Lycosid spiders and alternative food: Feeding behavior and implications for biological control

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ABSTRACT

The extent to which generalist arthropod predators feed on natural populations of alternative prey, and how availability of such food influences biological control of agricultural pests, is largely unknown. A major reason is that direct estimation of arthropod predation in food webs is a methodological challenge. Here, we report the first use of DNA-technology to track predation by lycosid spiders on natural populations of springtails. Predators were collected in cereals and leys on organic farms in central Sweden. In parallel, the availability of springtails and other potential alternative prey was monitored. The collected spiders ($n = 469$) were analyzed using group-specific springtail PCR-primers. Spiders collected in cereals had previously been screened for consumption of an aphid pest, and by combining those data with availability of alternative prey, we tested if presence of alternative food affected aphid predation. In total, 20% of *Pardosa* were found to have preyed upon springtails. The proportion of spiders consuming springtails did not differ between habitats; 19% positive in leys and 22% in cereals. Springtail consumption was not correlated with springtail abundance. Our results demonstrate that springtails are an important source of alternative food for *Pardosa*. Thus, presence of springtails may contribute to spider population maintenance and, indirectly, to enhanced predation pressure on co-occurring pests. However, we also found evidence that high abundances of alternative prey may interfere with aphid predation. We suggest that changes in the spiders̍ foraging behavior, rather than increased springtail consumption, is the underlying mechanism.

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1. Introduction

The diet of generalist arthropod predators includes major agricultural pests such as aphids (Sunderland et al., 1987; Chiverton, 1987; Kuusk et al., 2008), caterpillars (Ma et al., 2005), planthoppers (Fournier et al., 2008) and slugs (Dodd et al., 2003). If the predation pressure is high enough early in the season, when pest densities are low, assemblages of generalist predators have the capacity to maintain pest populations below economic thresholds (Edwards et al., 1979; Chiverton, 1986; Settle et al., 1996; Östman et al., 2001). Consequently, they are a valuable component of the natural enemy group that can contribute to conservation biological control.

In addition to pest herbivores, generalist predators are confronted with a wide range of potential non-pest prey. If such alternative food attracts generalist predators to a crop field, and predation rates on co-occurring pest species increases, then biological control may improve (Holt and Lawton, 1994). Such aggregative numerical responses are particularly important in annual cropping systems where natural enemies have to recolonize the crop fields after sowing and other disturbances (Harmon and Andow, 2004; Thorbek and Bilde, 2004; Öberg and Ekbom, 2006). Consumption rates of pests may also be elevated if ingestion of alternative prey causes a reproductive numerical response i.e., enhances predator fitness and the overall predator population size (Polis and Strong, 1996). Reproductive responses are more long-term than aggregative effects (Holt and Lawton, 1994), and likely involve other habitats than the crop area. For example, when annual crops are disturbed by different management practices, generalist predators can find refuge in adjacent, more extensively managed, environments such as field margins, leys and pastures (Pfiffner and Luka, 2000; Schmidt and Tscharntke, 2005; Öberg et al., 2007). Consequently, these areas may be important foraging sites, where predators can find alternative prey, and contribute to population maintenance of natural enemies. Although a handful of studies have demonstrated that generalist predators exploit natural populations of alternative prey (Agustí et al., 2003; Juen and Traugott, 2007; Harwood et al., 2007a,b, 2009), this area of research is still new. Information for most combinations of predator and prey is lacking.

Although there may be positive effects attributed to presence of alternative prey there may also, from a biological control perspective, be negative aspects. If the relative abundances of prey species

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changes generalist predators may switch from feeding on one prey species to another (Holt and Lawton, 1994). Consequently, in a situation where alternative food diverts predators away from feeding on an herbivorous pest, biological control may be disrupted. This has been observed in studies in which densities of generalist predators and/or prey have been manipulated (Musser and Shelton 2003; Koss and Snyder 2005; Prasad and Snyder 2006; Birkhofer et al., 2008). However, reports of negative correlations between pest consumption by generalist predators and availability of alternative prey, in undisturbed habitats, are sparse (but see Harwood et al., 2004).

Wolf spiders (Araneae: Lycosidae) are common generalist predators in European agroecosystems (Samu and Szinetár, 2002; Schmidt et al., 2005; Öberg et al., 2007) and in the current study we focus on the diurnal genus *Pardosa*. The members of this genus live almost exclusively on the ground surface where they hunt for food either by lying in ambush or by roaming around (Lowrie, 1973; Foelix, 1996). In a previous study, using DNA-based gut-content analysis, we demonstrated that *Pardosa* spiders feed on the bird cherry-oat aphid (*Rhopalosiphum padi* L., Hompotera: Aphididae) in spring-sown cereals at low pest densities, suggesting that they may be important natural enemies of this major pest (Kuusk et al., 2008). There was a large variation in aphid predation rates between farms, and because aphid densities did not differ between sites we suggested that the variation might be influenced by the availability of alternative prey. In the current study we tested this hypothesis by combining the aphid consumption PCR-data from Kuusk et al. (2008) with population monitoring of alternative prey, which was carried out in parallel.

Springtails (Arthropoda: Collembola) are small, detritivorous organisms that often occur in very high densities in soil and leaf litter (Hopkin, 1997). These organisms may constitute a major source of potential alternative food for ground-living generalist predators. Laboratory studies have shown that some springtails are high-quality food for wolf spiders (Toft and Wise, 1999; Oelbermann and Scheu, 2002) and inputs of detrital subsidies have caused a simultaneous increase in springtail and wolf spider abundances, suggesting that the spiders are exploiting springtails (Chen and Wise, 1999; Halaj and Wise, 2002; Oelbermann et al., 2008). It has also been observed that wolf spiders carry springtails in their chelicerae under natural field conditions (Edgar, 1970; Nyffeler and Benz, 1988). Despite such evidence, doubts have been raised as to whether or not this alternative prey forms a significant part of the diet of large, non-web based spiders such as *Pardosa* (Halaj and Wise, 2002; Harwood et al., 2005).

Arthropod predation is generally difficult to observe and estimate directly for obvious reasons: predators and prey are often small, mobile and/or live beneath dense vegetation. In the current study, we chose to investigate springtail predation by analyzing the gut-contents of field-collected *Pardosa* spiders using the polymerase chain reaction (PCR)-technique. This method enables precise amplification of minute amounts of prey-specific DNA-remains in a predator's stomach content, and provides direct evidence of trophic interactions that have occurred under minimal experimental disturbance (Sheppard and Harwood, 2005; King et al., 2009). When working in habitats where the diversity of a potential prey group is high, and when knowledge about the links between a predator and different species within the prey group is sparse, group-specific PCR-primers, having a broad specificity across a range of species in a given higher taxon, can be a powerful tool (Jarman et al., 2004; Admassu et al., 2006). We conducted our survey in spring-sown cereals and leys in central Sweden. Previous studies in similar habitats have shown that the species composition of springtails is relatively diverse with more than 20 identified species representing various families from both springtail suborders; Arthropleona (elongated springtails) and Symphypleona

(globular springtails) (Curry, 1986; Lagerlöf and Andrén, 1991). For this reason, we decided to utilize group-specific springtail primers designed by Kuusk and Agustí (2008).

The purpose of this work was to elucidate to what extent *Pardosa* spiders prey on natural populations of springtails in spring-sown cereals and leys using a combination of DNA-based gut-content analysis and population monitoring of prey availability. We hypothesized that *Pardosa* exploit springtails in both habitats and that *Pardosa* prey upon springtails in relation to availability. We also asked if presence of springtails or other alternative prey affected aphid predation by *Pardosa* spiders in spring-sown cereals. We hypothesized that high densities of alternative prey could have a negative impact on biological control of cereal aphids. Detailed knowledge about which species of alternative prey are exploited by generalist predators under natural field conditions, and how presence of such food is influencing consumption of co-occurring pest species, is necessary before effective and sustainable biological control programs, based on the action of local generalist predators, can be established.

2. Materials and methods

2.1. Detection success of springtail DNA in laboratory-fed Pardosa

To ascertain that it was possible to detect springtail DNA in *Pardosa* spiders we conducted a laboratory feeding experiment. As we wanted to know if spiders consumed springtails during the 24 h period proceeding capture in the field, we wanted to make sure that springtails consumed before that period would not be detected. Therefore spiders were tested immediately after consumption and after 24 h of digestion. The prey, adult *Isotoma* spp., was extracted from soil cores collected in a set-aside outside Uppsala in April 2007. The springtails were transferred to plastic vessels with a charcoal and plaster of Paris base to maintain high humidity and were fed dry yeast. After molting, the springtails were frozen and stored in −70 °C. The predators, adult *Pardosa* spp., were collected in the same set-aside the last week in May 2007. They were individually enclosed in small, aerated plastic vessels containing moist sand. After starvation for one week at room temperature, each spider was transferred to a clean Petri Dish (diameter 47 mm) containing one adult prey placed on a moistened filter paper. The spiders were observed until feeding started and ceased, which typically took 5–20 min. Half of the fed predators were frozen immediately (0 h) after ingestion, and the other half after 24 h in a clean dish in a climate chamber at 15 ± 2 °C representing local average temperatures in late May to June (SMHI webpage, 2009). All predators were stored at −70 °C until DNA extraction. To obtain 12 fed spiders per digestion period (0 and 24 h) the feeding trial was conducted twice on two consecutive days with completely different batches of starved spiders. For each setup, two starved unfed spiders were included and later used as negative controls in the PCR-analysis. Prior to DNA extraction, all spiders were briefly handled to determine species and sex. All analyzed specimens ($n = 28$ including four controls) were females consisting of 89% *Pardosa agrestis* (Westring), 7% *Pardosa palustris* (L.), and 4% *Pardosa prativaga* (L. Koch).

2.2. Collection of predators in leys and spring-sown cereals

Adult *Pardosa* spiders of both sexes were randomly collected from four leys and three fields of spring-sown cereals at organic farms near Uppsala, Sweden in 2005 (Table 1).

The leys were sown using a standard seed mix of *Trifolium pratense* (L.), *Trifolium repens* (L.), *Festuca pratensis* (L.) and *Phleum pratense* (L.), and had been established one year previously by