingly, females carrying eggsacs were not caught in the pitfall traps; considering occurrence of juveniles, *A. cuneata* most likely carried eggsacs in May and June.

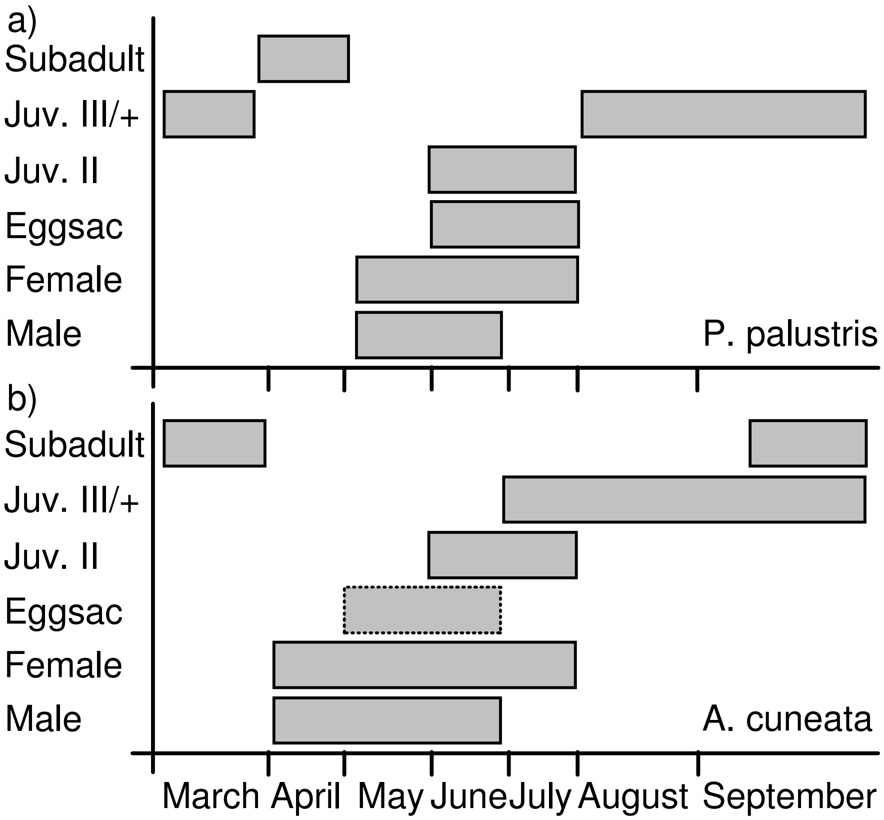

Fig. 1.1: **Occurrences of different life stages of *Pardosa palustris* (a) and *Alopecosa cuneata* (b) during the season '01 – '02. (Juv. II: second instar juveniles; Juv. III/+: third instar and older juveniles). Assumed occurrence of eggsacs in *A. cuneata* is indicated by a broken bar.**

III.2 Prey Availability

Abundances

Detritivores: Density of Collembola changed during the season (Table 2.1) decreasing from 104 Ind./m^2 in June to 37 Ind./m^2 in August. The density of Collembola was affected by grazing while the effect of grazing tended to change with time (Table 2.1, Fig. 2.1a; for a detailed list of arthropod abundances see Appendix I). In June, densities of springtails were strongly increased on grazed sites ($F_{1,7} = 11.50$, $p = 0.0116$), while in August densities did not differ significantly between grazed and non-grazed sites ($F_{1,7} = 3.18$, $p = 0.1178$).

While densities of *Lepidocyrtus cyaneus* (Entomobryidae) were not affected by grazing (Between Subjects Effect: $F_{1,7} = 2.08$, $p = 0.1925$) or prey addition (Between Subjects Effect: $F_{1,7} = 0.22$, $p = 0.6506$), *Entomobrya nivalis* (Entomobryidae) and *Isotoma viridis* (Isotomidae) tended to be more abundant on grazed sites (Between Subjects Effect: *E. nivalis*: $F_{1,7} = 5.09$, $p = 0.0586$; *I. viridis*: $F_{1,7} = 5.13$, $p = 0.0579$).

Table 2.1: Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on densities of detritivores (Collembola) and herbivores (Auchenorrhyncha, juvenile Auchenorrhyncha and Heteroptera) of a xeric grassland; block refers to the two different areas the experiment was established in (randomized complete block design).

			Collembola		Auchenorrh.		juv. Auchenorrh.		Heteroptera	
		DF	F	P	F	P	F	P	F	P
between subjects effects	block	1,7	1.31	0.2906	0.05	0.8284	0.01	0.9383	7.85	0.0265
	grazing	1,7	20.91	0.0026	0.67	0.4387	1.54	0.2546	2.60	0.1506
	prey addition	1,7	0.05	0.8255	0.77	0.4099	0.61	0.4617	0.04	0.8496
	grazing*prey addition	1,7	0.01	0.9078	0.03	0.8728	0.04	0.8451	0.02	0.8893
within subjects effects	time	1,7	23.23	0.0019	106.06	<0.0001	117.50	<0.0001	15.29	0.0058
	time*grazing	1,7	5.12	0.0582	0.34	0.5807	0.33	0.5848	1.57	0.2498
	time*prey addition	1,7	0.96	0.3599	22.64	0.0021	13.02	0.0086	0.55	0.4808
	time*grazing *prey addition	1,7	0.12	0.7391	5.84	0.0463	7.56	0.0285	0.69	0.4342
	time*block	1,7	1.53	0.2563	0.33	0.5810	0.63	0.4519	15.77	0.0054

Herbivores: The density of the most abundant Auchenorrhyncha (*Anaceratagallia* cf. *ribauti*, *Artianus interstitialis*, *Doratura stylata*, *Jassargus obtusivalvis*, and juvenile Auchenorrhyncha) strongly decreased from 30 Ind./m^2 in June to 10 Ind./m^2 in August (Table 2.1). Additionally, the effect of prey addition changed with time, as did the effect of grazing and prey addition (Table 2.1, Fig. 2.1b), which was reflected in densities of juvenile Auchenorrhyncha (Table 2.1). In June, prey addition caused an increase in density of Auchenorrhyncha, whereas in August the density of juvenile Auchenorrhyncha decreased on sites with prey addition and/or when grazing was abandoned.

Densities of *A. ribauti* (Within Subjects Effect: $F_{1,7} = 19.57$, $p = 0.0031$) and juvenile Auchenorrhyncha (Table 2.1) decreased most strongly from June to August and density of juvenile Auchenorrhyncha in August tended to be negatively correlated with density of juvenile spiders ($R^2 = 0.3244$; $F_{1,9} = 4.32$, $p = 0.0674$).

The density of Heteroptera also decreased significantly from June (6 Ind./m²) to August (4 Ind./m²) (Table 2.1). But densities were neither affected by grazing nor by prey addition (Table 2.1).

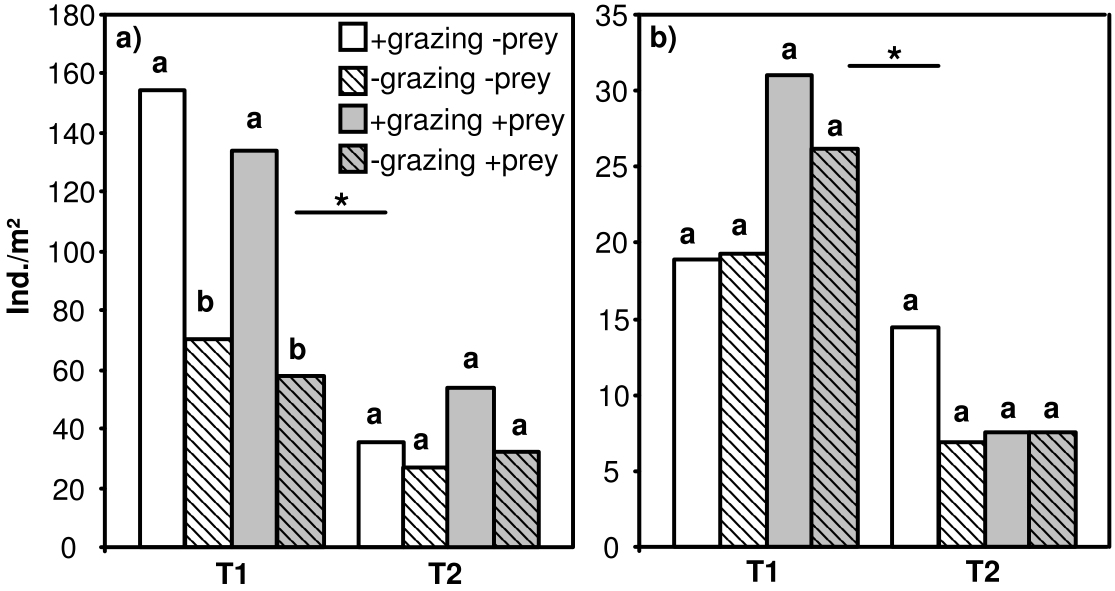

Fig. 2.1: **Over all density of Collembola (a) and Auchenorrhyncha (b) as affected by grazing and prey addition in June (T1) and August (T2). Bars of each date sharing the same letter indicate that densities are not significantly different. Asterisks indicate significant differences between sampling dates. For further statistical analyses of interactions see text.**

Predators: The overall density of spiders tended to be increased on grazed sites (Table 2.2). The effect was based on the densities of the two most abundant wolf spiders (Lycosidae) *Alopecosa cuneata* and *Pardosa palustris* (Table 2.2) and resulted from a strong increase in abundances on grazed sites in June ($F_{1,7} = 16.90$, $p = 0.0045$) (Fig. 2.2a). Furthermore, the number of eggsacs of *P. palustris* significantly decreased from June to August, but was significantly increased on grazed sites (Table 2.2, Fig. 2.2b). The effect of grazing on the number of egg sacs changed with time (Table 2.2); the positive effect of grazing only occurred in June ($F_{1,7} = 16.57$, $p = 0.0047$). Clutch size of *P. palustris* in June was neither affected by prey addition ($F_{1,21} = 1.95$, $p = 0.1771$) nor by grazing ($F_{1,21} = 3.34$, $p = 0.0817$).

The overall density of Carabidae was neither affected by grazing nor by prey addition (Table 2.2).

Table 2.2: Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on densities of predators (Araneae, Lycosidae: *Pardosa palustris* and *Alopecosa cuneata*, female *P. palustris* carrying eggsacs; Carabidae) of a xeric grassland; block refers to the two different areas the experiment was established in (randomized complete block design).

			Araneae		Lycosidae*		eggsacs**		Carabidae	
		DF	F	P	F	P	F	P	F	P
between subjects effects	block	1,7	7.69	0.0275	6.30	0.04	6.52	0.0379	9.36	0.0183
	grazing	1,7	4.90	0.0624	5.87	0.046	16.36	0.0049	0.82	0.3946
	prey addition	1,7	0.28	0.6136	0.08	0.787	0.75	0.4148	0.03	0.8660
	grazing*prey addition	1,7	0.17	0.6900	0.05	0.835	0.08	0.7810	0.02	0.8902
within subjects effects	time	1,7	0.36	0.5683	3.82	0.092	17.32	0.0042	1.20	0.3099
	time*grazing	1,7	0.28	0.6160	0.74	0.419	13.69	0.0077	2.05	0.1956
	time*prey addition	1,7	0.31	0.5976	0.02	0.897	1.81	0.2204	0.16	0.7020
	time*grazing*prey addition	1,7	0.50	0.5026	0.93	0.366	1.81	0.2204	3.43	0.1063
	time*block	1,7	0.70	0.4307	3.25	0.115	3.18	0.1176	0.03	0.8730

*: densities of *Pardosa palustris* and *Alopecosa cuneata*

**: female *P. palustris* carrying eggsacs

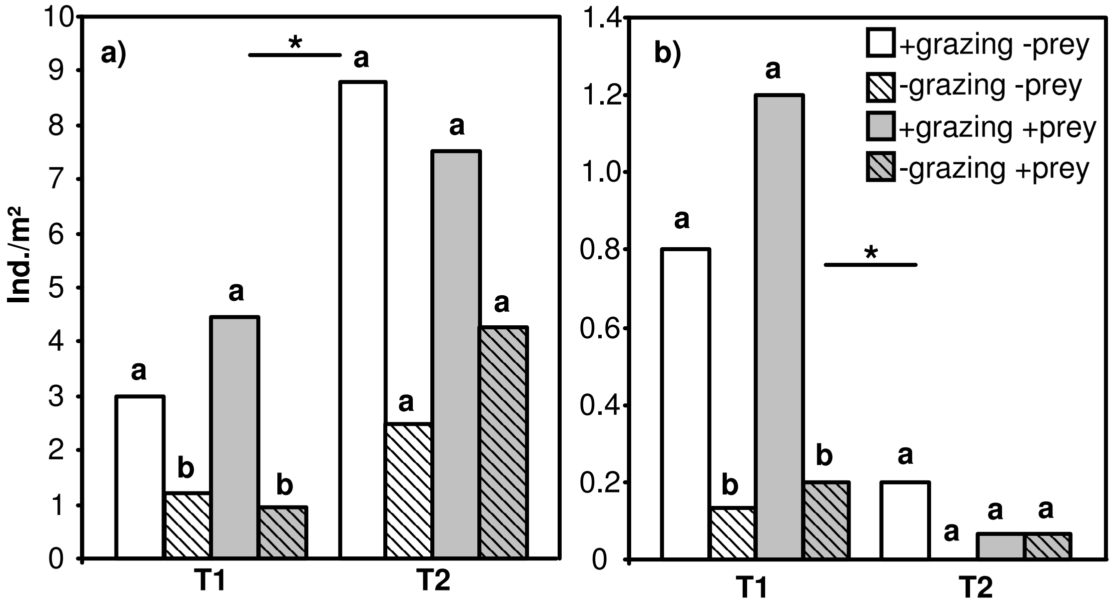

Fig. 2.2: Density of *Alopecosa cuneata* and *Pardosa palustris* (a) and density of female *P. palustris* carrying eggsacs (b) as affected by grazing and prey addition in June (T1) and August (T2). Bars of each date sharing the same letter indicate that densities are not significantly different. Asterisks indicate significant differences between sampling dates. For further statistical analyses of interactions see text.

Stable isotopes

Detritivores: *E. nivalis* was significantly depleted in ^{13}C on grazed sites and δ^{13}C ratios decreased from the first to the second sampling (Table 2.3, Fig. 2.3a). Both, grazing and prey addition affected δ^{15}N ratios of *E. nivalis* (Table 2.3, Fig. 2.4a). In June, *E. nivalis* was significantly enriched in ^{15}N by 0.81 ‰ on grazed sites ($F_{1,7} = 9.49$, $p = 0.0178$), while in August it was significantly enriched in ^{15}N by 0.94 ‰ on sites with prey addition ($F_{1,7} = 9.35$, $p = 0.0184$).

In general, grazing decreased δ^{13}C ratios of *I. viridis*, while prey addition did not affect δ^{13}C ratios (Table 2.3, Fig. 2.3b). *I. viridis* was significantly enriched in ^{15}N on grazed sites and also significantly enriched on sites with prey addition (Table 2.3, Fig. 2.4b).

Table 2.3: Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on δ^{13}C and δ^{15}N ratios of Collembola (*Entomobrya nivalis* and *Isotoma viridis*) of a xeric grassland.

		Entomobrya nivalis						*Isotoma viridis*					
		δ^{13}C			δ^{15}N			δ^{13}C			δ^{15}N		
		DF	F	P	DF	F	P	DF	F	P	DF	F	P
between subjects effects	grazing	1,6	36.78	0.0009	1,7	17.21	0.0043	1,6	11.98	0.0134	1,6	45.66	0.0005
	prey addition	1,6	0.24	0.6424	1,7	16.75	0.0046	1,6	3.05	0.1315	1,6	15.63	0.0075
	grazing*prey addition	1,6	3.38	0.1157	1,7	0.26	0.6276	1,6	2.21	0.1877	1,6	0.96	0.3651
within subjects effects	time	1,6	6.08	0.0488	1,7	1.44	0.2697	1,6	0.55	0.4869	1,6	2.90	0.1393
	time*grazing	1,6	0.00	0.9492	1,7	0.37	0.5639	1,6	0.26	0.6271	1,6	0.03	0.8784
	time*prey addition	1,6	0.03	0.8662	1,7	1.88	0.2130	1,6	1.00	0.3549	1,6	1.16	0.3236
	time*grazing *prey addition	1,6	0.03	0.8673	1,7	0.54	0.4865	1,6	1.55	0.2600	1,6	0.28	0.6143

Grazing decreased δ^{13}C ratios of *L. cyaneus* and δ^{13}C ratios increased from the first to the second sampling (Table 2.4, Fig. 2.3c). Furthermore, the effect of grazing grew stronger from June to August (Table 2.4). Neither grazing nor prey addition affected δ^{15}N ratios of *L. cyaneus*, but δ^{15}N ratios increased from the first to the second sampling (Table 2.4, Fig. 2.4c).

Table 2.4: Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on $\delta^{13}C$ and $\delta^{15}N$ ratios of *Lepidocyrtus cyaneus* (Collembola) of a xeric grassland.

		Lepidocyrtus cyaneus					
		$\delta^{13}C$			$\delta^{15}N$		
		DF	F	P	DF	F	P
between subjects effects	grazing	1,8	113.39	<0.0001	1,8	2.23	0.1740
	prey addition	1,8	0.13	0.7267	1,8	2.90	0.1269
	grazing*prey addition	1,8	0.49	0.5051	1,8	0.31	0.5920
within subjects effects	time	1,8	62.64	<0.0001	1,8	9.74	0.0142
	time*grazing	1,8	8.04	0.0219	1,8	0.22	0.6532
	time*prey addition	1,8	0.32	0.5870	1,8	1.72	0.2265
	time*grazing*prey addition	1,8	0.67	0.4354	1,8	1.32	0.2831

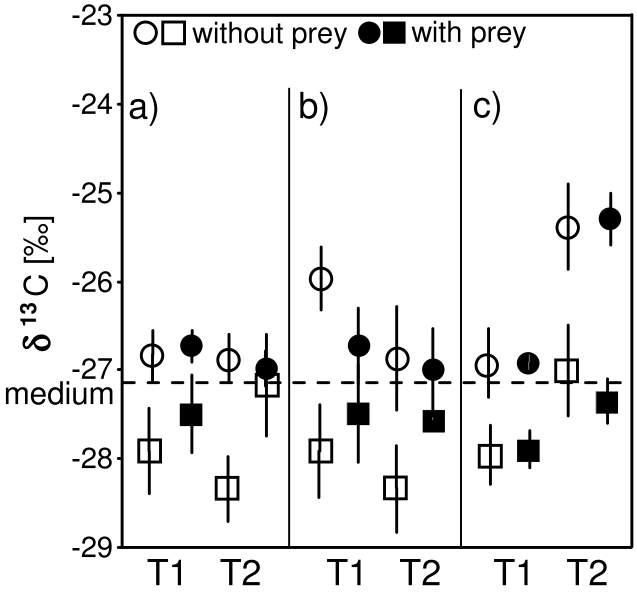

Fig. 2.3: $\delta^{13}C$ ratios (± SD) of detritivores (Collembola) as affected by grazing (circles: without grazing; squares: with grazing) and prey addition in June (T1) and August (T2). $\delta^{13}C$ ratio of the culture medium is indicated by a horizontal line. (a) *Entomobrya nivalis*, (b) *Isotoma viridis*, (c) *Lepidocyrtus cyaneus*

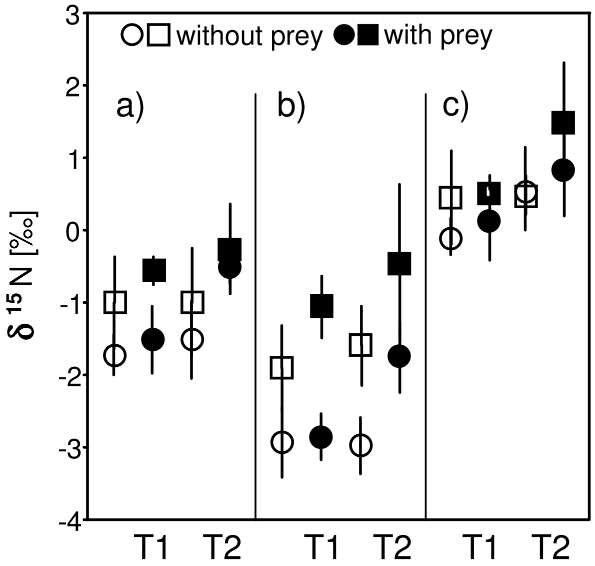

Fig. 2.4: δ^{15}N ratios (± SD) of detritivores (Collembola) as affected by grazing (circles: without grazing; squares: with grazing) and prey addition in June (T1) and August (T2). (a) *Entomobrya nivalis*, (b) *Isotoma viridis*, (c) *Lepidocyrtus cyaneus*

Herbivores: δ^{13}C ratios of *A. ribauti* in June were neither affected by grazing ($F_{1,6} = 0.26$; $p = 0.6270$) nor by prey addition ($F_{1,6} = 0.62$; $p = 0.4603$) and averaged -25.78 ± 0.96 ‰. Similarly, δ^{15}N ratios of *A. ribauti* in June were neither affected by grazing ($F_{1,6} = 0.03$; $p = 0.8761$) nor by prey addition ($F_{1,6} = 0.38$; $p = 0.5624$) averaging -1.06 ± 0.52 ‰.

Juvenile leafhoppers were depleted in ^{13}C on grazed sites, but δ^{13}C ratios were not affected by prey addition (Table 2.5, Fig. 2.5a). δ^{15}N ratios of juvenile leafhoppers were neither affected by grazing nor prey addition (Table 2.5) with the δ^{15}N ratio averaging -3.96 ± 1.12 ‰.

δ^{13}C ratios of *J. obtusivalvis* were neither affected by grazing nor by prey addition (Table 2.5, Fig. 2.5b). In contrast, *J. obtusivalvis* tended to be enriched in ^{15}N on grazed sites (Table 2.5); on grazed sites average δ^{15}N ratio was -3.73 ± 0.46 ‰ and on sites without grazing -3.37 ± 0.46 ‰. Prey addition did not affect δ^{15}N ratios (Table 2.5).

Table 2.5: **Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on $\delta^{13}C$ and $\delta^{15}N$ ratios of Auchenorrhyncha (juvenile Auchenorrhyncha and *Jassargus obtusivalvis*) of a xeric grassland.**

		juvenile Auchenorrhyncha						*Jassargus obtusivalvis*					
		$\delta^{13}C$			$\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
		DF	F	P	DF	F	P	DF	F	P	DF	F	P
between subjects effects	grazing	1,4	15.87	0.0164	1,4	1.75	0.2565	1,4	0.04	0.8579	1,7	5.37	0.0535
	prey addition	1,4	1.57	0.2779	1,4	0.00	0.9857	1,4	2.87	0.1655	1,7	0.00	0.9566
	grazing*prey addition	1,4	0.00	0.9577	1,4	1.21	0.3323	1,4	0.01	0.9169	1,7	0.37	0.5646
within subjects effects	time	1,4	2.51	0.1882	1,4	1.86	0.2444	1,4	6.17	0.0679	1,7	0.63	0.4551
	time*grazing	1,4	0.39	0.5332	1,4	2.58	0.1837	1,4	0.02	0.8981	1,7	0.33	0.5859
	time*prey addition	1,4	0.07	0.5681	1,4	0.55	0.4999	1,4	0.96	0.3836	1,7	0.03	0.8714
	time*grazing *prey addition	1,4	0.03	0.8112	1,4	0.01	0.9337	1,4	1.43	0.2973	1,7	0.27	0.6194

$\delta^{13}C$ ratios of *D. stylata* were not affected by grazing or prey addition (Table 2.6) with an average $\delta^{13}C$ ratio of -24.49 ± 0.74 ‰. Also, neither grazing nor prey addition affected $\delta^{15}N$ ratios of *D. stylata* with an average $\delta^{15}N$ ratio of -4.09 ± 0.80 ‰ (Table 2.6).

In June, *A. interstitialis* was significantly increased in ^{13}C by 8.50 ‰ on sites without grazing ($F_{1,5} = 138.31$, $p < 0.0001$), while in August $\delta^{13}C$ ratios were neither affected by grazing ($F_{1,5} = 0.26$, $p = 0.6295$) nor by prey addition ($F_{1,5} = 1.93$, $p = 0.2238$) (Fig. 2.5c). In August, neither grazing ($F_{1,6} = 0.69$, $p = 0.4388$) nor prey addition ($F_{1,6} = 0.75$, $p = 0.4203$) affected $\delta^{15}N$ ratios averaging -3.63 ± 0.46 ‰.

In general, grazing tended to increase $\delta^{13}C$ ratios of *N. tipularius* (Table 2.6); *N. tipularius* was significantly enriched in ^{13}C by 1.15 ‰ on grazed sites in June ($F_{1,6} = 8.20$, $p = 0.0287$) (Fig. 2.5d). In contrast, neither grazing nor prey addition affected $\delta^{15}N$ ratios of *N. tipularius* with an average $\delta^{15}N$ ratio of -2.46 ± 1.25 ‰ (Table 2.6).

Table 2.6: **Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on $\delta^{13}C$ and $\delta^{15}N$ ratios of *Doratura stylata* (Auchenorrhyncha) and *Neides tipularius* (Heteroptera) of a xeric grassland.**

		Doratura stylata						*Neides tipularius*					
		$\delta^{13}C$			$\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
		DF	F	P	DF	F	P	DF	F	P	DF	F	P
between subjects effects	grazing	1,7	2.55	0.1542	1,6	0.29	0.6101	1,6	5.21	0.0625	1,7	0.20	0.6697
	prey addition	1,7	1.77	0.2253	1,6	0.25	0.6330	1,6	0.41	0.5479	1,7	1.96	0.2044
	grazing*prey addition	1,7	0.64	0.4511	1,6	0.00	0.9579	1,6	3.06	0.1308	1,7	0.22	0.6520
within subjects effects	time	1,7	0.06	0.8151	1,6	0.00	0.9686	1,6	0.62	0.4621	1,7	1.06	0.3372
	time*grazing	1,7	0.14	0.7175	1,6	0.09	0.7761	1,6	1.61	0.2508	1,7	0.00	0.9599
	time*prey addition	1,7	0.45	0.5243	1,6	0.53	0.4921	1,6	0.11	0.7556	1,7	0.03	0.8760
	time*grazing *prey addition	1,7	0.26	0.6259	1,6	0.08	0.7860	1,6	1.52	0.2643	1,7	2.18	0.1832

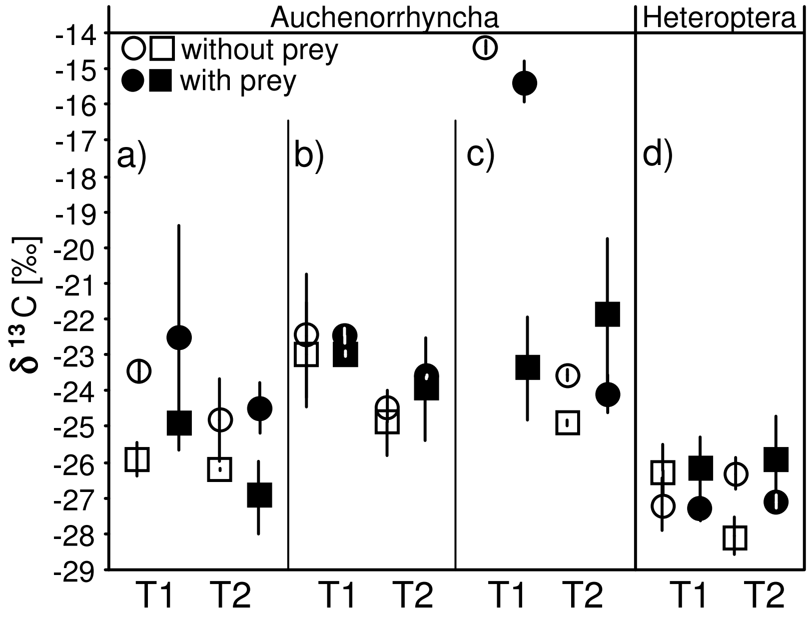

Fig. 2.5: **$\delta^{13}C$ ratios (± SD) of herbivores (Auchenorrhyncha & Heteroptera) as affected by grazing (circles: without grazing; squares: with grazing) and prey addition in June (T1) and August (T2). (a) juvenile Auchenorrhyncha, (b) *Jassargus obtusivalvis*, (c) *Artianus interstitialis,* (d) *Neides tipularius***

Predators: $\delta^{13}C$ ratios of female *P. palustris* were neither affected by grazing nor prey addition and ratios did not differ between the first and the second sampling (Table 2.7, Fig. 2.6a). However, in June, prey addition increased $\delta^{13}C$ ratios of female *P. palustris* on grazed sites, whereas in August $\delta^{13}C$ ratios of females were similar on grazed and non-grazed sites (Table 2.7). Both grazing and prey addition affected $\delta^{15}N$ ratios of female *P. palustris* (Fig. 2.7a); females on grazed sites were significantly enriched in ^{15}N and tended to be enriched in ^{15}N in presence of *D. melanogaster* (Table 2.7). Interestingly, eggsacs were strongly enriched in ^{13}C (Fig. 2.6b) by 1.85 ‰ ($F_{1,18} = 93.86$, $p < 0.0001$) and ^{15}N (Fig. 2.7b) by 1.83 ‰ ($F_{1,18} = 32.52$, $p < 0.0001$) compared to females. $\delta^{13}C$ ratios of second instar juveniles of *P. palustris* on grazed sites were not affected by prey addition ($F_{1,4} = 6.08$, $p = 0.0904$) (Fig. 2.6c), but juveniles were significantly enriched in ^{15}N when *D. melanogaster* was added ($F_{1,4} = 100.23$, $p = 0.0021$) (Fig. 2.7c). Later instars of *P. palustris* were significantly depleted in ^{13}C by 0.66 ‰ on grazed sites ($F_{1,7} = 5.66$, $p = 0.0489$) (Fig. 2.6d), resulting from the pronounced difference when alternative prey was present (grazing x prey interaction; $F_{1,7} = 6.23$, $p = 0.0413$). Furthermore, later instars were significantly enriched in ^{15}N on grazed sites by 1.38 ‰ ($F_{1,6} = 21.38$, $p = 0.0036$) and enriched by 0.79 ‰ when *D. melanogaster* was present ($F_{1,6} = 8.39$, $p = 0.0275$) (Fig. 2.7d). The enrichment tended to be more pronounced on grazed sites when prey was added ($F_{1,6} = 5.59$, $p = 0.0560$).

Table 2.7: Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on $\delta^{13}C$ and $\delta^{15}N$ ratios of Lycosidae (*Pardosa palustris* and *Alopecosa cuneata*) of a xeric grassland.

		Pardosa palustris						*Alopecosa cuneata*					
		$\delta^{13}C$			$\delta^{15}N$			$\delta^{13}C$			$\delta^{15}N$		
		DF	F	P	DF	F	P	DF	F	P	DF	F	P
between subjects effects	grazing	1,6	0.41	0.5449	1,6	11.19	0.0155	1,4	0.61	0.4779	1,4	0.56	0.4945
	prey addition	1,6	0.18	0.6846	1,6	5.47	0.0579	1,4	0.92	0.3928	1,4	19.04	0.0120
	grazing*prey addition	1,6	0.00	0.9962	1,6	1.66	0.2453	1,4	0.05	0.8393	1,4	2.56	0.1851
within subjects effects	time	1,6	0.52	0.4983	1,6	3.47	0.1118	1,4	1.11	0.3515	1,4	0.97	0.3803
	time*grazing	1,6	0.22	0.6560	1,6	1.70	0.2404	1,4	0.08	0.7854	1,4	0.14	0.7231
	time*prey addition	1,6	0.00	0.9619	1,6	1.53	0.2629	1,4	2.80	0.1695	1,4	0.94	0.3380
	time*grazing *prey addition	1,6	7.18	0.0365	1,6	0.20	0.6667	1,4	2.45	0.1925	1,4	0.08	0.7855

Female *A. cuneata* were significantly enriched in ^{13}C compared to female *P. palustris* ($F_{1,43} = 39.90$, $p < 0.0001$), but did not differ in ^{15}N from female *P. palustris* ($F_{1,41} = 0.07$, $p = 0.7977$). Furthermore, δ^{13}C ratios of female *A. cuneata* were neither affected by grazing nor by addition of *D. melanogaster* and did not differ between the first and the second sampling (Table 2.7, Fig. 2.6e). In contrast, prey addition affected δ^{15}N ratios of females, resulting in an increase in ^{15}N (Table 2.7, Fig. 2.7e). Second instar juveniles of *A. cuneata* were enriched in ^{13}C when *D. melanogaster* was added ($F_{1,6} = 6.69$, $p = 0.0415$) (Fig. 2.6f), while grazing affected neither δ^{13}C ($F_{1,6} = 2.43$, $p = 0.1701$) nor δ^{15}N ratios of second instar juveniles ($F_{1,4} = 1.91$, $p = 0.2390$) (Fig. 2.7f). In contrast, second instar juveniles were significantly enriched in ^{15}N by 0.45 ‰ when prey was added ($F_{1,4} = 10.70$, $p = 0.0308$), and the enrichment tended to be more pronounced on grazed sites (grazing x prey interaction; $F_{1,4} = 6.82$, $p = 0.0593$) (Fig. 2.7f). δ^{13}C ratios of later instars of *A. cuneata* did not differ between grazed and ungrazed sites ($F_{1,8} = 1.20$, $p = 0.3046$) or sites with and without additional prey ($F_{1,8} = 0.97$, $p = 0.3532$) (Fig. 2.6g). However, later instars on grazed sites and on sites with alternative prey were enriched in ^{15}N by 0.87 ‰ ($F_{1,8} = 16.70$, $p = 0.0035$) and by 0.67 ‰ ($F_{1,8} = 11.87$, $p = 0.0088$), respectively (Fig. 2.7g).

δ^{13}C ratios of *C. cinctus* were significantly reduced on grazed sites and the effect of prey addition on δ^{13}C ratios changed with time (Table 2.8, Fig. 2.6h). While *C. cinctus* was significantly depleted in ^{13}C by 1.68 ‰ on sites with additional prey in June ($F_{1,2} = 31.13$, $p = 0.0307$), δ^{13}C ratios in August were not affected by prey addition ($F_{1,2} = 0.20$, $p = 0.7007$). *C. cinctus* tended to be enriched in ^{15}N when additional prey was provided (Table 2.8) reflecting an enrichment of 1.94 ‰ in June ($F_{1,2} = 18.97$, $p = 0.0489$) (Fig. 2.7h).

Table 2.8: Repeated measures ANOVA table of F-values on the effect of grazing, prey addition and time on δ^{13}C and δ^{15}N ratios of Carabidae (*Calathus cinctus* and *Trechus obtusus*) of a xeric grassland.

		Calathus cinctus						*Trechus obtusus*					
		δ^{13}C			δ^{15}N			δ^{13}C			δ^{15}N		
		DF	F	P	DF	F	P	DF	F	P	DF	F	P
between subjects effects	grazing	1,2	24.11	0.0391	1,2	3.47	0.2036	1,2	2.03	0.2903	1,4	5.45	0.0799
	prey addition	1,2	8.75	0.0978	1,2	15.65	0.0583	1,2	2.36	0.2642	1,4	0.01	0.9461
	grazing*prey addition	1,2	0.93	0.4370	1,2	0.73	0.4829	1,2	0.11	0.7740	1,4	1.12	0.3505
within subjects effects	time	1,2	1.59	0.3342	1,2	0.01	0.9143	1,2	3.82	0.1897	1,4	2.21	0.2115
	time*grazing	1,2	0.44	0.5755	1,2	0.77	0.4718	1,2	0.21	0.6944	1,4	1.30	0.3185
	time*prey addition	1,2	27.18	0.0349	1,2	0.87	0.4498	1,2	16.37	0.0560	1,4	0.23	0.6539
	time*grazing *prey addition	1,2	0.41	0.5871	1,2	5.06	0.1533	1,2	0.16	0.7296	1,4	2.48	0.1907

In general, δ^{13}C ratios of *T. obtusus* were neither affected by grazing nor by prey addition (Table 2.8), even though at the first sampling *T. obtusus* was significantly depleted in ^{13}C by 0.52 ‰ and 1.17 ‰ on grazed sites ($F_{1,2} = 22.53$, $p = 0.0416$) and on sites with additional prey ($F_{1,2} = 143.08$, $p = 0.0069$), respectively (Fig. 2.6i). Thus, the effect of additional prey tended to change with time (Table 2.8), as *T. obtusus* was depleted in ^{13}C on sites with prey addition in June, but δ^{13}C ratios were not affected by prey addition in August ($F_{1,2} = 0.61$, $p = 0.5154$). Finally, *T. obtusus* tended to be enriched in ^{15}N on grazed sites (Table 2.8), due to a significant enrichment in ^{15}N by 1.28 ‰ on grazed sites in August ($F_{1,4} = 9.92$, $p = 0.0345$) (Fig. 2.7i).

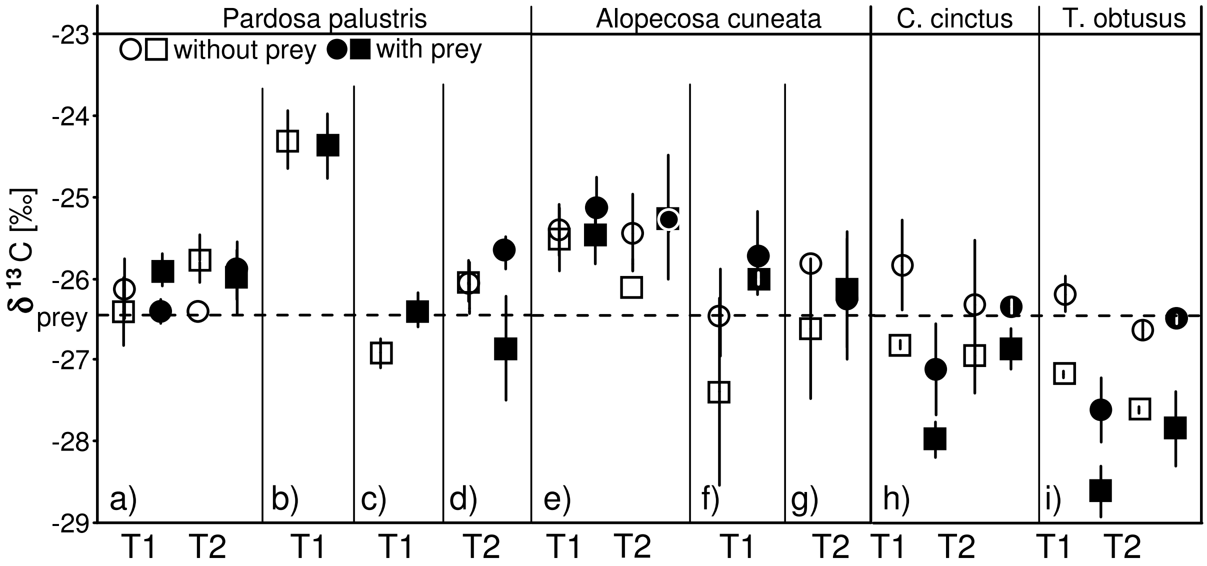

Fig. 2.6: δ^{13}C ratios (± SD) of predators as affected by grazing (circles: without grazing; squares: with grazing) and prey addition in June (T1) and August (T2). δ^{13}C ratio of *Drosophila melanogaster* is indicated by a horizontal line. *Pardosa palustris*: (a) females, (b) egg sacs, (c) second instar juveniles, (d) third/ later instar juveniles; *Alopecosa cuneata*: (e) females, (f) second instar juveniles, (g) third/ later instar juveniles; *Calathus cinctus* (h); *Trechus obtusus* (i)

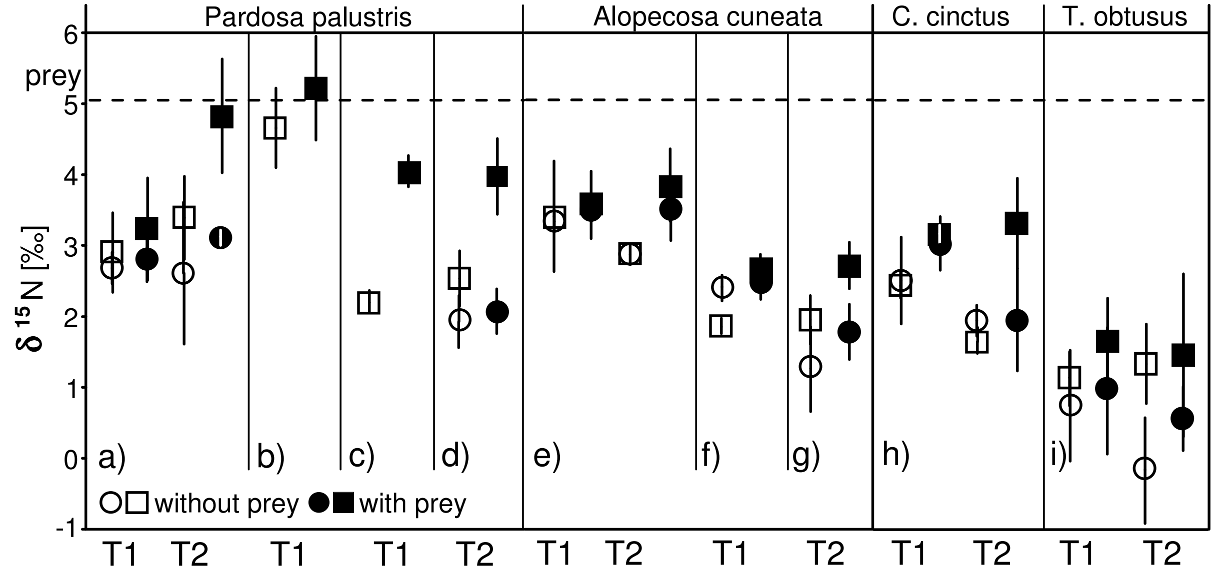

Fig. 2.7: **δ^{15}N ratios (± SD) of predators as affected by grazing (circles: without grazing; squares: with grazing) and prey addition in June (T1) and August (T2). δ^{15}N ratio of *Drosophila melanogaster* is indicated by a horizontal line. *Pardosa palustris*: (a) females, (b) eggsacs, (c) second instar juveniles, (d) third/ later instar juveniles; *Alopecosa cuneata*: (e) females, (f) second instar juveniles, (g) third/ later instar juveniles; *Calathus cinctus* (h); *Trechus obtusus* (i)**

III.3 Allochthonous Resources

Vegetation

The most abundant grass on the foredune and dominating plant was *Ammophila arenaria* (Poaceae), which is native to Europe and was introduced all over the world in order to stabilise sand (Zitat). *Carpobrotus rossii* (Aizoaceae), *Acaena novae-zelandiae* (Rosaceae) and *Lupinus arboreus* (Fabaceae) were the most abundant herbs. *Macrocystis* spec. (kelp; Lessoniaceae) was periodically washed ashore together with *Zostera* spec. (sea grass; Zosteraceae) and deposition was heaviest around the traps in-between the shoreline and the base of the foredune (personal observation). Plants differed strongly in $\delta^{15}N$ ($F_{9,20} = 21.96$, $p < 0.0001$) and $\delta^{13}C$ ($F_{9,20} = 30.86$, $p < 0.0001$), while the mixture of kelp and sea grass differed significantly from other plants (Fig. 3.1). The mixture of kelp and sea grass was enriched in ^{15}N by 7.02 ‰ and enriched in ^{13}C by 11.30 ‰, as compared to the foredune vegetation.

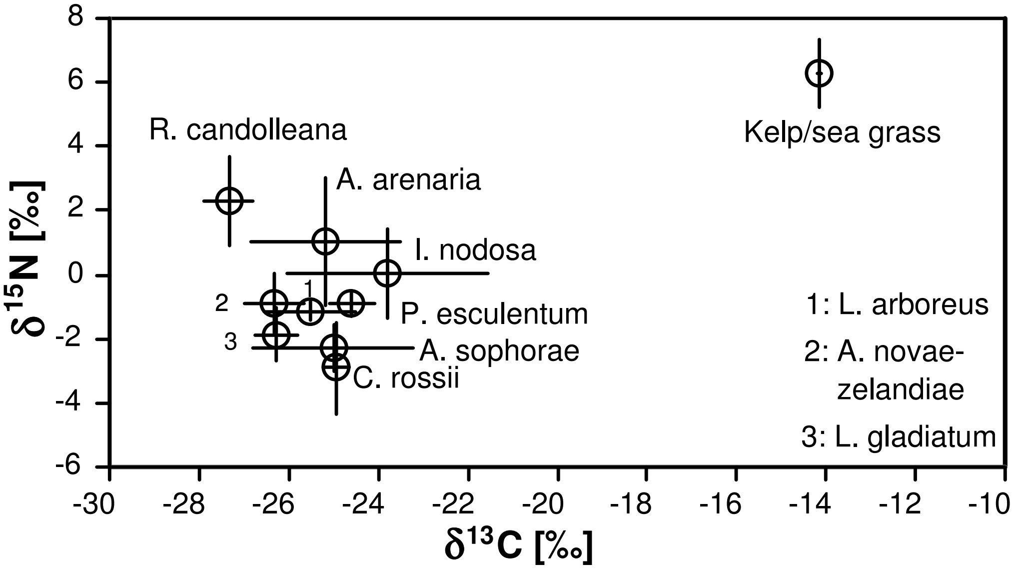

Fig. 3.1: **$\delta^{13}C$ and $\delta^{15}N$ signatures (± SD) of plants collected on the beach and foredune at Marion Bay: *Acacia sophorae* (Mimosaceae); *Acaena novae-zelandiae* (Rosaceae); *Ammophila arenaria* (Poaceae); *Carpobrotus rossii* (Aizoaceae); *Isolepis nodosa*, *Lepodosperma gladiatum* (Cyperaceae); *Lupinus arboreus* (Fabaceae); *Pteridium esculentum* (Dennstaedtiaceae); *Rhagodia candolleana* (Chenopodiaceae).**

Animals

A total of 4213 arthropods were collected within 9 days. Most important arthropods belonged to Crustacea (e.g. amphipods and isopods) and Insecta (e.g. beetles and flies) (Fig. 3.2; for detailed data on arthropod abundances see Appendix II).

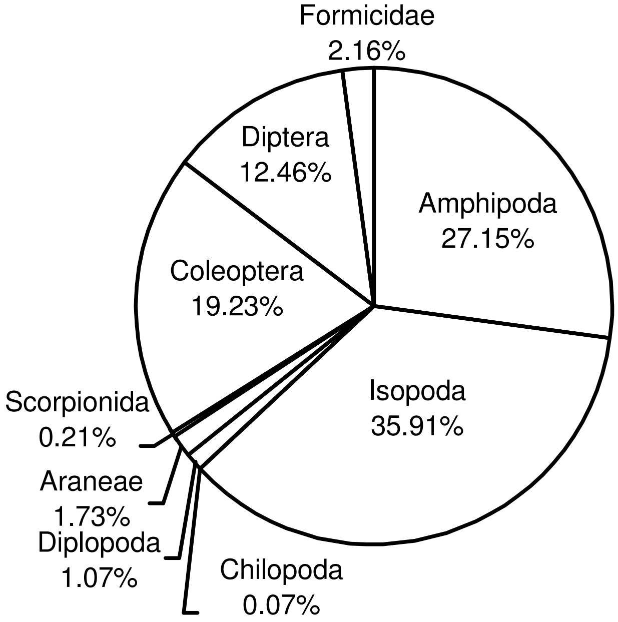

Fig. 3.2: Abundance distribution of arthropod groups from pitfall trap catches on the beach and foredune at Marion Bay.

Species were not equally distributed on the shore and foredune and were separated into the beach community (a-c) and the foredune community (d-e) along a gradient at the first axis (Eigenvalue 0.70; Fig. 3.3). *Actaecia thompsoni* (Isopoda) and the talitrid amphipods *Talorchestia* 2 (5-dentate sandhopper), *T. marmota* (5-dentate sandhopper) and *Orchestia* spec. as well as juvenile Amphipoda were most abundant on the shoreline (a, b), while the talitrid amphipod *Talorchestia* 1 (4-dentate sandhopper "longhorn") and *Porcellio scaber* (Isopoda) were found on the foredune (d, e). Most beetles were found on the foredune (d, e) with the exception of *Cafius* 2 (Staphylinidae), *Phycosecis littoralis* (Phycosecidae) and Halticinae 1 (Chrysomelidae). Similarly, most flies were trapped on the foredune (d, e) with the exception of some species of Brachycera (Scatophagidae 1, B4, B9, B11, and B28). Polydesmidae (Diplopoda), ants and the scorpion *Cercophonius squama* (Bothuridae) were restricted to the foredune (d, e). *Tetralycosa oraria* (Lycosidae) was the most abundant spider with a restricted occurrence on the beach (a-c) similar to *Tuoba laticeps*, the only chilopod caught. Generally, the foredune community included more species, than the beach community and only few species such as the fly Brachycera 29 and the weevils *Timareta* 6 and *Mandalotus* 8, occurred in both communities.

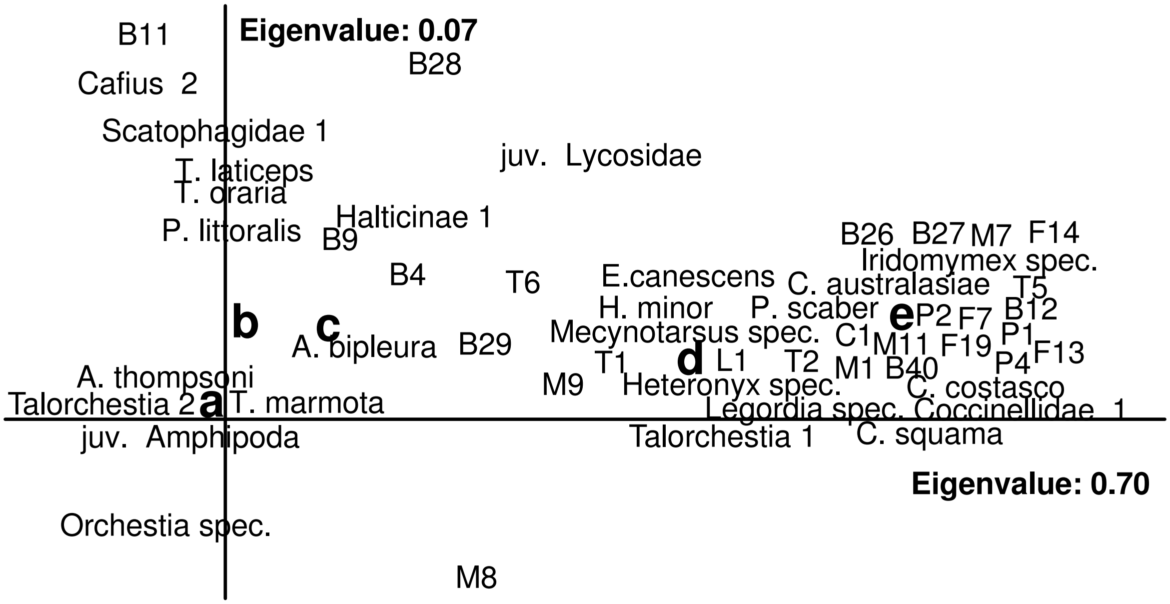

Fig. 3.3: Ordination of arthropods (log-transformed mean activity abundance data) and sampling sites along a transect (a-e) across the beach and foredune at Marion Bay. B: Brachycera (Diptera); F: Formicidae (Hymenoptera); Coleoptera (Curculionidae): M: *Mandalotus*; T: *Timareta*; P: Polydesmidae (Diplopoda). For description of the sampling sites see CHAPTER II.3; for complete species names see Appendix II.

Stable carbon and nitrogen ratios differed between the beach and the foredune communities. Within the beach community δ^{15}N signatures of animals ranged from 5.44 ‰ (*T. marmota*; Amphipoda) to 12.76 ‰ (*T. oraria* ♂; Araneae) (Fig. 3.4a). δ^{13}C signatures ranged from -21.83 ‰ (*P. littoralis*; Coleoptera) to -12.79 ‰ (*Actaecia bipleura*; Isopoda) (Fig. 3.4a). Therefore, the proportion of carbon derived from kelp and sea grass varied between 32.01 % (*P. littoralis*) and 111.83 % (*A. bipleura*) (Table 3.1).

Table 3.1: Proportion of carbon (± SD) derived from kelp and sea grass in arthropods from the beach at Marion Bay as calculated by a two-source mixing model (see text). For complete species names see Appendix II.

Taxon	carbon derived from kelp/ sea grass [%]	Taxon	carbon derived from kelp/ sea grass [%]
P. littoralis	32.01 ± 5.46	juvenile amphipods	76.62 ± 3.97
Myrmeleonidae	35.10 ± 5.10	*Orchestia* spec.	80.06 ± 5.91
Scatophagidae 1	53.46 ± 20.71	*Cafius* 2	84.53 ± 3.19
A. thompsoni	57.10 ± 12.41	*T. marmota*	87.55 ± 2.87
Talorchestia 2	69.93 ± 2.73	*T. laticeps*	93.06
T. oraria ♀	70.59 ± 7.95	*A. bipleura*	111.84 ± 4.53
T. oraria ♂	75.38 ± 6.74		

In contrast, $\delta^{15}N$ signatures of animals from the foredune community ranged from -3.76 ‰ (Polydesmidae 1; Diplopoda) to 8.78 ‰ (*Mecynotarsus* spec.; Coleoptera) (Fig. 3.4b). $\delta^{13}C$ signatures ranged from -25.50 ‰ (Entomobryidae; Collembola) to -21.24 ‰ (Polydesmidae 1; Diplopoda) (Fig. 3.4b) with proportions of carbon derived from kelp ranging from 0.00 % to a maximum of 37.14 % (Table 3.2).

Table 3.2: Proportion of carbon (± SD) derived from kelp and sea grass in arthropods from the foredune at Marion Bay as calculated by a two-source mixing model (see text). For complete species names see Appendix II.

Taxon	carbon derived from kelp/ sea grass [%]	Taxon	carbon derived from kelp/ sea grass [%]
Entomobryidae	-0.49 ± 2.36	*Heteronyx* spec.	12.89 ± 1.87
Timareta 6	5.37 ± 7.22	*Mecynotarsus* spec.	15.73 ± 6.59
E. canescens	6.44 ± 2.67	Myrmecinae	16.05 ± 9.26
C. costasco	7.68 ± 3.35	*H. minor*	16.28 ± 0.81
Mandalotus 9	8.54 ± 6.17	*Iridomymex* spec.	17.30 ± 5.54
Trombidiidae	8.56 ± 2.94	Cryptorhynchinae 1	20.22 ± 9.25
C. squama	9.95 ± 1.41	*Talorchestia* 1	27.01 ± 10.29
C. australasiae	12.35 ± 12.37	Polydesmidae 1	37.14 ± 8.99

In order to keep the data comprehensible, I focus on general stable isotope patterns and on the importance of the marine subsidies. Consequently, only the most important feeding links depending on allochthonous resources are described in detail below.

Beach Community

Most amphipods (juveniles, *T. marmota* and *Orchestia* spec.) and *A. bipleura* (Isopoda) hardly differed in $\delta^{15}N$ signature from kelp and sea grass, while Scatophagidae 1 (Diptera) as well as the wolf spiders (male and female *T. oraria*) were enriched in ^{15}N by 5.10 - 6.47 ‰ compared to kelp and sea grass. Interestingly, the isopod *A. thompsoni* and the amphipod *Talorchestia* 2 were enriched in ^{15}N by 2.65 and 3.34 ‰, respectively, compared to the signature of kelp and sea grass, and differed in stable isotope signatures from those of other amphipod and isopod species. $\delta^{15}N$ signatures of female and male *T. oraria* differed by 2.79 and 3.14 ‰, respectively, from those in *Talorchestia* 2, while $\delta^{13}C$ signatures differed by only 0.62 and 0.07 ‰, respectively, from those in the talitrid amphipod. Major food source of *T. oraria* was *Talorchestia* 2 (1-99th percentile: 69 – 88 %) and other amphipods and isopods contributed only little to the diet of the wolf spiders. In contrast to wolf spiders, *T. laticeps*

(Chilopoda) was enriched in ^{15}N by 2.98 ± 0.26 ‰ as compared to the average δ^{15}N signature of juvenile amphipods, *Orchestia* spec. and *A. bipleura* that I considered to be the most probable prey. Furthermore, δ^{13}C signature of the chilopod was increased by only 0.4 ‰ as compared to the average signature of the three crustacean groups in focus (δ^{13}C = -15.32 ± 2.20 ‰). Interestingly, *A. bipleura* and *T. marmota* appeared to constitute the majority of the diet of *T. laticeps* (1-99th percentile: 32 – 42 % and 22 – 51 %, respectively), and the other potential food sources contributing only little to its diet. *Cafius* 2 was enriched in ^{15}N by 3.61 ± 0.25 ‰ and depleted in ^{13}C by 0.56 ± 2.20 ‰, as compared to the average signature of juvenile amphipods, *Orchestia* spec. and *A. bipleura*. The latter appeared to contribute most to the diet of *Cafius* (1-99th percentile: 14 – 32 %), followed by the beachflea *Orchestia* and juvenile amphipods (0 – 57 % and 0 – 62 %, respectively).

Interestingly, antlions were slightly depleted in ^{15}N by 0.56 ‰ and strongly depleted in ^{13}C by 2.49 ‰ as compared to *A. thompsoni*, the prey with most similar stable isotope signature. In contrast, antlions were enriched in ^{15}N by 2.04 and 3.14 ‰, as well as enriched in ^{13}C by 2.01 and 2.51 ‰, as compared to the ants *Iridomymex* spec. and Myrmecinae from the foredune, respectively. Myrmecinae and *T. marmota* appeared to constitute the majority of the diet of antlions (1-99th percentile: 58 – 78 % and 11 – 30 %, respectively) and *Iridomymex* represented only a minor part of the diet (0 – 14 %), while the other amphipods and isopods were virtually not included in the diet of antlions. *P. littoralis* and Brachycera 1 were enriched in ^{15}N by 4.86 and 5.10 ‰, respectively compared to kelp. Furthermore, *P. littoralis* was strongly depleted in ^{13}C by 7.69 ‰, while Scatophagidae 1 was only depleted by 3.95 ‰. The latter seemed to feed predominately on *A. thompsoni* (1-99th percentile: 63 – 74 %) and to a minor part on *T. marmota* (8 – 26 %), while the other amphipods and isopods contributed only little to its diet.

Foredune Community

In contrast to the beach community animals from the foredune rather aggregated according to δ^{13}C ratios. *Heteronyx* spec. (Coleoptera), Cryptorhynchinae 1 (Coleoptera) and *Talorchestia* 1 (Amphipoda) were on average enriched in ^{15}N by 1.76 ‰ compared to plants on the foredune. In contrast, some beetles (*Mecynotarsus* spec., *Edylius canescens, Conoderus australasiae*) the ants (*Iridomymex* spec. & Myrmecinae spec.), *Cercophonius squama* (Scorpionida) and Trombidiidae (Acari) were enriched in ^{15}N by 5.98 - 8.78 ‰ compared to plants from the foredune. Interestingly, Polydesmidae 1 (Diplopoda) was depleted in ^{15}N by 3.02 ‰ compared to plants.

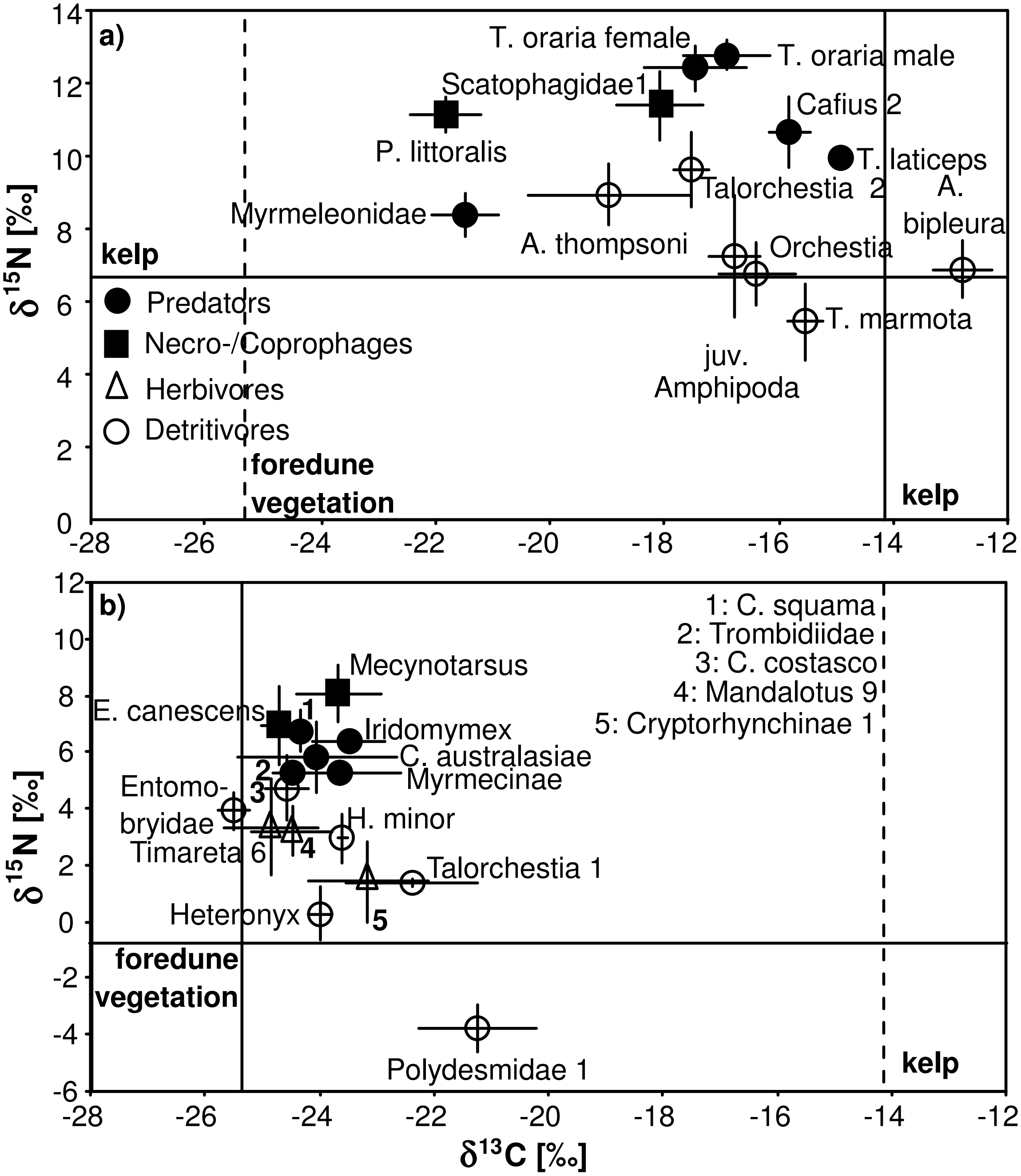

Fig. 3.4: **$\delta^{13}C$ and $\delta^{15}N$ signatures (± SD) of animals from the beach (a) and the foredune (b) at Marion Bay. $\delta^{15}N$ and $\delta^{13}C$ signatures of kelp/sea grass and vegetation on the foredune are indicated by vertical and horizontal lines. For complete species names see Appendix II.**

III.4 Food Quality

Female performance and offspring production

An average of 43.54 ± 8.22 spiderlings hatched from the first eggsacs (n = 76) that left their mothers 3.08 ± 1.14 days later. The number of juveniles was only slightly positively correlated to prosoma width of females ($r^2 = 0.062$, $F_{1,79} = 5.21$, $p = 0.025$), but there was a strong positive correlation between the weight of gravid females and the number of juveniles ($r^2 = 0.163$, $F_{1,79} = 15.43$, $p = 0.00018$; Fig. 4.1).

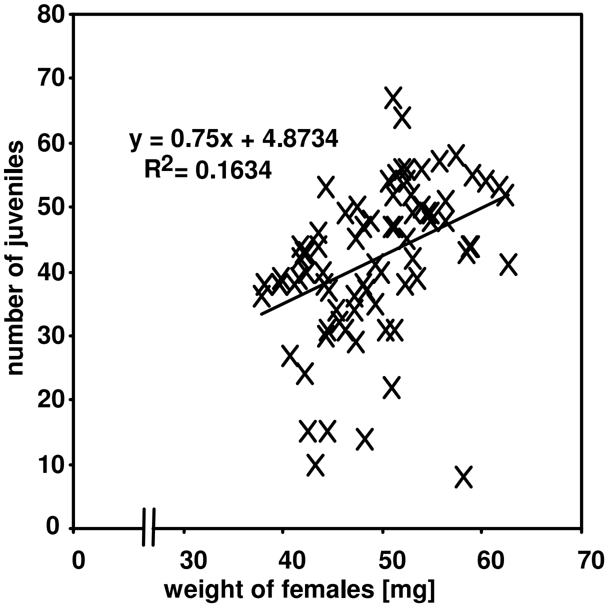

Fig. 4.1: Correlation of biomass of gravid females of *Pardosa lugubris* and number of juveniles in the first eggsac.

There was no correlation between weight of gravid females and mean dry weight of juveniles ($r^2 = 0.022$, $F_{1,34} = 0.76$, $p = 0.389$) or clutch size and mean juvenile weight per eggsac ($r^2 = 0.015$, $F_{1,34} = 0.50$, $p = 0.482$). Only females fed diets without *F. candida* produced a second eggsac on average 12.03 ± 4.02 days later (n = 41), while time until production differed between feeding treatments ($F_{2,33} = 3.73$, $p = 0.0347$). Females fed a diet containing *D. melanogaster* (D; DH) produced eggsacs earlier than those fed *H. nitidus* (H) (Fig. 4.2).

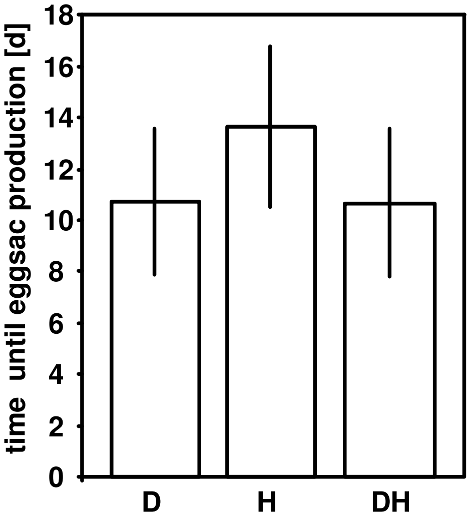

Fig. 4.2: Time until production (± SD) of the second eggsac as affected by different diets; D: single diet *Drosophila melanogaster*; H: single diet *Heteromurus nitidus*; DH: mixed diet of *D. melanogaster* and *H. nitidus*.

Females carried the eggsacs for 23.24 ± 1.65 days until they were opened for hatching of juveniles and there was no difference between the diet treatments in the duration eggsacs were carried ($F_{2,39} = 0.06$, $p = 0.943$). Between 9 and 23 spiderlings hatched from the second eggsacs. Spiderling number differed significantly between the first and the second eggsacs (Within Subjects Effect: $F_{1,27} = 206.74$, $p < 0.0001$), but did not differ between diets (Between Subjects Effect: $F_{2,27} = 1.97$, $p = 0.159$). In the second eggsac juvenile number (18.71 ± 7.62) dropped to less than half the number in the first eggsac (43.54 ± 8.22). Width of prosoma of juveniles did not differ between feeding treatments (Between Subjects Effect: $F_{2,15} = 0.83$, $p = 0.454$), but differed slightly between the first and the second eggsac (Within Subjects Effect: $F_{1,15} = 4.84$, $p = 0.044$). Prosoma width of juveniles declined from 0.72 ± 0.02 mm in the first to 0.71 ± 0.03 mm in the second eggsac. Average dry weight of juveniles also differed between the first and the second eggsacs (Within Subjects Effect: $F_{2,28} = 30.81$, $p < 0.0001$): Juveniles of the first eggsac weighed on average 0.172 ± 0.033 mg, while those of the second eggsac weighed only 0.125 ± 0.045 mg. After starvation the weight of juveniles dropped to 0.108 ± 0.022 mg, but this difference was not significant ($F_{1,14} = 0.67$, $p = 0.426$). Furthermore, the weight of juveniles did not differ between diets (Between Subject Effect: $F_{2,14} = 0.27$, $p = 0.770$). Survival of juveniles of the second eggsac ranged between 5 and 11 days and did not differ between diets either ($F_{2,28} = 1.48$, $p = 0.244$). Yet, survival of adults differed strongly between feeding treatments (Fig. 4.3): Females fed diets without *F. candida* (D; H; DH) survived until the end of the experiment, while females in treatments with *F. candida* (F; DF) had died after 61 days. Survival of females fed *F. candida* only (F) and a mixed of *D. melanogaster* and *F. candida* (DF) did not differ between treatments ($F_{1,28} = 1.49$, $p = 0.232$).

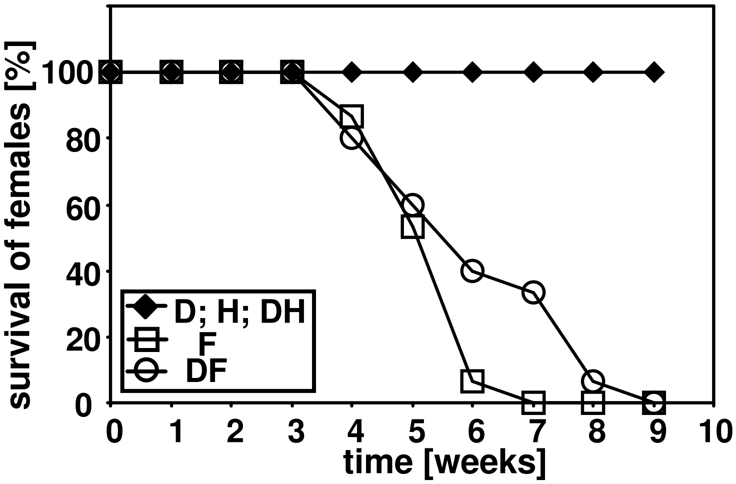

Fig. 4.3: Survival of female *Pardosa lugubris* fed different diets; D: single diet *Drosophila melanogaster*; H: single diet *Heteromurus nitidus*; F: single diet *Folsomia candida*; DH: mixed diet of *D. melanogaster* and *H. nitidus*; DF: mixed diet of *D. melanogaster* and *F. candida*.

Dry weight of females at the end of the experiment differed strongly between diets ($F_{4,70} = 12.75$, $p < 0.0001$). Females fed diets containing *F. candida* were less heavy compared to the other feeding treatments, with females fed *D. melanogaster* only (D) being the heaviest (Fig. 4.4).

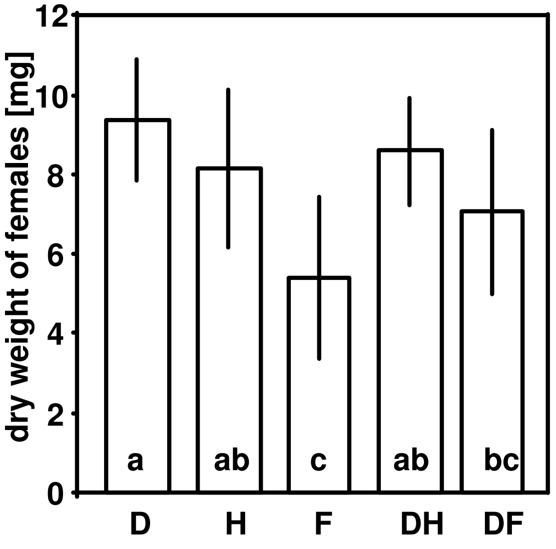

Fig. 4.4: Dry weight (± SD) of female *Pardosa lugubris* fed different diets. (For legend see Fig. 4.3)

C:N ratio and stable isotopes

The carbon-to-nitrogen (C:N) ratio of females differed significantly between treatments ($F_{5,12} = 4.39$, $p = 0.0167$). In females fed *D. melanogaster* only (D) it was highest, whereas in those fed *F. candida* only (F) and a mixed diet of *D. melanogaster* and *H. nitidus* (DH) it was lowest (Fig. 4.5). The C:N ratio of juveniles of the first eggsac did not differ between diet treatments ($F_{4,9} = 0.30$, $p = 0.8684$). Differences in C:N ratios calculated between females and juveniles of the second eggsac did not differ between feeding treatments either ($F_{2,6} = 3.41$, $p = 0.1025$). In contrast, starved juveniles of the second eggsac had significantly lower C:N ratios compared to those that had just dispersed from their mothers (Within Subjects Effect: $F_{1,6} = 45.99$, $p = 0.0005$) (Fig. 4.5), while C:N ratios did not differ between feeding treatments (Between Subjects Effect: $F_{1,6} = 0.46$, $p = 0.6536$).

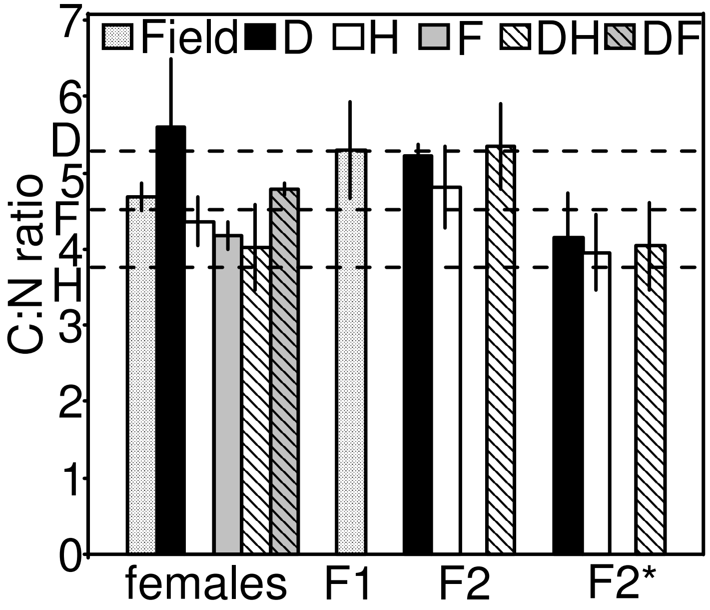

Fig. 4.5: C:N ratios (± SD) of female *Pardosa lugubris* and juvenile wolf spiders of the first (F1) and the second eggsac (F2), as well as starved juveniles of the second eggsac (F2*) as affected by different diets. (For legend see Fig. 4.3)

$\delta^{13}C$ ratios of females fed in the laboratory differed strongly between feeding treatments ($F_{5,12} = 25.28$; $p < 0.0001$). While $\delta^{13}C$ signatures of females kept on C_3 diet (H; F) and on a mixed diet of *D. melanogaster* and *F. candida* (DF) did not differ significantly from the initial signature, females fed *D. melanogaster* only (D) and a mixed diet of *D. melanogaster* and *H. nitidus* (DH) were enriched in ^{13}C by 7.31 and 2.52 ‰, respectively (Fig. 4.6). Feeding treatments also affected $\delta^{15}N$ ratios of females ($F_{5,12} = 6.85$, $p = 0.003$). Females fed a mixed diet of *D. melanogaster* and *F. candida* (DF) were significantly depleted in ^{15}N by 2.32 ‰ compared to the initial signature, while females of other feeding treatments did not differ from the initial signature (Fig. 4.7).

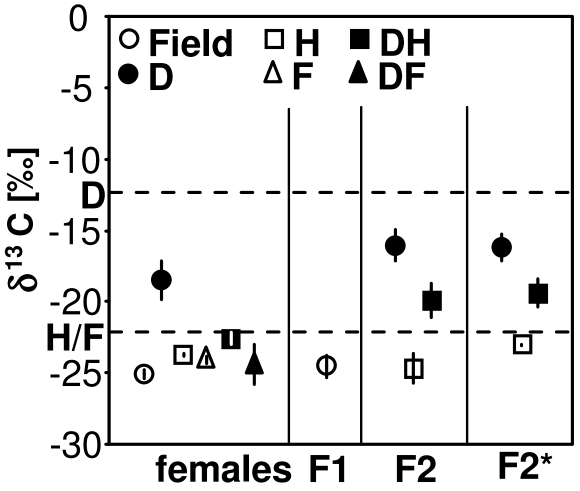

Fig. 4.6: **$\delta^{13}C$ ratios (±SD) of female *Pardosa lugubris* and juvenile wolf spiders of the first (F1) and the second eggsac (F2), as well as starved juveniles of the second eggsac (F2*) as affected by different diets. $\delta^{13}C$ ratios of prey are indicated by horizontal lines. (For legend see Fig. 4.3)**

In general, females were enriched in ^{13}C and ^{15}N as compared to their first offspring (1st eggsacs; Fig. 4.6 & 4.7) and stable isotope signatures of these juveniles did not differ between diets ($\delta^{13}C$: $F_{4,9} = 0.99$, $p = 0.4581$; $\delta^{15}N$: $F_{4,9} = 1.12$, $p = 0.4050$). In contrast, enrichment in ^{13}C of juveniles of the second eggsacs differed between feeding treatments ($F_{2,6} = 9.48$, $p = 0.139$). Juveniles of females fed *D. melanogaster* only (D) and a mixed diet *D. melanogaster* and *H. nitidus* (DH) were similarly enriched in ^{13}C by 2.65 ‰ and 2.47 ‰, respectively, while juveniles of females fed *H. nitidus* only (H) were slightly depleted by 0.97 ‰ (Fig. 4.6).

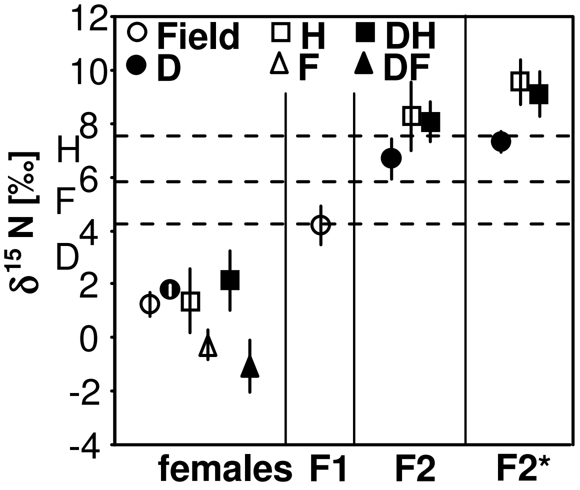

Fig. 4.7: **$\delta^{15}N$ ratios (±SD) of female *Pardosa lugubris* and juvenile wolf spiders of the first (F1) and the second eggsac (F2), as well as starved juveniles of the second eggsac (F2*) as affected by different diets. $\delta^{15}N$ ratios of prey are indicated by horizontal lines. (For legend see Fig. 4.3)**

Juveniles of the second eggsacs were generally enriched in ^{15}N and the enrichment did not differ between treatments ($F_{2,6} = 2.70$, $p = 0.146$), even though it was somewhat more pronounced in diets containing *H. nitidus* (Fig. 4.7). Starvation affected δ^{13}C ratios of second instar juveniles (2nd eggsacs) differently (starvation x food interaction: $F_{2,6} = 5.82$, $p = 0.039$). Starved juveniles of females fed *D. melanogaster* only (D) were slightly depleted in ^{13}C, while those of females fed diets containing *H. nitidus* (H; DH) were slightly enriched in ^{13}C (Fig. 4.6). δ^{15}N ratios were also affected by starvation ($F_{1,6} = 14.91$, $p = 0.008$); starved juveniles were uniformly enriched in ^{15}N compared to those that had just left their mother (Fig. 4.7).

III.5 Cannibalism

Cannibalism among second instar juveniles

Per capita mortality rate of juvenile spiders increased with time ($F_{5,68} = 200.14$, $p < 0.0001$; Fig. 5.1). Presence of alternative prey strongly decreased per capita mortality ($F_{1,72} = 282.33$, $p < 0.0001$); the effect increased during the first 12 days and then remained constant (time x prey interaction; $F_{5,68} = 38.69$, $p < 0.0001$). After 18 days per capita mortality of juveniles in treatments without alternative prey reached 95 %, while in treatments with alternative prey it was only 46 %. At higher density the mortality was significantly increased ($F_{1,72} = 6.77$, $p = 0.0113$), but this tended to be more pronounced in treatments with alternative prey (alternative prey x density interaction; $F_{1,72} = 3.34$, $p = 0.0717$; Fig. 5.1).

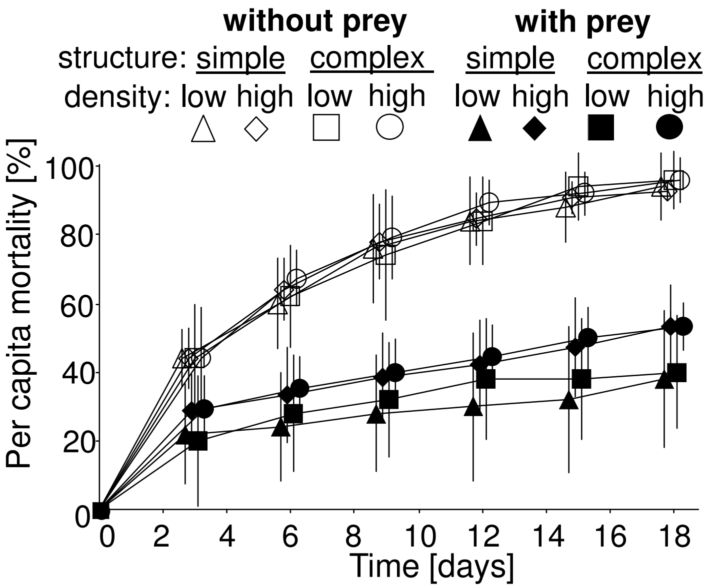

Fig. 5.1: Cumulative per capita mortality of juvenile spiders (± SD) as affected by habitat structure (simple, complex), density (low, high) and prey availability (without, with *Heteromurus nitidus*) during 18 days.

Presence of alternative prey resulted in a significantly increased body weight of spiderlings at the end of the experiment ($F_{1,52} = 86.56$, $p < 0.0001$; Fig. 5.2). However, the increase tended to be more pronounced at low density and complex habitat structure (habitat structure x density x alternative prey interaction; $F_{1,52} = 3.64$, $p = 0.0619$). At low density without alternative prey, spiderlings in complex habitat structure were almost twice as heavy as those in simple habitat structure, while at high density without alternative prey weights were similar regardless of habitat structure.

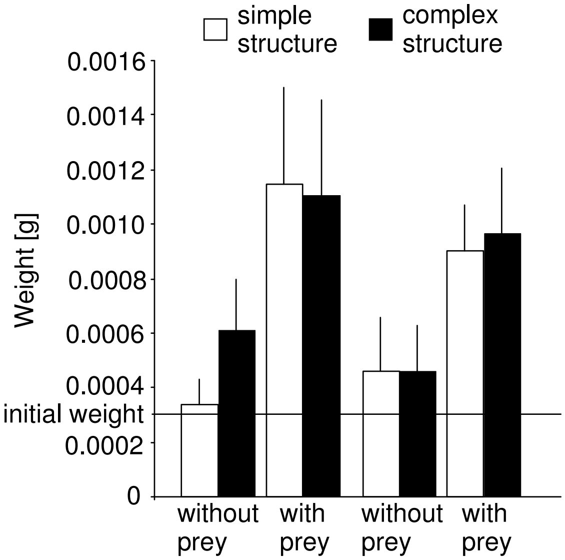

Fig. 5.2: Weight of juvenile spiders (+ SD) as affected by habitat structure (simple, complex), density (low, high) and prey availability (without, with *Heteromurus nitidus*) after 18 days.

Cannibalism between females and juveniles

Mortality of spiderlings was high after the first three days and ranged between 60 % (simple habitat structure with alternative prey) and 90 % (simple habitat structure without alternative prey) (Fig. 5.3). After 11 days only 4 out of 320 spiderlings had survived. Generally, mortality of spiderlings increased significantly from day 3 to day 5 ($F_{1,36} = 46.10$, $p < 0.0001$; Fig. 5.3). Only in the simple habitat structure treatment the absence of alternative prey significantly increased mortality of juvenile spiders (habitat structure x alternative prey interaction; $F_{1,36} = 12.22$, $p = 0.0013$).

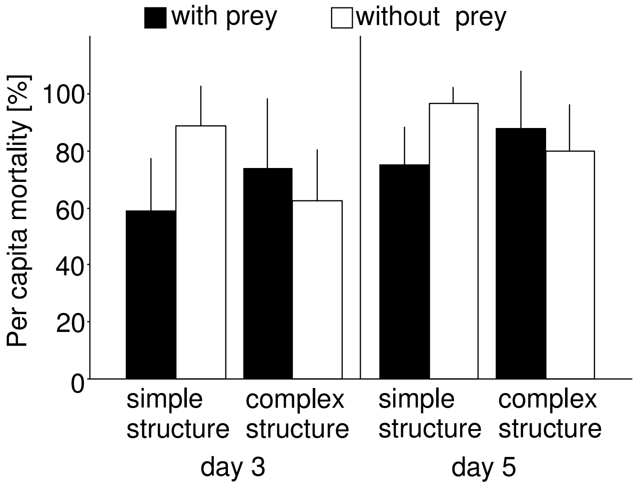

Fig. 5.3: Cumulative per capita mortality of juvenile spiders (+ SD) in presence of one adult female as affected by habitat structure and alternative prey (*Drosophila melanogaster*) after 3 and 5 days.

At the end of the experiment (after 11 days) mortality of females in treatments without alternative prey ranged between 60 and 70 %. In the alternative prey treatments all females survived with some even producing eggsacs. Without alternative prey, mortality of females increased during the experiment, but females died earlier in the complex habitat structure treatment: after 7 days 50 % of females had died in the complex habitat structure, while in the simple habitat structure all females were still alive ($G_{1,20} = 7.78$, $p < 0.05$). After 9 days 60 % of females in the complex habitat structure had died, while in the simple habitat structure only 10 % were dead ($G_{1,20} = 5.30$, $p < 0.05$). At the end of the experiment (after 11 days) mortality was similar in simple and complex habitat structure treatments without alternative prey.

Generally, alternative prey caused an increase in biomass of females ($F_{1,23} = 34.52$, $p < 0.0001$) (Fig. 5.4). However, the differences in weight were more pronounced in the complex habitat structure due to the decline in body weight in the complex structure treatment without alternative prey (significant alternative prey x habitat structure interaction; $F_{1,23} = 16.93$, $p = 0.0004$).

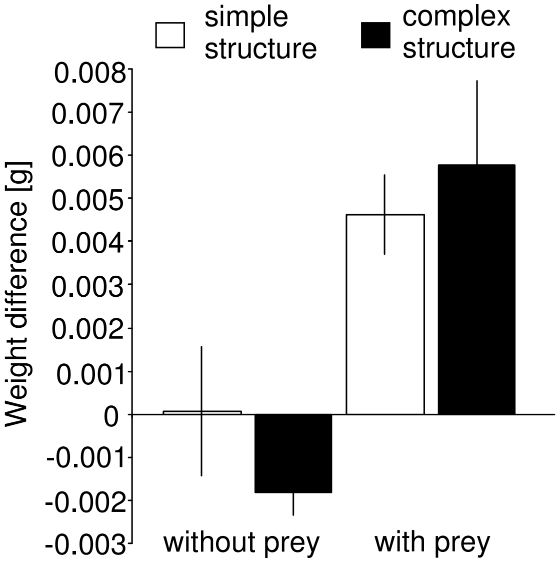

Fig. 5.4: Differences in weight of female spiders before and at the end of the experiment (± SD) as affected by habitat structure (simple, complex) and availability of alternative prey (without, with *Drosophila melanogaster*).

III.6 IGP

Mortality of *P. palustris* increased during the experiment (Table 6.1; Fig. 6.1), it was highest at simple habitat structure without alternative prey. Generally, mortality of second instar *P. palustris* was affected by the availability of alternative prey as well as the interaction of alternative prey and habitat structure (Table 6.1).

Table 6.1: Within and between subjects effects of a repeated measures GLM; influence of habitat structure (simple; complex) and alternative prey (absence; presence) on mortality of *P. palustris*.

	treatment	Df model	Df error	F	p
between subjects effects	structure	1	35	0.07	0.7889
	alternative prey	1	35	23.58	< 0.0001
	structure*alternative prey	1	35	4.96	0.0352
within subjects effects	time	6	210	102.16	< 0.0001
	time*structure	6	210	0.67	0.6766
	time*alternative prey	6	210	11.47	< 0.0001
	time*structure*alternative prey	6	210	0.70	0.6475

The effect of alternative prey changed with time: during the first 6 days, absence of alternative prey increased mortality of *P. palustris* only at simple habitat structure (prey x habitat structure interaction), while after 8 days, mortality increased also at complex habitat structure without alternative prey (Table 6.1; Fig. 6.1).

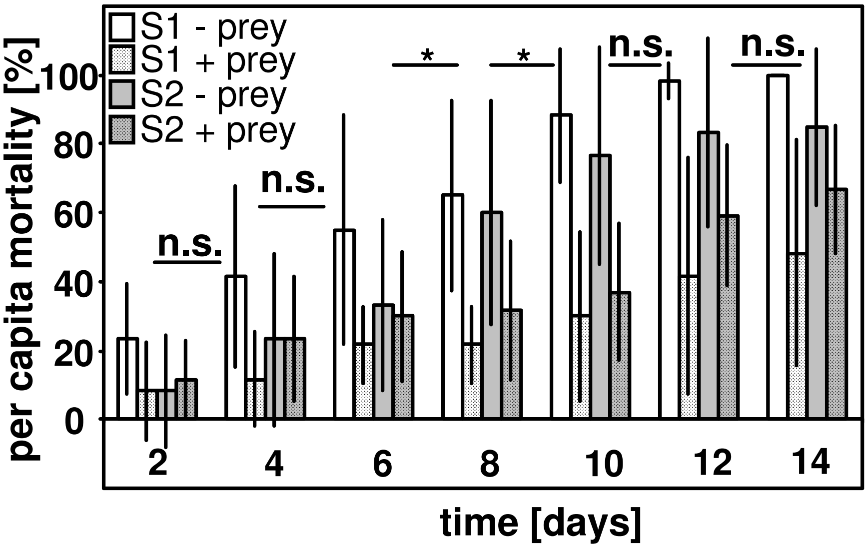

Fig. 6.1: Cumulative mortality (± SD) of juvenile *Pardosa palustris* as affected by habitat structure (S1: simple structure; S2: complex structure) and availability of alternative prey during two weeks. Asterisks indicate significant differences between time intervals. For further statistics of interactions see text.

After 10 days, mortality of juvenile *P. palustris* increased strongly when alternative prey was missing (Fig. 6.1). In treatments with IGP and alternative prey all individuals of *A. cuneata* survived until the end of the experiment. Without prey, *A. cuneata* started to die after 10 days and mortality was pronounced in simple habitat structure ($G_{1,20} = 6.97$, $p < 0.01$) (Fig. 6.2).

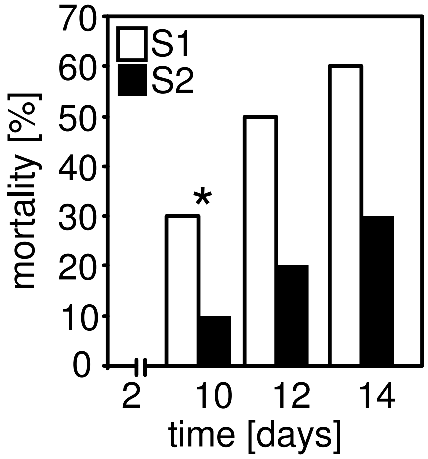

Fig. 6.2*:* **Cumulative mortality of starving juvenile *Alopecosa cuneata* as affected by habitat structure (S1: simple structure; S2: complex structure). Asterisks indicate significant differences between treatments.**

Bodyweight of *A. cuneata* also differed between treatments ($F_{7,69} = 60.31$, $p < 0.0001$; Fig. 6.3). In treatments with IGP and in those with alternative prey weight gain of spiders was significantly increased from 1.12 mg to 2.02 mg ($F_{1,69} = 50.70$, $p < 0.0001$) and from 0.39 mg to 2.69 mg ($F_{1,69} = 357.27$, $p < 0.0001$), respectively. In treatments with alternative prey the increase in body weight was more pronounced at complex habitat structure (habitat structure x alternative prey interaction; $F_{1,69} = 8.88$, $p = 0.0040$) and also when both alternative prey and IGP were available (habitat structure x prey x IGP interaction; $F_{1,69} = 4.58$, $p = 0.0359$).

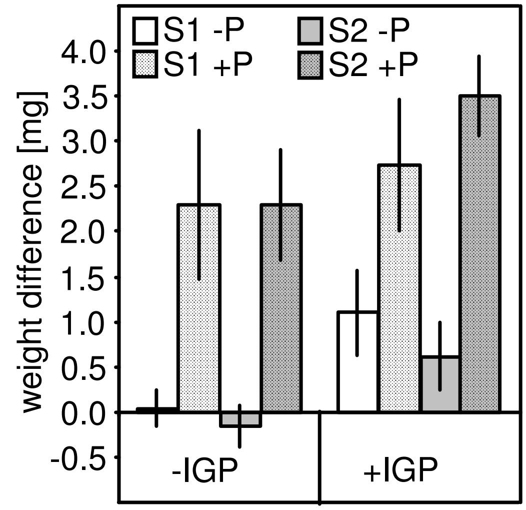

Fig. 6.3: Weight differences (± SD) of juvenile *Alopecosa cuneata* as affected by IGP, alternative prey (-P: without prey; +P: with prey) and habitat structure (S1: simple structure; S2: complex structure).

Even though juvenile *P. palustris* seemed to gain weight in treatments with alternative prey, changes in body weight of individual spiderlings within treatments were very high, resulting in high standard deviations in simple habitat structure with alternative prey (0.23 ±0.43 mg) and in complex structure with alternative prey (0.22 ± 0.25 mg). Consequently, differences between treatments were not significant ($F_{2,19} = 0.80$, $p = 0.4634$).

C:N ratio and stable isotopes

The C:N ratio of juvenile *A. cuneata* was significantly increased when alternative prey was available ($F_{1,44} = 59.34$, $p < 0.0001$) (Fig. 6.4). Furthermore, the C:N ratio of juvenile *P. palustris* was significantly increased at complex habitat structure without alternative prey as compared to complex habitat structure with alternative prey ($F_{2,19} = 4.14$, $p = 0.0267$) (Fig. 6.4).

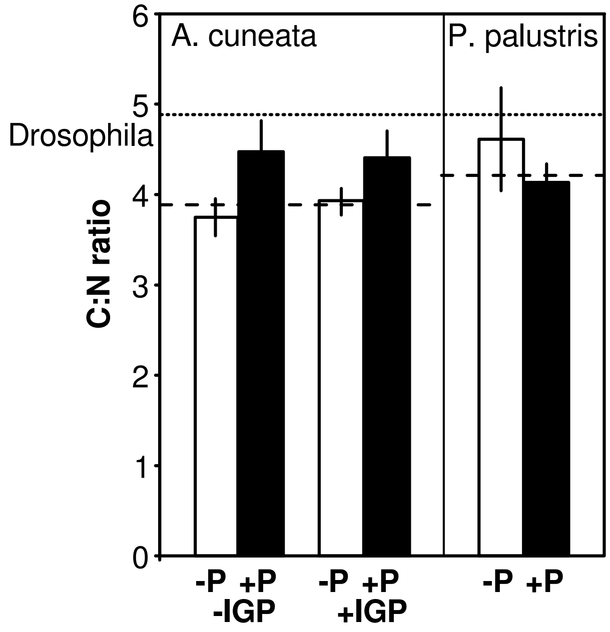

Fig. 6.4: C:N ratio (± SD) of juvenile *Alopecosa cuneata* and *Pardosa palustris* as affected by IGP and/or alternative prey (-P: without prey; +P: with prey). Initial C:N ratios of *A. cuneata*, *P. palustris* and their prey *Drosophila melanogaster* are indicated by horizontal lines.

$\delta^{13}C$ ratios of *A. cuneata* varied with the availability of intraguild prey (*P. palustris*) and alternative prey (*D. melanogaster*) (Fig. 6.5a). While feeding on juvenile *P. palustris* resulted only in slightly higher $\delta^{13}C$ ratios ($\Delta^{13}C = 0.06$ ‰; $F_{1,44} = 21.32$, $p < 0.0001$), feeding on alternative prey resulted in strongly increased $\delta^{13}C$ ratios ($\Delta^{13}C = 98.14$ ‰; $F_{1,44} = 2526.90$, $p < 0.0001$) and the increase was most pronounced without intraguild prey ($F_{1,44} = 24.12$, $p < 0.0001$). Feeding on intraguild prey (*P. palustris*) and alternative prey (*D. melanogaster*) affected $\delta^{15}N$ ratios of *A. cuneata* differently (Fig. 6.5b). While spiderlings feeding on *D. melanogaster* were slightly depleted in ^{15}N ($\Delta^{15}N = -0.85$ ‰; $F_{1,44} = 5.82$, $p = 0.0201$) spiderlings feeding on *P. palustris* were enriched ($\Delta^{15}N = 0.63$ ‰; $F_{1,44} = 11.45$, $p = 0.0015$) and the increase was most pronounced without alternative prey ($F_{1,44} = 6.15$, $p = 0.0170$). $\delta^{15}N$ ratios of *P. palustris* did not differ between treatments ($F_{2,19} = 1.93$, $p = 0.1713$) (Fig. 6.5b). In contrast, $\delta^{13}C$ ratios of *P. palustris* were significantly increased in treatments with alternative prey ($F_{2,19} = 5.95$, $p = 0.0098$) and differed strongly within these treatments resulting in pronounced standard deviations (Fig. 6.5a). $\delta^{13}C$ ratios were positively correlated with the body weight of juvenile *P. palustris* at the end of the experiment at simple habitat structure with alternative prey ($r^2 = 0.72$, $F_{1,4} = 10.41$, $p = 0.0320$) (Fig. 6.6), but not at complex habitat structure with alternative prey ($r^2 = 0.20$, $F_{1,4} = 1.02$, $p = 0.3702$). Habitat structure did not affect C:N ratios or stable isotope signatures of *A. cuneata* and *P. palustris* (Fig. 6.4 & 6.5).

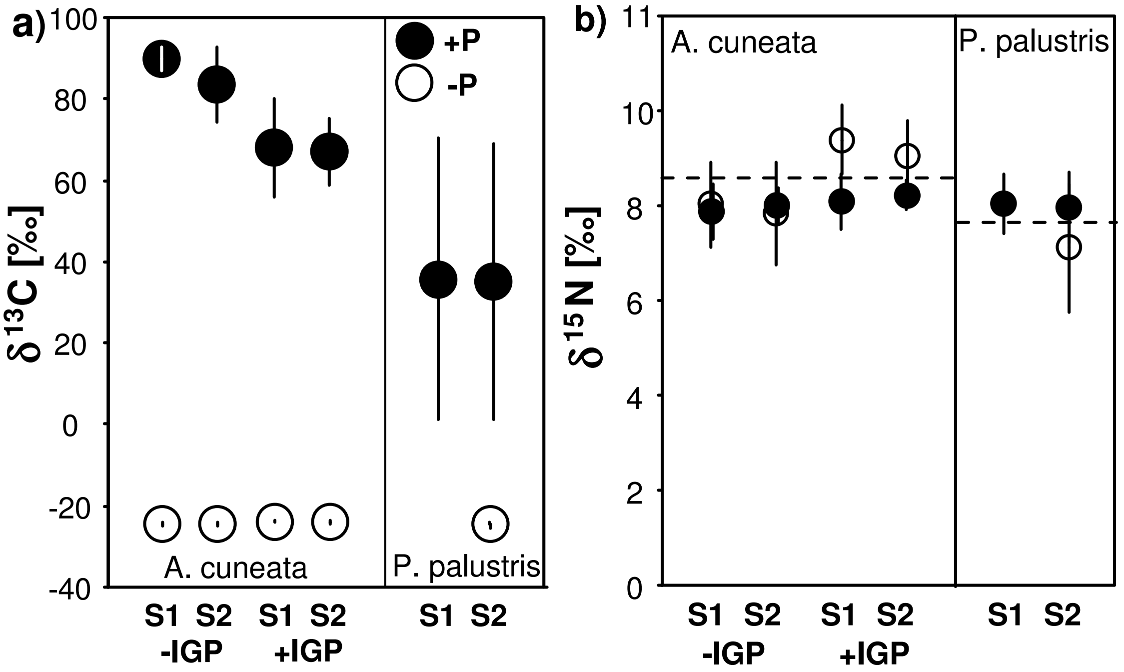

Fig. 6.5: $\delta^{13}C$ ratio (± SD) (a) and $\delta^{15}N$ ratio (± SD) (b) of juvenile *Alopecosa cuneata* and *Pardosa palustris* as affected by IGP, alternative prey (-P: without prey; +P: with prey) and habitat structure (S1: simple structure; S2: complex structure). $\delta^{15}N$ ratio of *Drosophila melanogaster* is indicated by a horizontal line.

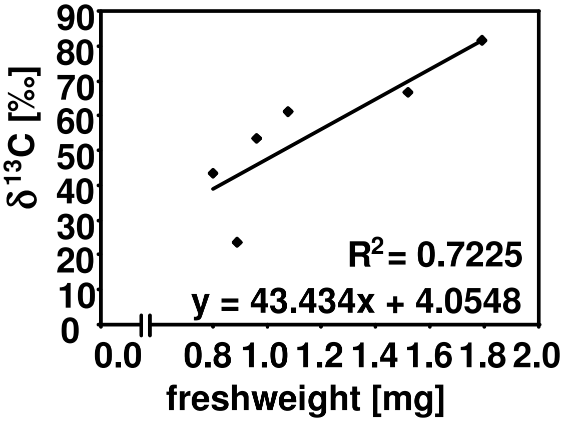

Fig. 6.6: Correlation between weight of juvenile *Pardosa palustris* and $\delta^{13}C$ ratio at simple habitat structure with alternative prey.

IV Discussion

IV.1 Phenology

I refrained from presenting data on activity density of juveniles, since the interpretation of pitfall trap catches of individuals with limited walking distances in complex habitat structure should be handled with great care (MELBOURNE 1999; HOLLAND & SMITH 1999; STANDEN 2000). Consequently, probability of catches with pitfall traps of small spiders in a very heterogeneous habitat, such as the grasslands of the former airfield, presumably is very low.

Both wolf spider species seem to be univoltin and complete their development within one year. Furthermore, in both spiders male individuals die shortly after mating and consequently disappear in June. Nevertheless, phenologies differ strongly between *P. palustris* and *A. cuneata*. The bigger spider *A. cuneata* overwinters predominately as subadult spiders and they mature already in April, which is why *A. cuneata* reproduces somewhat earlier than the smaller wolf spider. As in *P. palustris* juvenile stages overwinter and those mature not before May, reproduction is somewhat delayed. Probably, the bigger *A. cuneata* is a superior competitor limiting prey availability for the smaller spider resulting in prolonged development of *P. palustris*.

The fact, that female *A. cuneata* carrying eggsacs could not be captured with pitfall traps is not surprising, since *Alopecosa* retreats to a web burrow after eggsac production and reduces activity (ROBERTS 1995; CHAPTER II.6). Yet, female *A. cuneata* leave their burrow from time to time to expose the eggsac to the sun and was observed occasionally during the field season 2003 and 2005. Interestingly, during the prey addition experiment 2002 (CHAPTER III.2) female *P. palustris* with eggsacs were captured in August, suggesting the production of second eggsacs in the field. *P. palustris* is known to produce second eggsacs in grasslands, probably depending on resource availability and abiotic conditions (BAYRAM 2000).

Reliable data on the occurrence of second eggsacs and accurate estimates for juvenile density in the field can only be derived from more time intensive methods such as mark and recapture studies and hand searching in the field. Nevertheless, using monthly pitfall trap catches during one field season yielded an overview of the life cycle of both *P. palustris* and *A. cuneata* and revealed clear differences between both coexisting species. The knowledge of the time of mating and reproduction was crucial for field and laboratory experiments that included *A. cuneata* and/or *P. palustris*.

IV.2 Prey Availability

Effects of prey addition

Detritivores: Abundances of Collembola were not affected by prey addition, indicating that either Collembola were not top-down controlled, or prey addition did not relax predation pressure. Despite the absence of effects on detritivore abundance, stable isotope signatures of Collembola changed in the prey addition treatment, i.e. *E. nivalis* and *I. viridis* were enriched in ^{15}N. The fruit flies were cultivated on a medium rich in ^{15}N (δ^{15}N = 3.08 ‰) and the culture medium containing pupae and larvae of *D. melanogaster* was added to the plots together with adult flies to increase fruit fly density. Presumably, both Collembola species used the culture medium as a food resource. In contrast, as indicated by δ^{15}N ratios *L. cyaneus* did not feed on this alternative resource. Collembola predominantly graze on fungi, but also ingest detritus, algae and in part even higher plants and other animals (MOORE et al. 1987; CHEN et al. 1995). Based on its ^{15}N signature, SCHEU & FALCA (2000) classified *Lepidocyrtus* spec. as secondary decomposer. For *L. cyaneus* very similar nitrogen isotope ratios were measured in this study confirming the earlier classification. Lower δ^{15}N values of *I. viridis* and *E. nivalis* indicate that they directly feed on detritus and therefore function as primary decomposers.

Herbivores: In general, densities and stable isotope signatures of herbivores were not affected by the presence of *D. melanogaster*. Yet, significant changes in the effect of prey addition on densities of juvenile Auchenorrhyncha between June and August occurred that depended on grazing. In June, juvenile leafhoppers were most abundant on sites with prey addition, indicating reduced predation pressure when alternative prey was available for predators. In August however, densities of juveniles declined strongly in all treatments except for the grazed treatment without additional prey. From June to August densities of juvenile Auchenorrhyncha decline since most species reproduce early in the summer (WALLUS 2002). In August, most of the vegetation has dried out and especially on the non-grazed sites, where the neophytic grass *C. dactylon* is most abundant, resource availability for Auchenorrhyncha is presumably low. The pronounced decline on grazed sites with additional prey suggests that predation pressure strongly increased from June to August especially when *D. melanogaster* was added. In August, juvenile spiders may have preyed on juvenile Auchenorrhyncha as indicated by the nearly significant negative correlation between the density of juvenile Auchenorrhyncha and juvenile spiders. However, density of spiderlings was not significantly increased on sites with additional prey.

Predators: Neither the density nor the fecundity of wolf spiders was affected by the addition of prey, which is in contrast to other studies (SPILLER 1992; CHEN & WISE 1999; KREITER & WISE 2001). However, the addition of *D. melanogaster* significantly affected stable isotope signatures of predators proving that they were preying on *D. melanogaster*. Female *P. palustris* incorporated little nitrogen from *D. melanogaster*, but second instar juveniles were significantly enriched in ^{15}N. Females invest most of the ingested nutrients into egg production (CHAPTER IV.4), suggesting that females substantially fed on *D. melanogaster* that was rich in ^{15}N and transferred most of the ingested nitrogen into their offspring. Later instars of *P. palustris* were also enriched in ^{15}N in the prey addition treatment, documenting predation of the spiderlings on *D. melanogaster*. However, the enrichment in ^{15}N only occurred on grazed sites, indicating that spider predation on *D. melanogaster* was restricted to grazed sites. This is supported by a strong decrease in ^{13}C in older juveniles on grazed sites with prey addition, with the δ^{13}C signature approaching that of *D. melanogaster*. Even if alternative prey was provided, older spiderlings on non-grazed sites obviously preyed predominately on indigenous prey such as *L. cyaneus*, resulting in a similar δ^{13}C signature to that of the springtail ($\Delta^{13}C = 0.36$ ‰), but the low difference in δ^{15}N signature ($\Delta^{15}N = 1.19$ ‰) suggests that additional prey with lower δ^{15}N signatures was consumed, too. Female *A. cuneata* also incorporated nitrogen from *D. melanogaster*, which was most obvious in August. In June however, second instar juveniles of *A. cuneata* were slightly enriched in ^{15}N and ^{13}C on sites with additional prey reflecting the consumption of *D. melanogaster* (with increased δ^{15}N signature) by female *A. cuneata* during egg production. The enrichment in ^{15}N of second instar juveniles was lower compared to second instar juveniles of *P. palustris,* and juvenile *A. cuenata* were enriched in ^{13}C instead of depleted, suggesting that female *A. cuneata* fed predominately on indigenous prey (with higher δ^{13}C signature) during egg production. *A. cuneata* reproduces somewhat earlier than *P. palustris* (CHAPTER IV.1), which is why compared to *P. palustris*, *A. cuneata* had less time to prey on *D. melanogaster* before eggsac production. The enrichment in ^{15}N of second instar juveniles of *A. cuneata* tended to be more pronounced on grazed sites, indicating enhanced success of females on grazed sites capturing *D. melanogaster*. Later instars of *A. cuneata* were also enriched in ^{15}N, suggesting that *D. melanogaster* was included into their diet. Summarizing, both adult and juvenile spiders of *P. palustris* and *A. cuneata* fed on *D. melanogaster* that was added as alternative prey. Nitrogen isotope signatures of female *P. palustris* as well as nitrogen and carbon isotope signatures of later instars of *P. palustris* document that capturing *D. melanogaster* on grazed sites significantly exceeded that on non-grazed sites. Since litter is accumulating on sites without sheep grazing (McIntosh et al. 1997; Xi & Wittig 2004), habitat structure is increased, providing shelter for *D. melanogaster* from predation by wolf spiders.

Ground beetle abundance did not react to prey addition, even though positive effects of additional prey on densities of Carabidae are known (Halaj & Wise 2002). Presumably, prey addition started too late to increase survival of beetle larvae. Therefore, beneficial effects of prey addition could have been detected in the next generation only. However, changes in stable isotope composition documented that *C. cinctus* included *D. melanogaster* into its diet in June, resulting in an increase in $\delta^{15}N$ and a decrease in $\delta^{13}C$ signatures. In August, *D. melanogaster* did not contribute to its diet, as indicated by similar stable isotope signatures in plots with and without additional prey. In June, *T. obtusus* was significantly depleted in ^{13}C and seemed enriched in ^{15}N when additional prey was provided, suggesting predation on *D. melanogaster*.

The fact that *D. melanogaster* was integrated into the diet of the predators suggests that Collembola populations of the studied grassland were not top-down controlled, since Collembola densities were not increased by prey addition. This is in contrast to a study in a forest ecosystem, where densities of springtails were controlled by generalist predators (Wise 2004).

Effects of grazing

Detritivores: In June, densities of the primary decomposers *E. nivalis* and *I. viridis* were strongly increased on grazed sites, corroborating findings from Ferguson & Joly (2002). Grazing is known to change the abundance of soil biota including Collembola (Bardgett et al. 1993; Bardgett et al. 1998; Dombos 2001), since litter quality and habitat characteristics change due to grazing (Semmartin et al. 2004). Food quality of C_4 plants is generally low due to a high content of cellulose and a low content of nitrogen (Caswell et al. 1973; Haddad et al. 2001). Since abandonment of grazing increased the density of the C_4 grass *C. dactylon* and negative effects of *C. dactylon* on springtail densities have been observed (Rickers 2002), resource availability for Collembola presumably was higher on grazed sites. Density of the secondary decomposer *L. cyaneus* was not affected by grazing, but springtails were strongly enriched in ^{13}C on sites without grazing in August. This indicates that *L. cyaneus* used fungi growing on litter of *C. dactylon* as a resource on the non-grazed sites in August where the grass was most abundant. This suggests that feeding on fungi secondary decomposers are able to exploit food resources that are unpalatable for primary decomposers. Both *E. nivalis* and *L. cyaneus* were not enriched in ^{13}C in August, and generally depleted on grazed sites confirming avoidance of litter of *C. dactylon*. Furthermore, *E. nivalis* and *I. viridis* were enriched in ^{15}N on grazed sites. Legumes benefit from sheep grazing on the studied grassland resulting in higher abundance compared to non-grazed sites (STORM & BERGMANN 2004). Consequently, primary decomposers, such as *E. nivalis* and *I. viridis*, were enriched in ^{15}N on grazed sites, since the δ^{15}N signature of legumes approaches that in air due to their symbiosis with nitrogen-fixers (PETERSON & FRY 1987; HANDLEY & SCRIMGEOUR 1997).

Herbivores: Grazing generally did not affect densities of herbivores. This is in contrast to studies that document negative impacts of grazing on phytophagous insects (HUNTLY 1991; KRUESS & TSCHARNTKE 2002; NICKEL & HILDEBRANDT 2003). Furthermore, stable isotope signatures in *A. ribauti* and *D. stylata* were not affected by grazing indicating similar availability of resources on both the grazed and the non-grazed sites. *A. ribauti* is known to feed on *Plantago* (Plantaginaceae) and legumes (BIEDERMANN & NIEDRINGHAUS 2004). Since densities of *P. lanceolata* were very low at the study sites (personal observation), *A. ribauti* likely predominately fed on legumes, which is confirmed by stable isotope signatures; δ^{15}N signature of *A. ribauti* was higher than that of other phytophagous insects and close to that of legumes. *D. stylata* is known to feed on *Festuca ovina* (Poaceae) (BIEDERMANN & NIEDRINGHAUS 2004), a grass that reaches between 2 – 15 % of ground cover at the study site (RICKERS 2002). Since stable isotope signatures of *D. stylata* were similar to those of *F. ovina* (WALLUS 2002), it is likely that *D. stylata* infact predominately fed on *F. ovina*.
In contrast to *A. ribauti* and *D. stylata*, grazing significantly affected stable isotope signatures of juvenile leafhoppers and *N. tipularius*, which were depleted in ^{13}C on grazed sites. Juvenile leafhoppers and *N. tipularius* obviously predominately fed on C_3 grasses and ingested less carbon from *C. dactylon* on grazed sites. *N. tipularius* is a typical species of xeric grasslands feeding on grasses, *Artemisia* (Asteraceae) and *Geranium* (Geraniaceae) (SAUER 1996). The most abundant leafhopper *J. obtusivalvis* tended to be enriched in ^{15}N on grazed sites. Since *J. obtusivalvis* feeds on *Bromus erectus* and *Brachypodium pinnatum* (BIEDERMANN & NIEDRINGHAUS 2004) and species of the genus *Jassargus* in general are rather specialised on grasses (BIEDERMANN & NIEDRINGHAUS 2004), feeding on legumes (with high δ^{15}N signature) is unlikely. Grazing affects plant productivity and nutrient content (MOORE & CLEMENTS 1984; SEASTEDT 1985; HOLLAND et al. 1992) and *J. obtusivalvis* may have fed on grasses that became enriched in ^{15}N due to grazing. δ^{13}C signatures in *A. interstitialis* were strongly decreased in grazed plots. Without grazing, *A. interstitialis* obviously predominately

fed on *C. dactylon* in June approaching the signature of the C_4 grass. On grazed sites, *A. interstitialis* switched to feeding on C_3 grasses presumably due to the lower biomass of *C. dactylon*. *A. interstitialis* is known to feed on tall grasses, such as *Festuca* and *Elymus repens* (BIEDERMANN & NIEDRINGHAUS 2004). The dietary switch to *C. dactylon* on non-grazed sites is surprising since *E. repens* reached similar abundance to *C. dactylon* at these sites two years before (RICKERS 2002), but probably densities of *C. dactylon* have increased in 2002. In August, however, *A. interstitialis* also switched to a C_3 plant diet on non-grazed sites, presumably, because *C. dactylon* dried in early August.

Predators: Abundances of ground beetles were generally not affected by grazing. This is in contrast to the observed negative impact of grazing on beetle communities at other sites (DENNIS et al. 1997; GARDNER et al. 1997). Obviously, beetle species of the studied xeric grassland are adapted to disturbance, such as grazing by sheep. However, grazing affected stable isotope signature of beetles; *C. cinctus* was depleted in ^{13}C indicating that its prey fed on *C. dactylon* to some extent. δ^{15}N and δ^{13}C signatures of *T. obtusus* suggest predation on Collembola by *T. obtusus*. Collembola are an important prey for Carabidae (HENGEVELD 1980; POLLET & DESENDER 1987) and the most abundant springtail *L. cyaneus* is known to be of high food quality for the ground beetle *Bembidion lampros* (BILDE et al. 2000).

Wolf spider populations benefited from grazing resulting in enhanced eggsac production of *P. palustris* and enhanced densities of *A. cuneata* and *P. palustris* on grazed sites. This is in contrast to studies that document negative effects of grazing on spider communities due to impoverished vegetation structure and lower height of plants (GIBSON et al. 1992; DENNIS et al. 2001). As the grassland is grazed only moderately on a rotational basis, beneficial effects of grazing and abundant prey from the detritus food web may override potential negative direct (e.g. trampling) and indirect effects (e.g. reduction of the herbivore community) of grazing. Furthermore, both *A. cuneata* and *P. palustris* often occur on open grasslands (ROBERTS 1995) and ambush predators known to be more abundant in patchier vegetation caused by moderate grazing (DENNIS et al. 2001). Consequently, wolf spiders are probably adapted to heterogeneous habitats created by grazing that also provide beneficial microclimatic conditions for egg development.

In *P. palustris*, females as well as later instars were enriched in ^{15}N on grazed sites and later instars were additionally depleted in ^{13}C on grazed sites. Presumably, Collembola represented a major food resource for *P. palustris* showing the same pattern of enrichment in ^{15}N and depletion in ^{13}C on grazed sites. Low ^{15}N signatures of second instar juveniles on grazed sites without prey addition also indicate that female *P. palustris* predominately fed on Collembola during egg production. In contrast to *P. palustris*, female *A. cuneata* fed little on Collembola as indicated by dissimilar stable isotope signatures. Also, stable isotope signatures of second instar juveniles of *A. cuneata* were not affected by grazing. The size range of prey consumed by spiders depends on spider size (NENTWIG & WISSEL 1986) with larger spiders preying on larger prey. Since insect herbivores represent larger prey compared to Collembola, herbivores presumably become more important prey for adult *A. cuneata* than detritivores. In contrast, later instars of *A. cuneata* were enriched in ^{15}N on grazed sites, suggesting that Collembola formed a substantial part in their diet, and this is supported by δ^{13}C signature on grazed sites without alternative prey. This is in line with other studies documenting that spider populations are subsidized by the detrital food web (TURNBULL 1966; CHEN & WISE 1999; AGUSTI et al. 2003) and stressing the importance of Collembola for juvenile spiders (MCNABB et al. 2001). Furthermore, an increase in detritivore densities may foster biological control of herbivorous insects by spiders (SETTLE et al. 1996; WISE et al. 1999; WISE et al. in review), but this was not the case on the studied xeric grassland site. Probably, detritivores and herbivores were rather limited by density independent factors such as precipitation (LENSING et al. 2005) that was unusually high on the xeric grasslands in 2002 (personal observation).

NEILSON et al. (2002) documented an enrichment of ^{15}N in beetles and spiders due to grazing and suggested that belowground food chains were longer on grazed sites. Unfortunately, neither stable isotope data of the most common plants, nor of microfauna or potential prey of ground beetles and spiders were presented. Thus, essential data on the food web is missing. My study clearly demonstrated that effects of grazing strongly depend on plant composition that account for the enrichment in ^{15}N, since legumes (rich in ^{15}N) were more abundant on grazed sites. In conclusion, inferring changes in chain length of belowground food webs from changes in ^{15}N of aboveground generalist predators is impossible if important data on the food web components are neglected.

IV.3 Allochthonous Resources

As expected, arthropods reflected the gradient from the shoreline to the foredune with decreasing number of crustaceans and increasing number of insect species and density. This is in line with other studies (DAHL 1952; MCLACHLAN 1990; HAYNES & QUINN 1995; RICHARDSON et al. 1999). Animals formed discrete communities on the beach and the foredune and only few taxa were part in both communities.

Beach Community

Amphipods were most abundant in the traps closest to the shoreline, with only the exception of the sandhopper *Talorchestia* 1 that was found at the top of the foredune. In general, crustaceans dominated the food web in numbers, and species specific diet of amphipod and isopod taxa could be documented by stable isotope analysis. *Talorchestia* 2 forages for small particulate matter, such as diatoms, on the sand during night (JOHNSTON et al. 2005). Presumably, diatoms at Marion Bay were enriched in ^{15}N and depleted in ^{13}C compared to kelp resulting in increased δ^{15}N signatures and decreased δ^{13}C signatures of *Talorchestia* 2. Similarly, *A. thompsoni* was enriched in ^{15}N and depleted in ^{13}C as compared to kelp, suggesting that the isopod fed on diatoms, too. In contrast, *Talorchestia marmota* is known to burrow beneath the kelp patches, emerging at night to feed on wrack (JOHNSTON et al. 2005). Feeding directly on kelp is documented by a high proportion of carbon derived from kelp. Similarly, the amphipod *Orchestia* spec. and the isopod *A. bipleura* depend on kelp as major resource as reflected in high proportions of carbon derived from kelp. Since juvenile amphipods could not be identified to species level, a mixture of individuals was analysed and consequently produced a mixture of the stable isotope signatures of adults (*T. marmota* & *Talorchestia* 2). In general, kelp feeders had similar δ^{15}N signatures compared to their diet, only *T. marmota* was slightly depleted in ^{15}N. Most crustaceans excrete ammonia (NH_3) and lack the biosynthetic processes of most terrestrial animals during which the lighter nitrogen isotope (^{14}N) is preferentially metabolised and finally excreted (FANTLE et al. 1999; VANDERKLIFT & PONSARD 2003). In addition, detritivores show only little fractionation of ^{15}N (VANDERKLIFT & PONSARD 2003) explaining the lack of fractionation in kelp feeding amphipods and isopods. This, however, is in contrast to a study on *Talitrus saltator* (Ampipoda, Talitridae) where trophic fractionation in ^{15}N of 3.4 ‰ was assumed to document feeding on stranded algae (ADIN & RIERA 2003). ADIN & RIERA (2003) sampled plants after recent deposition. However, the nutritional value of algae changes during decomposition (BUCHSBAUM et al. 1991) and signatures of decaying plants become enriched in ^{15}N compared to fresh plant material (HANDLEY & SCRIMGEOUR 1997). Presumably, algae become enriched in $\delta^{15}N$ during decomposition and *T. saltator* feeding on decaying plant material is similarly enriched in ^{15}N contradicting a trophic level fractionation of 3.4 ‰. In general, amphipods are regarded as the major agent in wrack degradation followed by bacteria, while other herbivores and detritivores at the drift line play only a minor part (GRIFFITHS et al. 1983; COLOMBINI et al. 2000). Stable isotope analyses in this study support the importance of amphipods (e.g. *T. marmota* and *Orchestia* spec.) as kelp feeders, but also show that isopods (e.g. *A. bipleura*) may be equally important, being smaller than the amphipods, but more abundant.

Most important terrestrial predators on the beach were *T. oraria* (Lycosidae) and *Cafius* 2 (Staphylinidae). The large wolf spider is a common predator on beaches of Australia (FRAMENAU et al. in press) and similarly beetles of the genus *Cafius* are commonly found in the littoral zone of sandy beaches (CHELAZZI et al. 1983; COLOMBINI et al. 1998, 2000). *T. laticeps* (Geophilomorpha) is the only centipede known for Tasmanian beaches and can be found under stones and in seaweed wrack at, or just below the high tide mark (MESIBOV 2004). Predators on the beach (*T. laticeps*, *Cafius* 2 and *T. oraria*) were enriched between 3.6 and 6.47 ‰ compared to the baseline of kelp. This is in line with a trophic level fractionation of 2.3 – 3.4 ‰ postulated in other food web studies (PETERSON & FRY 1987; POST 2002; MCCUTCHAN et al. 2003) and suggests that predators comprise two trophic levels at Marion Bay with *T. oraria* being the top predator. However, calculations in IsoSource revealed that *T. oraria* predominately fed on *Talorchestia* 2 with a high $\delta^{15}N$ signature documenting that *T. oraria* is also a first order predator. Furthermore, analyses documented that *T. laticeps* predominately fed on a mixture of *T. marmota* and *A. bipleura*. Thus, *Orchestia* and juvenile amphipods seem to be not important as prey for *T. laticeps*. Finally, *Cafius* 2 seemed to prey predominately on *A. bipleura,* which was unexpected, since stable carbon isotope signatures were dissimilar. For antlions, analysis in IsoSource suggested that both animals from the terrestrial food web (e.g. Myrmecinae) and the marine food web (e.g. *T. marmota*) belonged to their diet. Mass tolerance had to be increased to ± 0.5 % for antlions to produce feasible solutions suggesting that not all potential sources have been identified. Probably, other ants also contributed to antlion diet. Finally, high $\delta^{15}N$ signatures of *P. littoralis* (Coleoptera) and Scatophagidae 1 (Diptera) indicate that these species predominately fed on decaying animal tissue and faeces, respectively, while *P. littoralis* was more strongly linked to the terrestrial food web than Scatophagidae 1 as documented by low proportions of carbon derived from kelp and sea grass in *P. littoralis*. Both larvae and adult *Phycosecis* are known to feed on carrion (BEUTEL & POLLOCK 2000). Presumably, the beetles fed on bird carcasses that were frequently encountered on the beach (personal observation), where *P. littoralis* reached high abundance.

Since I used an average carbon isotope signature of various plant species to calculate proportions of carbon derived from kelp, obtained data can be regarded as rough estimates for the importance of kelp in the diet of animals, only. In general, crustaceans as well as most predators and coprophages had high proportions of carbon derived from kelp indicating a close link to the allochthonous resource. *P. littoralis* (Coleoptera) and Myrmeleonidae had distinctly lower proportions of carbon from kelp suggesting that they were linked to both, the foredune and the beach food web.

Expectations about feeding preferences of predators derived from a preliminary look at stable isotope data were not uniformly supported by analysis in IsoSource. Thus, presented data emphasize the importance of comprehensive data on potential prey organisms and the need for detailed analyses of stable isotope data with mixing models as soon as more than one potential source is concerned. Both, detailed data and thorough analysis were crucial for the interpretation of stable isotope data and feeding links.

Foredune Community

Insects dominated the foredune community and only the amphipod *Talorchestia* 1 occurred exclusively on the foredune. This species is regularly found among strandline vegetation and suggested to feed on decaying plant material (RICHARDSON et al. 1999). A proportion of 27.01 % of carbon was calculated to derive from kelp in this species, which is surprising since the amphipod is restricted to the foredune. Consequently, carbon also must have derived from feeding on plant litter being enriched in ^{13}C as compared to the average of the dune vegetation. In general, data on proportions of carbon in animals on the foredune derived from kelp presumably overestimated the contribution of kelp to carbon in animals, since average carbon isotope signatures of various plant species from the foredune were used for calculations. δ^{13}C signatures of plants on the foredune span over a range of 3.53 δ units and therefore calculations rather reflect the dependence of animals on plants with less negative δ^{13}C signatures other than kelp. For example Polydesmidae 1 (Diplopoda) had a calculated proportion of carbon from kelp of 37.14 %. But negative δ^{15}N signatures clearly document that the diplopods cannot depend on kelp (with high δ^{15}N signature) as a resource. Diplopoda are detritivores feeding on fungi and litter (MESIBOV 2004). Unfortunately, only fresh plant material was sampled and thus I can only speculate that Polydesmidae fed on a mixture of decaying litter including *I. nodosa* and *C. rossii*, plants with the most similar stable isotope signatures. However, Diplopoda still seem to be depleted in ^{15}N as compared to litter, which is in line with findings from a German forest (SCHEU & FALCA 2000), but mechanisms resulting in strong depletion in ^{15}N in diplopods are poorly understood.

According to $\delta^{15}N$ signatures, the predator assemblage on the foredune consisted of the scorpion *Cercophonius squama*, velvet mites (Trombidiidae), ants (*Iridomymex* spec. and Myrmecinae spec.), and the beetle *Conoderus australasiae* (Elateridae). *C. squama* is the only scorpion found on Tasmania and a very common species on mainland Australia (MARGULES et al. 1994). Elaterid larvae are well known pests on plant roots and adult beetles are omnivorous or predaceous (HARDE & SEVERA 1988), which is supported by high $\delta^{15}N$ signatures in *C. australasiae*. Both dark beetles (Tenebrionidae) *Cellibe costasco* and *Edylius canescens* fed on decaying material, while *C. costasco* presumably rather depended on plant and *E. canescens* rather on animal derived material as indicated by $\delta^{15}N$ signatures. Anthicidae are known to live on detritus mostly feeding on dead beetles (HARDE & SEVERA 1988), which is supported by high $\delta^{15}N$ signatures.

Since fractionation in detritivores and nitrogen limited herbivores is controversial (MCCUTCHAN et al. 2003; VANDERKLIFT & PONSARD 2003), feeding links of detritivores and herbivores on the foredune were impossible to assess with regard to the availability of multiple plant resources. However, two groups of detritivores and herbivores could be distinguished. The first group contains animals (*Heteronyx* spec., Cryptorhynchinae 1 and *Talorchestia* 1) that were only little enriched in ^{15}N from the average $\delta^{15}N$ signature of plants, while the second group, including springtails (Entomobryidae), weevils (*Mandalotus* 9 & *Timareta* 6) and an elaterid (*H. minor*), was somewhat more enriched in ^{15}N. Diet of animals in the first group likely contains *C. rossii* (Aizoaceae), *L. arboreus* (Fabaceae), *P. esculentum* (Dennstaedtiaceae) and *A. novae-zelandiae* (Rosaceae), plants with an average $\delta^{15}N$ signature of -1.67 ‰. For animals in the second group, *A. arenaria* (Poaceae), *I. nodosa* (Cyperaceae) and *R. candolleana* (Chenopodiaceae) with an average $\delta^{15}N$ of 1.12 ‰ were likely more important.

In general, stable isotopes document that that the community on the foredune was rather isolated from the beach community and lacked allochthonous input from the beach. This is in contrast to other studies that documented the importance of allochthonous resources for terrestrial arthropods (POLIS & HURD 1995; HENSCHEL et al. 2001; BASTOW et al. 2002).

IV.4 Food Quality

Relation of female size to juvenile and clutch size

Several studies documented that clutch size in spiders increases with female biomass (KESSLER 1973; MARSHALL & GITTLEMAN 1994; BROWN et al. 2003) and that clutch size reflects food availability of females (BRICEÑO 1987; WALKER et al. 2003). Our results support these findings in *P. lugubris* as biomass of females and clutch size of the first eggsac were closely correlated. In contrast, correlation between female prosoma width and offspring number was weak, indicating that prosoma width is a measure for resource availability during growth and development of the females (MIYASHITA 1968), while total biomass of reproducing females is a measure for the resource availability during reproduction. There was no correlation between female biomass and spiderling biomass or clutch size and average spiderling biomass, indicating that spiderling biomass is rather constant and additional resources are invested in clutch size instead of egg size. This is in contrast to the theory of a size-number trade-off, i.e. the larger the eggs, the fewer eggs per eggsac (SMITH & FRETWELL 1974; SIMPSON 1995; BROWN et al. 2003). IIDA (2003) argues that the small within clutch variance is a tactic developed by females to reduce sibling cannibalism; our finding of small variance in width of juvenile prosoma supports this conclusion. Compared to the first clutch the number of juveniles in subsequent clutches is commonly reduced in lycosid spiders (EDGAR 1971; KESSLER 1973; BROWN et al. 2003).

Effects of high food quality on females

Females thrived on diets containing *D. melanogaster* and/or *H. nitidus* and uniformly reproduced. For juveniles of *P. lugubris*, *D. melanogaster* is only of medium food quality, since it does not allow development to the adult stage (OELBERMANN & SCHEU 2002a). Yet, for adult females it was of high food quality, even higher than *H. nitidus*, as indicated by greater biomass and the fact that females produced eggsacs three days earlier than those fed *H. nitidus* only. Since the concentration of nitrogen in *D. melanogaster* was lower than that in *H. nitidus*, this indicates that food quality is not solely determined by nitrogen availability. Interestingly, there was no beneficial effect of the mixed diet of *H. nitidus* and *D. melanogaster* on female biomass and reproduction. This is in contrast to the finding of OELBERMANN & SCHEU (2002a), where a mixed diet of *D. melanogaster* and *H. nitidus* resulted in enhanced rates of development and survival of juvenile *P. lugubris*. Obviously, juveniles represent a more sensitive life stage with more specific nutritional demands than adult spiders.

During more than two months of feeding of female *P. lugubris* on ^{13}C enriched *D. melanogaster* in single and mixed diet with *H. nitidus* they incorporated the fruit fly carbon leading to an enrichment of ^{13}C in the single diet by 6.55 ‰ and in the mixed diet by 2.52 ‰. In the single diet this was equivalent to a replacement of 51 % of the body carbon of the females which was lower than expected. Low carbon incorporation might have resulted from the artificial diet of the prey. The importance of the preys' food resources for predators has been documented (MAYNTZ & TOFT 2001) and elemental composition influences the incorporation of dietary nitrogen and carbon isotopic signatures (PHILLIPS & KOCH 2002; PEARSON et al. 2003; HAUBERT et al. in press). Fruit flies in our study have been raised on a medium with a high content of carbohydrates and a low content of proteins resulting in a high tissue content of carbon (54 %) and a low content of nitrogen (10 %). Insect herbivores and fish fed nutrient-rich diets had a higher lipid content than those fed nutrient-poor diets (SLANSKY & WHEELER 1992; GAYE-SIESSEGGER et al. 2004) and during de novo fatty acid synthesis the lighter isotope is preferentially incorporated (DENIRO & EPSTEIN 1977). Furthermore, even compounds derived directly from the diet may exhibit significantly different δ^{13}C ratios when compared to the precursor compounds in the diet (CHAMBERLAIN et al. 2004). Probably, females invested the surplus of carbohydrates in synthesis of new fatty acids that were less enriched in ^{13}C. Surprisingly, females were not strongly enriched in ^{15}N, in spite of the high δ^{15}N ratios of their diet. Theoretically, females should have reached higher δ^{15}N ratios compared to the initial signature and to their diet (POST 2002; VANDERKLIFT & PONSARD 2003). Potentially, nitrogen anabolic metabolism was negligible in females after they reproduced resulting in only slight changes in ^{15}N signatures.

Effects of low food quality on females

Feeding on *F. candida* proved to be detrimental for adult females: none of them produced a second eggsac and feeding on *F. candida* was finally lethal. Low-quality food is known to affect reproduction in arthropod predators (BILDE & TOFT 1994, 2001; MAYNTZ et al. 2003), classifying *F. candida* as very low-quality or even toxic prey. Negative effects of the springtail are also reflected in the final dry weight of the females, as the biomass of females in treatments with *F. candida* was lower than in the other feeding treatments. Females grew thinner and lethargic shortly before they died (personal observation) and low biomass of females resulted from a disproportionately high loss of carbon compared to nitrogen as indicated by lower C:N ratios. Thus, the decline in the C:N ratio of females fed Collembola was caused by different mechanisms: when females preyed on *H. nitidus*, they incorporated nitrogen from their prey, while females fed *F. candida* predominately lost carbon, both resulting in lower C:N ratios. Interestingly, the body weight of females fed a mixed diet of *D. melanogaster* and *F. candida* were only slightly heavier than those fed *F. candida* only. Analogously, the C:N ratio differed only slightly between females fed *F. candida* in single and mixed diet, indicating that the loss of carbon of females was similar in both treatments. In addition, females fed a mixed diet of *D. melanogaster* and *F. candida* were not enriched in ^{13}C at all, indicating that females were not able to incorporate carbon from *D. melanogaster* in presence of *F. candida*. This supports the finding that females were not able to compensate the negative effects of *F. candida* on their metabolism. Furthermore, females fed *F. candida* were depleted in ^{15}N.

Biomass, C:N ratio and nitrogen stable isotopes documented that females fed a diet containing *F. candida* were catabolising their own body tissue. Starvation usually results in an enrichment of ^{15}N (OELBERMANN & SCHEU 2002b; VANDERKLIFT & PONSARD 2003) due to preferential excretion of the lighter stable nitrogen isotope (^{14}N), as also documented for the starved juveniles in our study. Depletion in ^{15}N of females presumably resulted from using up a major part of their body proteins with the remaining tissue consisting mainly of the exoskeleton, which is depleted in ^{15}N compared to other body tissues (BUNN et al. 1995). I suggest that the detrimental effect of *F. candida* is caused by toxins liberated during digesiton, since both *F. candida* and *D. melanogaster* were regularly preyed upon until females finally died. This is in line with FISKER & TOFT (2004) who documented increased feeding rates of juveniles on *D. melanogaster* in presence of *F. candida*, without a gain in biomass or enhanced survival of spiders. Thus, *P. lugubris* appears to be unable to recognize and avoid feeding on the unpalatable prey (*F. candida*). Interestingly, juveniles of *Schizocosa* spec. that were fed *D. melanogaster* with some *F. candida* showed induced resistance and were able to cope with the toxicity of the prey (TOFT & WISE 1999b). Due to continuous exposure to *F. candida* in our study, female *P. lugubris* were probably not able to recover from intoxication and did not have the chance to develop resistance. Furthermore, in the studies of TOFT & WISE (1999b) and FISKER & TOFT (2004) the negative impact of *F. candida* was pronounced in small juveniles, whereas in larger juveniles it was reduced. This is in stark contrast to our results; even mature females suffered irreparable damages from feeding on *F. candida* in our experiment.

Effects of food quality on juveniles

Offspring clutch size, juvenile weight, and juvenile survival did not differ between the high quality food treatments (D; H; DH). Since clutch size and juvenile weight are known to be sensitive to food quality (BILDE & TOFT 1994, 2001; MAYNTZ et al. 2003), this suggests that *D. melanogaster* and *H. nitidus* were of similar food quality.

Generally, starvation of juveniles from the second eggsac resulted in an enrichment in ^{15}N (see above) and a disproportionate loss of carbon compared to nitrogen as indicated by the increase in C:N ratio. During starvation ^{12}C was preferentially respired, since both juveniles of females fed *H. nitidus* and juveniles of females fed a mixture of *D. melanogaster* and *H. nitidus* were somewhat enriched in ^{13}C. This is in accordance with earlier results (OELBERMANN & SCHEU 2002b), but interestingly, the effect did not occur in juveniles of females fed ^{13}C labelled *D. melanogaster* only.

Apart from starved juveniles, C:N ratios differed neither between juveniles of the first and the second eggsac, nor between the feeding treatments. In contrast, stable isotope composition differed between diets. Compared to their mothers, juveniles from the first eggsac, which was produced in the field, were slightly depleted in ^{13}C and strongly depleted in ^{15}N. Similar results have been found previously (OELBERMANN & SCHEU 2002b; CHAPTER IV.2). In contrast, all juveniles from the second eggsac produced on diets in the laboratory were uniformly enriched in ^{15}N compared to their mothers. Only juveniles from females fed a diet containing *D. melanogaster* were also enriched in ^{13}C compared to their mothers. Even though $\delta^{13}C$ signatures of females fed *D. melanogaster* only and a mixed diet of *D. melanogaster* and *H. nitidus* differed strongly, juveniles were similarly enriched compared to their mothers. This indicates that females invested a similar amount of carbon from *D. melanogaster* into their offspring irrespective of the presence of alternative prey (*H. nitidus*). Both isotopic ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) of juveniles approached those of their mother's diet (and not their mother's tissue), suggesting that ingested nutrients were rooted predominately into offspring production. The metabolism of females for maintenance and for egg production obviously differs strongly in turnover rates and fractionation, as documented by the differential enrichment in ^{13}C and ^{15}N of adults and juveniles.

IV.5 Cannibalism

Intraspecific predation strongly depends on size differences between cannibal and victim (POLIS 1988; SAMU et al. 1999; BUDDLE et al. 2003; IIDA 2003). However, results of the present study suggest that even individuals of similar size are likely to prey on each other. Overall, high mortality of spiderlings in both experiments was presumably caused by cannibalism among juveniles as I can exclude starvation as a mortality factor early in the experiments. Without food spiderlings of *P. palustris* survived 9.86 (± 2.28) days; similar or even longer survival periods have been documented for *Schizocosa ocreata* (WAGNER & WISE 1996), *P. milvina* (WALKER et al. 1999) and *P. lugubris* (OELBERMANN & SCHEU 2002a). Since only successful cannibals were used for the experiments, mortality due to starvation was not important during the first week in both experiments. Later on, however, starvation and lack of high quality food likely contributed to mortality of spiderlings in treatments without alternative prey. Yet, absolute mortality rates are to be interpreted cautiously due to the preselection of successful cannibals. Results may be biased towards detecting a high incidence of cannibalism. Eggsacs of *P. palustris* contain up to 60 spiderlings resulting in a high density of spiderlings at dispersal and consequently in high encounter rates. Furthermore, the density of insect prey that is suitable for juvenile *P. palustris* (e.g. Collembola) is low at the studied xeric grassland site during summer (CHAPTER IV.2). Thus, preselection of cannibals as done in this study likely resembles natural conditions.

Availability of alternative prey

Mortality of spiderlings was strongly reduced when alternative prey was present, which is consistent with previous findings (WAGNER & WISE 1996; SAMU et al. 1999). Biomass of spiderlings in the experiment on cannibalism among juveniles showed a threefold increase in treatments with the collembolan *H. nitidus* during 18 days. The epigeic springtail has been documented to be a high-quality food for lycosid spiders (OELBERMANN & SCHEU 2002a).

Adult spiders did not prey on juveniles when alternative prey (*D. melanogaster*) was present, resulting in lower mortality of juvenile spiders in the simple habitat structure treatment. This is also reflected in the weight differences of the females. Even though prey was more accessible due to the lack of refuge in the treatment with simple habitat structure, females gained similar weight in treatments with simple and complex habitat structure with alternative prey.

Microhabitat structure

Cannibalism among juvenile spiderlings was not affected by habitat structure. Yet, at low spider density without alternative prey, biomass of spiderlings increased in complex habitat structure. This indicates that, given complex habitat structure, interference was reduced saving energy resources of spiderlings due to reduced metabolic activity. Interestingly, this did not occur at higher density. Presumably, the positive effect of habitat complexity decreases with density of spiderlings, whereas intensity of interference increases.

In contrast to cannibalism among juveniles, habitat structure affected mortality due to filial cannibalism. Females preyed on juveniles only in the simple habitat structure treatments without alternative prey, thereby increasing mortality of spiderlings. In the complex habitat structure treatments mortality was low with and without *D. melanogaster*, suggesting that even without alternative prey females did not prey on spiderlings. Obviously, the complex structure created refuges for spiderlings. Consequently, females in the complex habitat structure treatment without alternative prey died early from starvation and loss of biomass was pronounced. Even though adult mortality was similar in treatments without alternative prey by the end of the experiment, females in the simple structure treatment survived significantly longer than those in the complex structure treatment. Obviously, feeding on spiderlings only delayed female mortality, suggesting that spiderlings were of low food quality, and/or little was extracted, which is consistent with earlier studies (TOFT & WISE 1999b; OELBERMANN & SCHEU 2002a).

Density-dependence and wasteful killing

At higher density, per capita mortality rate of spiderlings was increased when alternative prey (*H. nitidus*) was available, suggesting higher activity and interference at higher density. Superfluous feeding (CONOVER 1966) by predators when prey is abundant was demonstrated for spiders (RIECHERT & MAUPIN 1998) and proposed as an indicator of aggression (MAUPIN & RIECHERT 2001). SAMU & BÍRÓ (1993) also documented wasteful killing for *P. hortensis* at high prey densities. Furthermore, cannibalism among second-instar *Hogna helluo* also increased in presence of alternative prey (ROBERTS et al. 2003). Presumably, in our experiment spiderlings increased the rate of attack when prey (*H. nitidus* and conspecifics) was abundant, which is also supported by the fact that juvenile *P. palustris* gained less weight at high compared to low density.

Kin-recognition?

Results of the present study document that even severely starved females prey little on conspecific spiderlings, rather they prefer to feed on alternative prey. True kin-recognition was documented for *S. ocreata*, but was restricted to two hours after demounting of juveniles from their mothers (ANTHONY 2003). Female *P. palustris* seem to avoid cannibalism for a longer period of time and the avoidance appears not to be restricted to close kin since in our experiment only non-kin juveniles were used. Filial relationships in *P. palustris* need further investigation.

IV.6 IGP

Effects of alternative and intraguild prey

In general, survival of *P. palustris* was enhanced, when alternative prey was available. This is in line with earlier findings that IGP is reduced when prey is abundant (LUCAS et al. 1998, CHEN & WISE 1999, MEYHÖFER & HINDAYAMA 2000). Feeding on *D. melanogaster* only, the biomass of *A. cuneata* increased almost threefold in biomass. As indicated by the enrichment in ^{13}C spiderlings incorporated a substantial amount of carbon form their prey. Presumably, due to the high C:N ratio of *D. melanogaster*, the C:N ratios of *A. cuneata* also increased. The enrichment in ^{13}C was less pronounced when intraguild prey was available. Either consuming both fruit flies and spiderlings led to a lower increase in ^{13}C due to additional ingestion of spiderlings with a lower δ^{13}C ratio, or *P. palustris* captured some of the fruit flies lowering the number of fruit flies available to *A. cuneata*. Indeed, δ^{13}C ratios of juvenile *P. palustris* suggest that most of the surviving individuals had preyed on *D. melanogaster*. This conclusion is supported by the pronounced weight gain of *P. palustris* when alternative prey was available. Furthermore, the strong correlation between δ^{13}C signatures and final weight of juvenile *P. palustris* at simple habitat structure with alternative prey indicates that juvenile growth mainly resulted from predation on *D. melanogaster*. In contrast, δ^{13}C signatures and the final weight of *P. palustris* were not related at simple structure with alternative prey suggesting a higher frequency of cannibalism since spiders gained similar weight as compared to those in complex structure.

Feeding on juvenile *P. palustris* instead of *D. melanogaster* resulted in lower C:N ratios and lower increase in biomass of *A. cuneata* due to lower C:N ratios of juvenile *P. palustris*. Furthermore, feeding on *P. palustris* caused an increase in δ^{15}N and this was more pronounced when alternative prey was missing suggesting that predation of *A. cuneata* on *P. palustris* was reduced in presence of alternative prey. Initially, *A. cuneata* were enriched by 0.90 ‰ compared to *P. palustris* increasing to 1.50 ‰ at the end of the experiment. IGP results in increased δ^{15}N ratios due to the consumption of prey on the same trophic level (HOBSON & WELCH 1995; PONSARD & ARDITI 2000; MCNABB et al. 2001). Fractionation was 1.41 ‰ at complex habitat structure and 1.75 ‰ at simple habitat structure, indicating increased predation on *P. palustris* at simple habitat structure (see below). Interestingly, juvenile *A. cuneata* were depleted in ^{15}N when feeding on *D. melanogaster*. Initially, juveniles of *A. cuneata* were enriched in ^{15}N by 1.07 ‰ and 4.30 ‰ compared to *H. nitidus* and *D. melanogaster*, respectively. The initial stable isotope signature reflected the feeding of *A. cuneata* on *H. nitidus* with a high δ^{15}N signature of 7.47 ‰ prior to the start of the experiment. Feeding on *D. melanogaster* ($\delta^{15}N$ = 6.25 ‰) resulted in lower $\delta^{15}N$ signatures ($\Delta^{15}N$ = 1.80 ‰) of *A. cuneata* approaching the trophic level fractionation of 2.54 - 3.4 ‰, which has been postulated in many food web studies (POST 2002; VANDERKLIFT & PONSARD 2003). *P. palustris* fed *H. nitidus* only were only slightly enriched in ^{15}N ($\Delta^{15}N$ =0.17 ‰) at the beginning of the experiment suggesting that only a small fraction of body nitrogen of *P. palustris* was replaced during feeding on *H. nitidus* for almost two weeks before the experiment. This is in line with trophic level fractionation of ca. 3 ‰ of juvenile *P. lugubris* after 11 weeks of feeding (OELBERMANN & SCHEU 2002b). The $\delta^{15}N$ signature of *P. palustris* only slightly increased when fed both *D. melanogaster* and conspecifics suggesting that the enrichment in ^{15}N due to cannibalism was levelled out by feeding on *D. melanogaster* depleted in ^{15}N.

Overall, feeding on a mixed diet of *D. melanogaster* and *P. palustris* resulted in a higher gain of biomass in *A. cuneata* at complex habitat structure. Beneficial effects of dietary mixing on growth and survival of generalist feeders is a common phenomenon (WALLIN et al. 1992; BERNAYS 1994; ACHARYA et al. 2004; SCHEU & FOLGER 2004) that has been documented for spiders (UETZ et al. 1992; TOFT 1999; OELBERMANN & SCHEU 2002a). Furthermore, spiders can increase their nitrogen intake and performance when supplementing their diet with IG prey (MATSUMURA et al. 2004). Yet, it remains unclear why this did not occur at simple habitat structure.

Effects of habitat structure

During the first week, mortality of juvenile *P. palustris* was only high at simple habitat structure without alternative prey. This indicates that both, alternative prey and complex habitat structure served as refuge for the smaller spiderlings of *P. palustris*. The latter is supported by the lower gain in biomass of *A. cuneata* in complex habitat structure without alternative prey and less enrichment in ^{15}N in this treatment. Habitat heterogeneity is known to lessen the strength of predator-prey interactions (DIEHL 1993; MARSHALL & RYPSTRA 1999; LEWIS & EBY 2002) and this likely was the case in our study. The finding that starving juveniles of *A. cuneata* experienced higher mortality in simple habitat structure is enigmatic, since loss in biomass and changes in stable isotope ratios of *A. cuneata* were similar regardless of habitat structure, suggesting similar activity of starving spiders.

The positive effect of complex habitat structure on survival of *P. palustris* only was evident during the first week; later mortality increased strongly in complex habitat structure without alternative prey. After one week of starvation cannibalism among *P. palustris* likely increased in treatments without alternative prey. Cannibalism is prevalent when food resources are limited and reduces competition for these resources (WAGNER & WISE 1996, 1997; SAMU et al. 1999). Starvation enhances cannibalism in juvenile *P. palustris* and complex habitat structure does not serve as shelter for juveniles of similar size (CHAPTER IV.5). Weight differences and high variability of δ^{15}N ratios of *P. palustris* at complex habitat structure without alternative prey also reflected starvation and/or cannibalism among *P. palustris*: some spiders lost weight due to starvation, while others were able to only slightly gain in weight due to cannibalism, since in wolf spiders conspecifics are known to be of poor food quality (TOFT & WISE 1999, OELBERMANN & SCHEU 2002a). Highly variable δ^{15}N ratios of juvenile *P. palustris* add to this conclusion: some juveniles were slightly enriched in ^{15}N due to the consumption of conspecifics, while on the other hand starving *P. palustris* were depleted in ^{15}N similar to *A. cuneata*. This finding is surprising since starvation usually results in an enrichment of ^{15}N in juvenile wolf spiders (OELBERMANN & SCHEU 2002b; CHAPTER IV.4) due to preferential excretion of the lighter stable nitrogen isotope (VANDERKLIFT & PONSARD 2003). Depletion in ^{15}N of juveniles presumably resulted from using up a major part of their body proteins with the remaining tissue consisting mainly of the exoskeleton, which is depleted in ^{15}N compared to other body tissues (BUNN et al. 1995). Finally, starvation may enhance activity and searching behaviour of wolf spiders (WALKER et al. 1999) increasing the likelihood for predation by *A. cuneata* during the second week.

V General Discussion & Prospects

Wolf spiders are important generalist predators in both agricultural and natural systems affecting prey populations (RIECHERT & BISHOP 1990; SNYDER & WISE 1999; CHEN & WISE 1999; WISE 2004) and ecosystem processes (KAJAK 1995; LAWRENCE & WISE 2004). In order to maximize the success of wolf spiders as biocontrol agents, factors increasing spider density in the field have to be identified. Consequently, mechanisms regulating wolf spider populations need to be understood in detail. Presented studies focussed on resource availability (autochthonous and allochthonous), cannibalism, IGP and microhabitat structure as key factors influencing wolf spider populations.

Prey Availability & Allochthonous Resources

Prey availability is one of the major determinants of animal abundance and distribution (WHITE 1978; HUNTER & PRICE 1992). Spiders often encounter periods of food shortage in the field (reviewed in WISE 1993) and reproduction in spiders is coupled with prey availability (KESSLER 1971; KREITER & WISE 2001) and quality (BILDE & TOFT 2001). While female *Pardosa lugubris* benefited from high quality prey, toxic prey, even if provided in a mixed diet with high quality prey, prevented reproduction and eventually caused death of spiders (CHAPTER IV.4; see below).

Furthermore, cannibalism (WAGNER & WISE 1996, 1997) and intraguild predation (HODGE 1999; CHEN & WISe 1999) are reduced in presence of alternative prey. Accordingly, juvenile *Pardosa palustris* benefited from the availability of alternative prey by reducing cannibalism among juveniles and between females and juveniles (CHAPTER IV.5), as well as reducing predation from juvenile *Alopecosa cuneata* (CHAPTER IV.6) (see below).

Despite the fact that prey availability increases reproduction and decreases strong biotic interactions, such as cannibalism and IGP, prey addition on xeric grasslands near Darmstadt did not result in an increase in the density of predators (CHAPTER IV.2). Presumably, the amount of prey added was not sufficient to significantly influence arthropod densities in addition to the strong positive effect of the sheep grazing management. Positive effects of grazing on spider abundance likely resulted from the increased availability of detritivore prey on grazed sites, suggesting that spider populations were indeed bottom-up controlled (CHAPTER IV.2).

Apart from autochthonous resources, animal communities also benefit from the input of allochthonous resources (POLIS & HURD 1995; HENSCHEL et al. 2001; BASTOW et al. 2002) fostering ecosystem stability (HUXEL & MCCANN 1998; HUXEL et al. 2002). Substantial amounts of kelp and sea grass are deposited on a sandy beach in south east Australia, resulting in high densities of kelp feeding amphipods and isopods (CHAPTER IV.3). In spite of this high amount of available prey on the beach, only one wolf spider *Tetralycosa oraria* (Araneae, Lycosidae) used this prey as resource; densities of other spiders in general were negligible. Rove beetles such as *Cafius* 2 were also important predators of amphipods and isopods, even if of much smaller size than the large wolf spider. Predators feeding on amphipods and isopods were restricted to the beach and seemed to be specialized on certain amphipods and isopods as suggested by stable isotope signatures. Consequently, the marine input remained limited to the food web directly on the beach and did not subsidize the terrestrial food web on the foredune. On the contrary, stable isotopes indicated that some animals on the beach were also sustained from the terrestrial system (e.g. Myrmeleonidae and *Phycosecis littoralis* (Coleoptera)). Thus, the availability of allochthonous resources is not necessarily important for arthropod food webs in the vicinity of ecosystem borders. Since the relative importance of allochthonous input depends on the extent of the productivity of the focal community (POLIS & HURD 1996 a,b; POLIS et al. 1997b; NAKANO & MURAKAMI 2001), productivity of the foredune community should be investigated; presumably, the foredune community is independent of allochthonous input due to abundant autochthonous resources.

Food Quality

Strong differences in prey quality for predators have been documented (TOFT 1999; SINGER & BERNAYS 2003) and dietary mixing fosters toxin dilution and nutritional balance (GREENSTONE 1979; SLANSKY & RODRIGUEZ 1987). Consequently, dietary mixing is beneficial for consumers (UETZ et al. 1992; BERNAYS 1994; ACHARYA et al. 2004) and even positive effects of mixing high- and low-quality prey have been documented (TOFT 1995; SCHEU & FOLGER 2004; SCHEU & SIMMERLING 2004). High prey quality results in enhanced survival and development of juvenile *Pardosa lugubris* (OELBERMANN & SCHEU 2002a) and resulted in shorter egg development in second eggsacs of *P. lugubris* (CHAPTER IV.4). However, prey mixing was not beneficial for *P. lugubris*, particularly if toxic prey was included in the diet (CHAPTER IV.4), which is in line with other studies (TOFT & WISE 1999a,b; OELBERMANN & SCHEU 2000a). The springtail *Folsomia candida* proved toxic for female *P. lugubris*, causing irreparable physiological damage in spiders that was finally lethal, even if high quality alternative prey, such as *Drosophila melanogaster*, was provided (CHAPTER IV.4). Avoidance of unpalatable prey and acquired aversion are documented for spiders (VASCONCELLOS-NETO & LEWISOHN 1984; TOFT 1997; STROHMEYER et al. 1998), but

P. lugubris neither ceased feeding on *F. candida* despite its negative physiological effects, nor selected the beneficial prey (*D. melanogaster*) (CHAPTER IV.4). Since prey availability is the major limiting factor for the diet of spiders (RIECHERT & LOCKLEY 1984; SLANSKY & RODRIGUEZ 1987; WISE 1993) and the encounter of prey is unpredictable in the field, spiders probably cannot afford not to catch and feed on prey, even if it is unpalatable or toxic. If encounters with unpalatable or toxic prey are rare in the field, physiological effects of the ingestion might be limited. Only if toxic prey is abundant, acquired aversion results in increased fitness of the predators. Unfortunately, there is virtually no study on the food quality of prey for spiders in the field. Given the high amount of detailed laboratory studies on food quality, information on the abundance of toxic prey in the field and its interaction with spiders in situ are crucial. Without such data one can only speculate about the ecological significance of the intriguing results from laboratory studies due to their artificiality, i.e. use of laboratory bred prey organisms. *Folsomia quadrioculata* is closely related to *F. candida* and a common springtail in forests in Europe (HOPKIN 1997). Consequently, it is a promising candidate for food quality studies with forest dwelling wolf spiders, such as *Pardosa lugubris*, that may reveal if toxicity of *F. candida* is species or genus specific.

Furthermore, future studies should examine effects of food quality on the production of the first eggsac in wolf spiders, since the first eggsac plays a major role in their reproduction (EDGAR 1971) and correlation between female fecundity (offspring number, size and survival) and quantity and/or quality of resources ingested by females after the winter might be even stronger.

Cannibalism, IGP and Importance of Habitat Structure

On xeric grasslands in near Darmstadt (Germany), mortality of juvenile *Pardosa palustris* is substantial, resulting in low numbers of adult spiders in the following spring despite of high fecundity of females in the field (personal observation). Cannibalism (CHAPTER IV.5) and intraguild predation (IGP; CHAPTER IV.6) were suggested to be major causes for juvenile mortality. Since starvation of spiders is common in the field (WISE 1993) cannibalism and IGP may reduce mortality from starvation for short periods of time; however, non-conspecific prey is essential for long-term survival of spiders and development of spiderlings (TOFT & WISE 1999; OELBERMANN & SCHEU 2002a; CHAPTER IV.5). Cannibalism is density dependent (POLIS 1981; WISE & WAGNER 1992) and enhanced when resources are limited (WAGNER & WISE 1996, 1997; SAMU et al. 1999). Eggsacs of *P. palustris* contain up to 60 spiderlings resulting in a high density of spiderlings at dispersal and consequently in high encounter rates of conspecifics. Interestingly, cannibalism between juveniles was only density-dependent when alternative prey was available (CHAPTER IV.5), supporting findings for juvenile *S. ocreata* and *P. milvina* of higher interference at higher density (WAGNER & WISE 1996; BUDDLE et al. 2003). Furthermore, the density of insect prey that is suitable for juvenile *P. palustris* (e.g. Collembola) is low at the studied xeric grassland site during summer (CHAPTER III.2) increasing the likelihood for cannibalism and IGP (HODGE 1999; CHEN & WISe 1999; MEYHÖFER & HINDAYAMA 2000; CHAPTER IV.5 & IV.6). Consequently, conspecifics and juveniles of other spider species abundant at the study site, such as *Xerolycosa miniata* (Lycosidae) and *Zelotes* sp. (Gnaphosidae) (Appendix I) may form a substantial part of the prey of juvenile *P. palustris*.

However, *P. palustris* is not only predator, but also prey for other spiders likely adding to mortality of *P. palustris* in the field. *Alopecosa cuneata*, being almost twice as large as *P. palustris*, reaches similar densities as *P. palustris* on grasslands near Darmstadt (CHAPTER IV.1). Third instar *A. cuneata* easily preyed on the smaller *P. palustris* in the laboratory, especially when alternative prey was missing (CHAPTER IV.6), and might therefore be an important mortality factor in the field, when availability of prey is low (see above).

Animals escape predation in spatial refuges (DIEHL 1993; FINKE & DENNO 2002; LEWIS & EBY 2002; LANGELLOTTO & DENNO 2004), since complex habitat structure may reduce interference due to lower encounter rates (CROWLEY et al. 1987; THOMPSON 1987; CONVEY 1988). Therefore, I hypothesised that cannibalism and IGP are reduced in complex habitat structure as compared to simple habitat structure. Habitat structure indeed provided shelter for second instar juvenile *P. palustris* from predation by female *P. palustris* (CHAPTER IV.5) and third instar *A. cuneata* (CHAPTER IV.6). However, cannibalism among second instar juveniles was not affected by habitat structure (CHAPTER IV.5). Consequently, the complex structured moss layer only served as shelter if size differences were pronounced (CHAPTER IV.5 & IV.6).

Cover of moss reaches often 100 % at xeric grasslands near Darmstadt (RICKERS 2002) providing spatial refugia that reduce predation on small juveniles by larger predators. Thus, juvenile *P. palustris* benefited from delayed eggsac production of their mothers (CHAPTER IV.1) as compared to *A. cuneata* that favours a strong size difference between juveniles of *A. cuneata* and *P. palustris*. In conclusion, I exclude IGP by *A. cuneata* as an important mortality factor for juvenile *P. palustris* in the field and suggest that rather cannibalism and/or IGP by other spider species of similar size reproducing simultaneously cause substantial mortality in *P. palustris*. Manipulations of conspecific and heterospecific spider densities in the field are necessary to clarify the importance of cannibalism and IGP in the field.

Stable Isotope Analysis

The analysis of natural variations in stable isotope signatures allows investigating food resources of organisms (PETERSON & FRY 1987; OSTROM et al. 1997; MAGNUSSON et al. 1999). Animal ^{13}C signatures are similar to their diet, since ^{13}C is little fractionated in food chains (DENIRO & EPSTEIN 1978; PETERSON & FRY 1987; WADA et al. 1991; POST 2002). Therefore, carbon isotope ratios indicate on what sources animals lived, if ^{13}C signatures of food resources differ (VANDER ZANDEN & RASMUSSEN 1999; MAGNUSSON et al. 1999; PONSARD & ARDITI 2000). For example C_3 plants are strongly depleted in ^{13}C, since RUBISCO, the CO_2 fixing enzyme, discriminates against the ^{13}C isotope and causes the lower $^{13}C/^{12}C$ ratio (GANNES et al. 1998). C_4 and CAM (Crassulacean Acid Metabolism) plants, in contrast, are less depleted in ^{13}C, because of their CO_2 fixing enzyme (PEP carboxylase) that discriminates ^{13}C less than RUBISCO (GANNES et al. 1998). A similar enrichment can be detected in algae, which is why the allochthonous input of algae into terrestrial ecosystems can be investigated using ^{13}C signatures (GANNES et al. 1998; BASTOW et al. 2002; STAPP & POLIS 2003a, b).

Nitrogen isotope ratios may be used to analyse the trophic structure of animal communities. Due to the preferential excretion of ^{14}N, animals are enriched in ^{15}N compared to their diet (PETERSON & FRY 1987; ADAMS & STERNER 2000). The enrichment per trophic level is assumed to be rather constant allowing tracing the trophic level of consumers (DENIRO & EPSTEIN 1981; WADA et al. 1991; POST 2002).

Finally, metabolic processes and tissue-specific fractionation have been investigated using stable isotope analysis (DENIRO & EPSTEIN 1977; TIESZEN et al. 1983; GANNES et al. 1998; SCHMIDT et al. 2004).

Food web structure: Stable isotope analysis documented that the most common predators on xeric grasslands near Darmstadt relied on the detrital food web (CHAPTER IV.2) which is in line with other ecosystems (CHEN & WISE 1999; MCNABB et al. 2001; AGUSTI et al. 2003). In addition, stable isotope signatures documented that sheep grazing did not change the structure of the food web on xeric grasslands near Darmstadt (CHAPTER IV.2), which is in contrast to the study of NEILSON et al. (2002). On the contrary, stable isotope analysis revealed changes in vegetation structure that propagated into stable isotope signatures of the studied trophic guilds (CHAPTER IV.2).

For sandy beaches in Tasmania, stable isotope analyses documented that marine subsidies on the beach were not important for the terrestrial arthropod community on the foredune (CHAPTER IV.3).

Prey choice: Differences in prey choice were detected in the most abundant predators of xeric grasslands in Germany (CHAPTER IV.2) and on a sandy beach of Tasmania (CHAPTER IV.3). While female *Pardosa palustris* on xeric grasslands near Darmstadt presumably predominately fed on Collembola, adult females of the bigger *A. cuneata* were not linked to the detrital food web (CHAPTER IV.2), however, juveniles of both wolf spiders were predominately feeding on Collembola. Thus, stable isotope analysis documented that the larger wolf spider (*A. cuneata*) switches from prey of the detritivore food web to herbivore prey from the grazing food web during ontogenesis.

Similarly, stable isotope analysis produced detailed data on the beach and the foredune food web (e.g. trophic position and resource of animals) in Tasmania (CHAPTER IV.3). Different feeding niches could be documented for *Tetralycosa oraria* (Lycosidae) and *Cafius* 2 (Staphylinidae) using IsoSource, a software package for calculating the contribution of different sources to animal diet. Even though spiders are widely regarded as generalist predators (WISE 1993), stable isotope analysis documented that *T. oraria* was rather specialized on *Orchestia* spec. and other abundant prey, such as other amphipods and isopods, were not important for wolf spider nutrition.

Biotic interaction: Stable isotope analyses successfully documented IGP on juvenile *Pardosa palustris* by third instar *Alopecosa cuneata* (CHAPTER IV.6). Furthermore, stable carbon and nitrogen isotopes provided intriguing information about predation among juvenile *P. palustris*, proving very helpful in interpreting survival and biomass data (CHAPTER IV.6).

Metabolism: Using stable isotope analysis I documented for the first time that female wolf spiders increase feeding rates prior to eggsac production in order to gain nutrients for egg production and that they direct dietary carbon and nitrogen into their offspring (CHAPTER IV.4). Furthermore, carbon isotope data revealed that *Folsomia candida* (Collembola) exerted post-ingestive physiological effects on female *Pardosa lugubris*, as *Drosophila melanogaster* (Diptera) was killed and consumed by *P. lugubris* in the mixed diet treatment (*F. candida* + *D. melanogaster*), but carbon derived from *D. melanogaster* could not be incorporated in spider tissue (CHAPTER IV.4).

Summarizing, stable isotope analysis proved a powerful tool to investigate natural food webs (CHAPTER IV.2 & IV.3) as well as biotic interactions (CHAPTER IV.6) and physiological processes of spiders in laboratory experiments (CHAPTER IV.4). Furthermore, results of this study emphasize the importance of comprehensive data on food web components and the necessity for detailed analyses using stable isotope mixing models (e.g. IsoSource) for understanding ecosystem processes.

Despite of the successful application of stable isotope analysis, limitations of this method have to be considered. Trophic level fractionation is still discussed controversially (MCCUTCHAN et al. 2003; VANDERKLIFT & POSNDARD 2003; SCHMIDT et al. 2004) and mixing models have to be chosen with care (PHILLIPS 2001; PHILLIPS & GREGG 2001; PHILLIPS & KOCH 2002; ROBBINS et al. 2002). Therefore, stable isotope data from the field have to be interpreted with caution. Further laboratory experiments are needed to understand fractionation processes in detail and to answer the questions that arise when dealing with stable isotope data both from the laboratory and from the field. For example, the issue of the effects of starvation on stable isotope ratios in animals has to be investigated further. Many studies document enrichment in ^{15}N due to starvation, arguing that body-own protein is metabolised and the lighter isotope, ^{14}N, is preferentially excreted (GANNES et al. 1998; OELBERMANN & SCHEU 2002b; VANDERKLIFT & PONSARD 2003). However, results of this study also document depletion in ^{15}N in some starving spiders (CHAPTER IV.4 & IV.6), indicating the occurrence of further physiological effects.

In conclusion, stable isotope analyses can provide intriguing information about food web processes and trophic structure; however, the ability to detect direct feeding links using this method is rather limited. Recently, DNA based molecular gut analysis has been successfully applied for the detection of prey in predators (SYMONDSON 2002; AGUSTI et al. 2003). This technique seems extremely useful for predators, such as wolf spiders, that digest prey extra-intestinally thereby masticating the prey organism. Once suitable gene regions have been identified and the half-life of genetic material in the gut of the spiders is determined, DNA based gut analysis can precisely assess diet choice of spiders in the field.

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VII Appendix

Appendix I: **Abundance (Ind./5 m² ± SD) of Collembola on sites with and without grazing and with and without prey addition in June and August on the xeric grasslands of the “Ehemaliger August-Euler-Flugplatz” in 2002.**

		June								August							
		without prey addition				with prey addition				without prey addition				with prey addition			
		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed	
Familie	Taxon	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Isotomidae	*Isotoma viridis*	57.0	14.8	24.0	5.0	88.7	93.2	33.3	20.0	41.3	32.1	29.3	5.5	54.0	13.0	21.3	12.7
Entomobryidae	*Entomobrya nivalis*	344.3	286.0	153.7	78.4	354.0	350.9	130.7	66.2	47.0	26.5	27.7	19.5	64.0	38.6	54.0	52.0
	Lepidocyrtus cyanaeus	371.0	409.4	175.3	262.1	228.7	211.4	125.3	181.7	90.0	96.6	77.0	74.3	150.0	130.2	86.0	77.1

Appendix I: **Continued. Abundance (Ind./5 m² ± SD) of Auchenorrhyncha (Cicadellidae) on sites with and without grazing and with and without prey addition in June and August on the xeric grasslands of the “Ehemaliger August-Euler-Flugplatz” in 2002.**

	June								August							
	without prey addition				with prey addition				without prey addition				with prey addition			
	grazed		ungrazed		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed	
Art	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Anaceratagallia cf. *ribauti*	17.3	14.0	6.0	3.6	16.7	13.4	7.3	5.0	2.0	2.0	1.3	2.3	1.0	0.0	0.0	0.0
Anoscopus serratulae	8.3	6.5	9.3	6.8	19.7	11.7	2.3	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6
Aphrodes bicinctus	1.3	1.2	1.3	0.6	2.3	2.1	0.0	0.0	1.3	1.5	0.0	0.0	0.7	1.2	0.0	0.0
Aphrodes spec.	11.3	13.6	8.7	2.9	14.0	5.6	3.7	1.2	1.7	1.2	0.3	0.6	1.7	2.1	1.0	1.7
Artianus interstitialis	0.3	0.6	1.3	1.5	0.7	0.6	1.3	1.2	4.0	2.6	4.3	4.9	5.3	6.7	2.7	1.2
Doratura stylata	3.3	3.2	1.7	1.5	1.0	1.0	2.7	2.9	1.0	1.7	3.7	2.1	0.7	1.2	2.7	2.5
Eupelix cuspidata	0.0	0.0	0.3	0.6	0.3	0.6	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Graphocraerus ventralis	6.7	5.5	4.3	2.3	5.3	2.5	1.7	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jassargus cf. *obtusivalvis*	36.7	33.6	48.7	13.6	63.0	25.5	77.7	15.9	25.3	18.8	9.7	3.5	11.0	5.2	21.3	6.7
Megophthalamus scanicus	5.3	5.1	4.7	4.7	6.7	4.0	5.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
juv. Auchenorrhyncha	37.0	44.2	39.0	1.0	73.7	0.6	42.0	13.0	40.0	21.0	15.7	11.4	19.7	17.5	11.3	3.2

Appendix I: Continued. Abundance (± SD; Ind./5 m²) of Heteroptera on sites with and without grazing and with and without prey addition in June and August on the xeric grasslands of the “Ehemaliger August-Euler-Flugplatz” in 2002.

		June								August							
		without prey addition				with prey addition				without prey addition				with prey addition			
		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed	
Family	Art	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Alydidae	*Alydus calcaraeus*	1.0	1.0	1.3	2.3	0.0	0.0	1.0	1.0	0.3	0.6	1.3	2.3	0.0	0.0	0.0	0.0
Berytidae	*Berytinus clavipes*	4.7	5.5	1.0	1.0	1.0	1.7	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Neides tipularius	3.3	3.2	1.3	1.2	3.3	5.8	3.0	1.7	2.7	1.5	2.7	2.5	2.7	1.2	1.0	1.7
Coreidae	*Arenocoris fallenii*	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Ceraleptus gracilicornis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.3	0.6
Lygaeidae	*Aphanus quadratus*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6
	Cymus melanocephalus	2.0	2.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Emblethis verbasci	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.2	0.0	0.0	0.3	0.6	0.7	0.6
	Megalonotus praetextatus	0.3	0.6	0.3	0.6	0.0	0.0	0.3	0.6	2.3	4.0	0.0	0.0	0.7	1.2	1.0	1.0
	Peritrechus geniculatus	0.7	0.6	1.0	1.0	0.3	0.6	1.3	2.3	0.7	1.2	0.7	1.2	1.0	1.0	0.0	0.0
	Rhyparochromus brevirostis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.2	0.3	0.6	0.3	0.6	0.0	0.0
Miridae	*Alloeonotus fulvipes*	4.0	4.0	0.0	0.0	5.3	6.1	0.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Myrmecoris gracilis	0.3	0.6	0.7	0.6	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0
	Psallus roseus	6.7	4.0	2.7	1.5	5.3	3.5	4.3	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Stenodema laevigatum	0.7	0.6	1.0	1.0	0.7	0.6	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nabidae	*Nabis rugosus*	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0
	Prostemma guttula	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.3	0.6	0.0	0.0
Pentatomidae	*Neottiglossa leporina*	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhopalidae	*Myrmus miriformes*	0.0	0.0	0.3	0.6	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6
Scutelleridae	*Odontoscelis fuliginosa*	2.3	4.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tingidae	*Acalypta gracilis*	1.7	1.5	0.0	0.0	0.3	0.6	0.3	0.6	2.7	2.1	7.3	4.0	5.7	4.6	9.3	11.0
	Acalypta marginata	5.3	9.2	3.3	5.8	11.0	18.2	9.7	16.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Derephysia foliacea	0.7	1.2	0.3	0.6	3.0	3.0	0.7	1.2	3.7	6.4	3.0	5.2	0.3	0.6	0.7	1.2
	juv. Heteroptera	5.3	2.1	6.3	2.1	8.0	4.4	4.3	1.5	8.7	11.7	4.3	1.5	12.0	12.5	2.3	1.2

Appendix I: **Continued. Abundance (Ind./5 m^2 ± SD) of ground beetles (Coleoptera; Carabidae) on sites with and without grazing and with and without prey addition in June and August on the xeric grasslands of the "Ehemaliger August-Euler-Flugplatz" in 2002.**

	June								August							
	without prey addition				with prey addition				without prey addition				with prey addition			
	grazed		ungrazed		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed	
Taxon	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Amara aena	8.7	7.5	1.0	1.0	7.7	4.9	0.0	0.0	1.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0
Calathus cinctus	5.0	7.8	11.0	9.5	4.3	4.0	3.3	2.9	15.0	11.4	12.0	11.5	16.7	22.0	17.7	7.5
Calathus fuscipes	0.7	0.6	0.7	0.6	0.3	0.6	0.3	0.6	3.7	3.1	0.3	0.6	0.7	0.6	1.0	1.0
Harpalus anxius	0.7	1.2	0.0	0.0	2.3	2.5	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Harpalus autumnalis	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Harpalus pumilus	0.3	0.6	0.3	0.6	0.3	0.6	0.7	1.2	0.3	0.6	0.3	0.6	0.0	0.0	0.0	0.0
Harpalus rubripes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.6	1.3	0.6
Harpalus serripes	2.0	1.0	1.0	1.7	6.7	5.5	2.7	4.6	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0
Harpalus tardus	0.3	0.6	0.3	0.6	0.7	0.6	0.7	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Parophonus maculicornis	0.7	1.2	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Syntomus foveatus	0.7	1.2	1.0	1.7	1.3	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.6	0.0	0.0
Trechus obtusus	1.0	1.0	1.0	1.0	2.0	3.5	1.7	0.6	2.7	3.8	4.3	1.2	1.0	1.0	7.0	7.8

Appendix I: **Continued. Abundance (Ind./5 m² ± SD) of spiders on sites with and without grazing and with and without prey addition in June and August on the xeric grasslands of the "Ehemaliger August-Euler-Flugplatz" in 2002.**

		June								August							
		without prey addition				with prey addition				without prey addition				with prey addition			
		Grazed		ungrazed		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed	
Family	Taxon	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Agelenidae	*Tegenaria agrestis*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0
	juv. Agelenidae	0.3	0.6	0.7	0.6	0.7	0.6	1.3	0.6	0.3	0.6	0.3	0.6	0.3	0.6	0.0	0.0
Clubionidae	*Clubiona neglecta*	0.0	0.0	0.3	0.6	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Cheiracanthum virescens	0.3	0.6	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	juv. Clubionidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.3	0.6	0.0	0.0
Dictyniidae	*Argenna subnigra*	1.0	1.7	2.3	2.1	3.0	1.0	1.3	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gnaphosidae	*Haplodrassus signifer*	2.0	1.0	1.7	1.5	3.0	0.0	1.3	0.6	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0
	Drassodes pubescens	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Drassodes lapidosus	0.3	0.6	0.0	0.0	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Zelotes electus	1.0	1.0	1.3	0.6	1.3	1.5	2.0	2.0	0.7	0.6	0.3	0.6	0.7	0.6	1.3	2.3
	Zelotes longipes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.6	0.3	0.6	1.0	1.7	0.0	0.0
	Zelotes praeficus	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Zelotes pusillus	1.7	0.6	0.7	1.2	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	juv. Gnaphosidae	0.3	0.6	2.3	1.5	0.3	0.6	0.3	0.6	5.3	3.1	12.0	2.0	2.3	1.5	10.0	7.0
Hahniidae	*Hahnia nava*	0.3	0.6	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Liocranidae	*Phrurolithus festivus*	1.0	1.0	5.7	3.5	3.0	1.7	5.3	2.1	0.0	0.0	1.3	1.5	0.3	0.6	0.7	1.2
Lycosidae	*Alopecosa cuneata*	2.3	1.5	0.7	0.6	4.0	2.0	1.7	1.5	0.3	0.6	0.7	1.2	0.7	0.6	2.7	2.5
	A. cuneata juv. II	3.3	4.0	15.0	13.2	4.0	4.6	29.7	25.7	0.0	0.0	0.3	0.6	4.7	8.1	0.0	0.0
	A. cuneata Juv. III/+	0.0	0.0	1.3	1.5	0.0	0.0	0.7	0.6	16.7	18.9	8.3	14.4	14.3	5.5	11.0	6.6
	Alopecosa striatipes	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.7	1.2	0.0	0.0	0.7	1.2	0.0	0.0
	Aulonia albimana	0.3	0.6	2.7	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Pardosa palustris	12.7	6.1	5.3	3.1	18.3	9.9	3.0	2.6	2.7	0.6	0.7	1.2	1.3	0.6	1.3	2.3
	P. palustris juv.II	22.0	29.9	2.3	2.1	38.0	26.2	0.3	0.6	6.7	11.5	0.0	0.0	8.7	15.0	0.0	0.0
	P. palustris juv. III/+	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	24.3	21.5	2.7	3.8	21.3	31.8	6.3	10.1
	Xerolycosa miniata	8.3	11.8	1.7	0.6	2.0	1.0	0.3	0.6	1.0	1.0	0.3	0.6	1.0	1.0	2.0	2.6
	X. miniata juv. II	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.3	24.8
	X. miniata juv. III/+	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.3	0.6	0.7	0.6	2.7	3.1
	juv. Lycosidae	1.0	1.0	1.0	1.0	2.0	3.5	2.7	3.8	2.0	2.0	2.0	1.7	1.3	1.2	3.3	5.8

Appendix I: Continued. Abundance (Ind./5 m² ± SD) of spiders on sites with and without grazing and with and without prey addition in June and August on the xeric grasslands of the "Ehemaliger August-Euler-Flugplatz" in 2002.

		June								August							
		without prey addition				with prey addition				without prey addition				with prey addition			
		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed		grazed		ungrazed	
Family	Taxon	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pisauridae	*Pisaura mirabilis*	1.3	2.3	0.7	1.2	1.3	2.3	1.0	0.0	0.7	1.2	0.3	0.6	0.3	0.6	0.3	0.6
	P. mirabilis juv. III/+	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	2.9
Salticidae	*Euophrys aequipes*	0.3	0.6	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Euophrys frontalis	0.0	0.0	1.3	1.2	0.0	0.0	3.3	2.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Heliophanus flavipes	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Phlegra fasciata	0.0	0.0	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	juv. Salticidae	0.3	0.6	0.7	0.6	0.0	0.0	0.0	0.0	0.7	1.2	0.3	0.6	0.3	0.6	1.3	1.2
Theridiidae	*Steatoda phalerata*	0.7	1.2	0.3	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Thomisidae	Oxyptila atomaria	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3	2.3	0.0	0.0	0.0	0.0
	Oxyptila scabricula	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.2	0.0	0.0	0.0	0.0
	Tibellus oblongus	0.0	0.0	0.3	0.6	0.0	0.0	0.7	1.2	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0
	Xysticus cristatus	0.3	0.6	0.0	0.0	0.0	0.0	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Xysticus kochi	0.7	1.2	0.0	0.0	0.7	1.2	1.0	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Xysticus striatipes	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.3	3.1	6.0	3.5	11.3	3.5	2.3	2.5
	juv. Thomisidae	0.7	0.6	1.3	1.5	0.7	1.2	2.0	1.7	3.3	1.2	4.0	1.7	3.7	4.6	4.0	5.3
Zodaridae	Zodarion italicum	0.3	0.6	0.3	0.6	0.7	0.6	0.7	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6

Appendix II: Activity density (± SD) of arthropods on a transect across a sandy beach and foredune at Marion Bay (Tasmania) in December 2004.

	Taxon	Transect a	Transect b	Transect c	Transect d	Transect e
Amphipoda	*Talorchestia marmota*	7.7 ± 7.8	6.7 ± 6.4	19.0 ± 6.2	0.0 ± 0.0	0.0 ± 0.0
	Talorchestia 1	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	1.8 ± 2.0	0.0 ± 0.0
	Talorchestia 2	79.0 ± 94.4	33.2 ± 28.1	24.2 + 24.9	0.0 ± 0.0	0.0 ± 0.0
	Orchestia spec.	7.2 ± 7.1	1.0 ± 2.0	0.5 ± 0.5	0.0 ± 0.0	0.0 ± 0.0
	juvenile Amphipods	4.5 ± 6.1	3.0 ± 3.0	2.5 ± 2.3	0.0 ± 0.0	0.0 ± 0.0
Isopoda	*Actaecia thompsoni*	44.3 ± 34.6	39.0 ± 40.0	9.5 ± 8.8	0.0 ± 0.0	0.0 ± 0.0
	Actaecia bipleura	43.8 ± 51.7	75.5 ± 109.9	27.7 ± 36.5	4.0 ± 5.8	2.5 ± 6.1
	Porcellio scaber	0.0 ± 0.0	0.2 ± 0.4	0.5 ± 0.8	0.8 ± 1.6	4.3 ± 4.6
Chilopoda	*Tuoba laticeps*	0.0 ± 0.0	0.2 ± 0.4	0.3 ± 0.8	0.0 ± 0.0	0.0 ± 0.0
Diplopoda	Polydesmidae 1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	3.2 ± 3.2
	Polydesmidae 2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.8 ± 2.0
	Polydesmidae 3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
	Polydesmidae 4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	3.0 ± 3.0
Scorpionida	*Cercophonius squama*	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5	1.2 ± 1.2
Diptera	Scatophagidae 1	0.0 ± 0.0	3.0 ± 2.2	4.7 ± 5.6	0.0 ± 0.0	0.0 ± 0.0
	Brachycera 2	0.0 ± 0.0	0.2 ± 0.4	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
	Brachycera 3	0.0 ± 0.0	0.0 ± 0.0	3.5 ± 7.1	1.0 ± 0.9	0.0 ± 0.0
	Brachycera 4	0.3 ± 0.8	1.5 ± 1.9	7.0 ± 6.2	2.0 ± 2.3	0.2 ± 0.4
	Brachycera 8	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.2	0.0 ± 0.0
	Brachycera 9	0.2 ± 0.8	0.8 ± 1.6	1.5 ± 1.8	0.5 ± 0.8	0.0 ± 0.0
	Brachycera 11	0.0 ± 0.0	0.3 ± 0.5	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
	Brachycera 12	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
	Brachycera 13	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
	Brachycera 17	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
	Brachycera 18	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.8
	Brachycera 23	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
	Brachycera 26	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 0.8	0.5 ± 1.2
	Brachycera 27	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.5 ± 1.2
	Brachycera 28	0.0 ± 0.0	0.5 ± 1.2	0.0 ± 0.0	0.3 ± 0.8	0.0 ± 0.0
	Brachycera 29	0.5 ± 0.8	0.5 ± 0.5	14.3 ± 18.3	15.8 ± 20.6	0.0 ± 0.0
	Brachycera 35	0.0 ± 0.0	0.0 ± 0.0	0.5 ± 1.2	0.0 ± 0.0	0.0 ± 0.0
	Brachycera 40	0.2 ± 0.4	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	22.7 ± 51.7
	Brachycera 41	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
	Brachycera 44	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
	Nematocera 3	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 1.2	0.3 ± 0.5	0.0 ± 0.0
	Nematocera 6	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0
Hymenoptera	Iridomymex spec.	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.8 ± 1.6	2.0 ± 3.5
	Myrmecia spec.	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0
	Myrmecinae	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.5 ± 2.3	6.7 ± 10.9
	Formicidae 13	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.8 ± 4.5
	Formicidae 14	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 2.9
	Formicidae 15	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0
	Formicidae 19	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.8	0.3 ± 0.8

Appendix II: Continued. Activity density (± SD) of spiders on a transect across a sandy beach and foredune at Marion Bay (Tasmania) in December 2004.

Family	Taxon	Transect a	Transect b	Transect c	Transect d	Transect e
Lycosidae	*T. oraria* ♀	0.0 ± 0.0	0.2 ± 0.4	0.3 ± 0.8	0.0 ± 0.0	0.0 ± 0.0
	T. oraria ♂	0.3 ± 0.5	2.5 ± 2.5	1.3 ± 1.5	0.2 ± 0.4	0.0 ± 0.0
	A. victoriensis ♀	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
	juv. Lycosidae	0.0 ± 0.0	0.8 ± 1.3	0.2 ± 0.4	0.5 ± 0.8	0.5 ± 0.5
Gnaphosidae	Gnaphosidae 1 ♀	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
	Gnaphosidae 2 ♀	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0
	Gnaphosidae 3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0
	Gnaphosidae 4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.8	0.2 ± 0.4
	juv. Gnaphosidae	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.7 ± 1.0	0.7 ± 1.6
Clubionidae	Clubionidae 1	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
Salticidae	Salticidae 1	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0
	Salticidae 2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.0 ± 0.0
	Theridiidae 2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5
Linyphiidae	Linyphiidae 1	0.2 ± 0.4	0.2 ± 0.4	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Thomisidae	Thomisidae 1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Corinnidae	*Supunna picta*	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4	0.5 ± 0.8
Nicodamidae	Nicodamidae 1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.4
Zoridae	Zoridae 1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.5

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Eidesstattliche Erklärung

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation ohne fremde Hilfe angefertigt und mich keiner anderen als die von mir angegebenen Schriften und Hilfsmittel bedient habe.

Ort, Datum

Unterschrift