Intraguild interactions, trophic ecology and dispersal in spider assemblages

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Intraguild interactions, trophic ecology and dispersal in spider assemblages

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Per optar al grau de Doctora

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A la meva família, d’aquí i d’allà

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Abstract

Spiders (Araneae) are a hyperdiverse predator group and are widespread in both natural and arable communities, where they prey on many different types of insects and play a role in biological control. Spiders occupy intermediate positions in food webs and are involved in intraguild interactions with other arthropod and vertebrate predators. However, most studies in ecology adopt an oversimplified approach by treating the spider assemblage as a single uniform group, thus ignoring the sheer diversity of species interactions and trophic links within arthropod communities. Food webs and population dynamics are also influenced by the dispersal of individuals through the landscape. Because dispersal is costly, individuals are expected to rely on multiple sources of information about habitat quality before making a dispersal decision, although research on the relative importance of different information sources is largely lacking. The goals of this PhD thesis were first, to study arthropod food webs and the interactions between spiders, ants and birds using a Mediterranean organic citrus grove as study system; second, to investigate the effect of information about food availability and of actual food supply on spider dispersal. There were six specific objectives, namely (1) to compare the relative effect of birds and ants on the spider assemblage; (2) to test the differential impact of bird predation on diurnal and nocturnal canopy spiders; (3) to study the long-term effects of canopy-foraging ants on the spider assemblage; (4) to unravel the structure of the arthropod food web of the grove with stable isotope analyses; (5) to test the effect of cues of food availability on site-selection and of prey supply on emigration decisions of the colonial spider *Cytrophora citricola*; and (6) to test the importance of direct and maternal food supply on long- and short-distance emigration decisions of *Erigone dentipalpis*. Over an almost 2-year period, we found that ants had a strong effect on some web-building spiders of the families Araneidae and Theridiidae, whereas we did not find any effect of birds. However, in a bird exclusion experiment where we used other sampling methods, we detected a reduction of araneids and theridiids caused by birds, emphasizing the influence of sampling on the outcome of ecological field experiments. Long-term data also provided essential information about ecological processes: whereas in the beginning of an 8-year ant-exclusion experiment ants did not have any effect on spiders, they did have a pervasive impact on the spider assemblage for the last 4 years: ants negatively affected the abundance of a wide range of spider species independently of the family the spiders belonged to. Stable isotope analyses retrieved the trophic positions of the 25 most common spider species and of the main species

of ants and other insects. The trophic level of spiders was much higher than that of their potential prey, suggesting a prevalence of omnivory and intraguild predation in the food web. Spider species from the same family belonged to different trophic groups, which, together with the aforementioned results, show the high value of species-level analyses. In both *C. citricola* and *E. dentipalpis*, indirect information of food availability (dead prey remains, maternal food supply), played a key role in dispersal, in contrast to the limited importance of immediate food intake. Moreover, the two species accurately weighed their decision whether to emigrate or not, according to the costs required by the dispersal strategy on the one hand and to the available source of information on the other hand. These information sources thus need to be considered together with intraguild interactions as factors influencing spider populations.

Resum

Les aranyes (Araneae) són un grup hiperdivers de depredadors àmpliament representat en comunitats naturals i en conreus, on s'alimenten de diferents tipus d'insectes i participen en el control biològic de plagues. Ocupen posicions intermèdies dins les xarxes tròfiques i estan implicades en interaccions intragremials amb altres depredadors, tant artròpodes com vertebrats. Tanmateix, la majoria d'estudis en ecologia adopten un enfocament sobresimplificat perquè tracten les aranyes com a un sol grup uniforme i, per tant, ignoren la gran diversitat d'interaccions interespecífiques i de connexions tròfiques que tenen lloc en les comunitats d'artròpodes. Les xarxes tròfiques i les dinàmiques poblacionals també estan influenciades per la dispersió dels individus a través del paisatge. Com que dispersar-se és costós, hom espera que els individus es basin en múltiples fonts d'informació sobre la qualitat de l'hàbitat abans de decidir dispersar-se, tot i que la recerca sobre la importància relativa de fonts d'informació diferents es troba en un estadi molt incipient. Els objectius d'aquesta tesi doctoral eren, primer, estudiar les xarxes tròfiques d'artròpodes i les interaccions entre aranyes, formigues i ocells utilitzant com a sistema d'estudi un cultiu ecològic mediterrani de cítrics; segon, investigar l'efecte de la informació sobre sobre disponibilitat d'aliment i del subministrament d'aliment en la dispersió de les aranyes. Hi havia sis objectius concrets, que eren (1) comparar l'efecte relatiu dels ocells i de les formigues en la comunitat d'aranyes; (2) comprovar l'impacte dels ocells en les aranyes diürnes i nocturnes de les capçades; (3) estudiar els efectes a llarg termini sobre la comunitat d'aranyes de les formigues que patrullen en les capçades; (4) desentrellar l'estructura de la xarxa tròfica dels artròpodes del cultiu amb anàlisis d'isòtops estables; (5) comprovar l'efecte dels indicadors de disponibilitat d'aliment en la selecció d'hàbitat i l'efecte del subministrament de preses en l'emigració de l'aranya colonial *Cyrtophora citricola*; i (6) contrastar la importància del subministrament de menjar a la mare i a la descendència en l'emigració a curta i a llarga distància d'*Erigone dentipalpis*. Durant un període de gairebé 2 anys, vam trobar que les formigues tenien un gran efecte sobre les aranyes constructores de teranyina de les famílies Araneidae and Theridiidae, mentre que no vam trobar cap efecte dels ocells. No obstant això, en un experiment d'exclusió d'ocells on vam utilitzar altres mètodes de mostreig, vam detectar una reducció dels aranèids i dels terídids causada pels ocells, la qual cosa emfasitza la importància del mostreig en el resultat dels experiments de camp en ecologia. Les dades sobre llargs períodes de temps també proporcionen informació essencial sobre processos ecològics: mentre que a l'inici d'un experiment de 8 anys d'exclusió de formigues,

aquestes no tenien cap efecte sobre les aranyes, sí que van tenir un impacte profund sobre la comunitat d'aranyes durant els últims 4 anys: les formigues van afectar negativament l'abundància d'un ampli rang d'espècies d'aranyes independentment de la família a la qual les aranyes pertanyien. Les anàlisis d'isòtops estables van mostrar la posició tròfica de les 25 espècies més comunes d'aranyes i de les principals espècies de formigues i d'altres insectes. El nivell tròfic de les aranyes era molt més alt que el de les seves preses potencials, suggerint la prevalença de l'omnivoria i de la depredació intragremial en la xarxa tròfica. Les espècies d'aranyes de la mateixa família pertanyien a grups tròfics diferents, cosa que, juntament amb els resultats esmentats abans, mostra l'alt valor de les anàlisis a nivell d'espècie. Tant en *C. citricola* com en *E. dentipalpis*, la informació indirecta sobre la disponibilitat de menjar (restes de preses mortes, subministrament de menjar a la mare), va tenir un paper clau en la dispersió, en contrast amb la importància limitada de la ingesta de menjar. A més a més, les dues espècies van sospesar acuradament les seves decisions sobre emigrar o no d'acord amb els costos requerits per cada estratègia de dispersió i amb la font d'informació disponible. Per tant, aquestes fonts d'informació han de ser considerades juntament amb les interaccions intragremials com a factors que influencien les poblacions d'aranyes.

1

General introduction

Introduction

With more than 43,000 described species (Platnick 2012), spiders (Araneae) are the most abundant predator group in terrestrial ecosystems all over the world (Turnbull 1973; Wise 1993). They display a staggering array of lifestyles, hunting modes and reproductive strategies that make them ideal model organisms to address questions about ecology, behaviour and evolution (Jocqué & Dippenaar-Schoeman 2006; Foelix 2010; Herberstein et al. 2011).

Spiders are also fundamental components of the fauna of arable land (Young & Edwards 1990; Marc & Canard 1997). Some spider species tend to become dominant in crops and are termed "agrobiont spiders" (Luczak 1979), but the spider fauna in agroecosystems can be very diverse, as has been documented in many types of crops (Marc et al. 1999; Samu & Szinetár 2002). Because most spiders are generalist predators, they play a role in the biological control of pests as part of a multi-species assemblage, as well as together with other predatory arthropods (Riechert 1999; Symondson et al. 2002; Fréchette et al. 2008). Farmland represents nowadays 40% of the earth surface and contains more than 25% of the global tree cover (Foley et al. 2005; Ellis & Ramankutty 2008), the rampant increase in agricultural intensification over the past four decades being one of the leading causes of the biodiversity loss worldwide (Tilman et al. 2001; Nentwig 2003; Hole et al. 2005). To counteract this trend, many countries are shifting towards more sustainable farming practices, such as organic agriculture and integrated pest management, in order to enhance abundance and biodiversity of spiders and other predators in agroecosystems, and hence biological control (Pekár 1999; Bengtsson et al. 2005; Schmidt et al. 2005; Winqvist et al. 2012). Nevertheless, research on spider assemblages in agricultural land is strongly dominated by studies performed in temperate areas in America and Europe, whereas those in Mediterranean agroecosystems remain understudied (Nyffeler & Sunderland 2003; Prieto-Benítez & Méndez 2011).

Intraguild interactions and trophic ecology of spiders

The guild concept (Root 1967) is a useful and intuitive way to group species within communities, although the exact interpretation of this term has been subject of much debate. Currently guilds are mostly regarded as non-phylogenetic groups that share resources, the definition of "resource" depending on the ecological question under study (Hawkins & MacMahon 1989; Wilson 1999; Blondel 2003). Despite their sheer species diversity, a number of spider classifications into guilds with different scopes have been proposed (Uetz et al. 1999; Cardoso et al. 2011). At a larger scale, spiders are part of the predator guild of the arthropod community in terrestrial food webs, together with predatory insects (Halaj et al. 1997; Finke & Denno 2003), but again, this definition of guild can be further extended to encompass insectivorous vertebrates like birds or lizards (Schoener & Spiller 1987; Spiller & Schoener 1988; Gunnarsson 2007), and even carnivorous plants (Jennings et al. 2010).

Intraguild interactions among predators are very varied and have a profound impact on the dynamic and structure of communities (Morin 2011). Among these interactions are interspecific competition (Gurevitch et al. 1992, 2000; Chase et al. 2002) and intraguild predation. Intraguild predation is a case of omnivory (feeding across multiple trophic levels [Pimm & Lawton 1978]) that combines predation and competition because the predator kills prey that uses the same resource (Polis et al 1989; Polis & Holt 1992; Holt & Polis 1997). Intraguild interactions are prevalent in both natural and agricultural arthropod communities (Arim & Marquet 2004) and can cause the effects of multiple predators on other organisms to be non-additive so that the resulting outcome is stronger (synergism) or weaker (antagonism) than the sum of all individual effects (Rosenheim 1998; Sih et al. 1998; Ives et al. 2005; Vance-Chalcraft & Soluk 2005). These effects have the potential to lower (Finke & Denno 2004, 2005; Vance-Chalcraft et al. 2007) or to enhance the strength of top-down trophic cascades involving the shared prey (Cardinale et al. 2003, 2006; Law & Rosenheim 2011), and consequently affect pest control and crop yield in agroecosystems (Halaj & Wise 2001; Symondson et al. 2002; Snyder et al. 2008; Hunter 2009). Because of the ubiquity of intraguild interactions and their widespread effects on food webs, testing them with manipulative field experiments is crucial to further our knowledge of arthropod communities. However, most studies on intraguild interactions have at most addressed these effects on two broad categories of spiders —hunters vs. web-builders— if not treated the whole species assemblage as a single group (Van Bael et al. 2003; Mooney 2006, 2007). Given the great differences in lifestyles between spider species, we think that these are oversimplified approaches that could overlook a suite of contrasting responses of different species towards a given intraguild pressure.

On the other hand, knowledge about the complex network of trophic interactions that configure arthropod food webs is increasing (Moya-Laraño & Wise 2007; Evans 2008; Birkhofer et al. 2011). Different methodologies have been employed over the past decades to determine the diet composition of spiders and calculate predation rates, such as field observations of feeding behaviour and of prey remains in webs, laboratory choice experiments, and more recently, DNA-based gut content analysis (Young 1989; Nyffeler et al. 1992; Nyffeler 1999; Symondson 2002; King et al. 2008). A broader, complementary approach is to analyse the stable isotope composition of the species in a food web to assign them to trophic levels (with $\delta^{15}N$) and to determine the origin of the source of energy they use (with $\delta^{13}C$; Tiunov et al. 2007; Boecklen et al. 2011). This way, a picture of the isotopic signatures of species (or higher taxa) emerges, giving insights into the structure of the food web, but there is a need of detailed studies of the trophic positions of spiders in food webs (Sanders & Platner 2007).

Prey availability and spider dispersal

The dispersal of individuals and propagules across several spatial scales has a key influence on gene flow, species evolution, population dynamics, and on the species composition of communities (Bowler & Benton 2005; Ronce 2007). It is a process with three phases: emigration (departure), transience (movement phase) and immigration (colonization); each of these is governed by multiple causes (Ims & Yoccoz 1997; Clobert et al. 2004) that ecologists are trying to discern in order to predict how species will react to biodiversity threats such as habitat disturbance and fragmentation (Trakhtenbrot et al. 2005; Kokko & López-Sepulcre 2006).

Most spider species have high dispersal abilities: apart from walking on the ground, they build silken bridges among the vegetation, a dispersal mode called "rappelling" (Bonte 2009). Many families also perform aeronautic dispersal, called "ballooning", which consists in a long-distance passive flight through the air using a short silk thread as a drag (Suter 1999; Bell et al. 2005). Ballooning enables spiders to promptly colonize distant new habitats such as crops (Bishop & Riechert 1990; Weyman et al. 2002), although neighbouring natural areas are also a source of spiders for agroecosystems and can serve as overwintering sites for spiders inhabiting ephemeral crops (Thomas & Jepson 1997; Schmidt & Tscharntke 2005; Sackett et al. 2009). Habitat quality is a major factor influencing spider dispersal behaviour: research has shown that physiological indicators of habitat quality such as starvation and temperature affect spider ballooning (Weyman et al. 1994; Bonte et al. 2008a,b), but also that abundance of prey and habitat disturbance play a role (Harwood et al. 2003; Entling et al. 2011).

Each phase of the dispersal process involves specific costs for individuals (Bonte et al. 2012). In spiders, emigration by ballooning bears a high risk because spiders cannot direct their flight, whereas selecting a novel site requires an investment of energy to build a web or a nest to forage (Suter 1999; Zschokke & Vollrath 2000). For this reason, individuals are not only expected to disperse as a reaction to immediate environmental conditions, but also to have evolved mechanisms to gather accurate information on the habitat in order to weigh the costs vs. the potential benefits of emigration and site selection (Ronce et al. 2001; Clobert et al. 2009). Known sources of information about habitat quality are conspecific presence, maternal effects and cues of prey availability, but the relative influence on dispersal of these sources of information compared to actual prey intake has rarely been tested (Pasquet et al. 1994; Massot et al. 2002).

Study system

We investigated the trophic ecology of spiders and the intraguild interactions between spiders, ants and birds in an organic citrus grove. Groves are simpler and more susceptible to ecological manipulations than natural systems, thereby favouring the detection of functional relationships that in nature might be obscured by a number of complex interactions (Greenstone & Sunderland 1999; Polis et al. 2000).

The grove is located at La Selva del Camp (Catalonia, NE Spain; 41º 13' 07″N, 1º 8' 35″E). The area has a typical Mediterranean climate, with a rainy spring and autumn and a dry winter and summer. The grove has around 300 Clementine trees (*Citrus clementina* var. *clemenules*) grafted on the hybrid rootstock Carrizo citrange (*Poncirus trifoliata* (L.) Raf. x *Citrus sinensis* (L.) Osb.). The trees are watered during the dry seasons (Fig. 1.1). Grasses and other weeds form a permanent ground cover that is mowed a few times every year. Between 2002 and 2004 the grove underwent a gradual transformation to organic agriculture: pesticides were last applied in 2002, and herbicides in 2003; mineral fertilizer was substituted by organic manure in 2004. Therefore, the grove complied with all organic agriculture standards from 2004 onwards. Since 2006, the irrigation system consists of micro-spray jets that keep large areas of soil damp to accelerate the mineralization of the organic fertilizer, in substitution of a system of localized drip irrigation that nevertheless used the same volume of water.

This PhD thesis is part of a long-term project about the interspecific interactions in the arthropod community of the grove. The project began in 2002 and first tested the effects of canopy-foraging ants on aphids. Though ants and aphids are known to engage in mutualistic interactions, ants turned out not to have a substantial influence on aphids in the grove, in contrast with earwigs, which reduced their densities (Piñol et al. 2009). Ants however, exert a great negative effect on the abundances of several arthropod groups, although this effect varies over the years (Piñol et al. 2012a). In 2006 the influence of birds on the arthropod assemblage was examined: they were far less important than ants, as they only affected earwig abundances (Piñol et al. 2010). The trophic relationships within the arthropod food web have started being studied with stable isotopes (of ants: Platner et al. unpublished) and DNA-based gut content analyses (of earwigs: Romeu-Dalmau et al. 2012).

In addition, the thesis addresses the impact of prey availability on spider dispersal. Like competition and intraguild predation, the dispersal of individuals is expected to affect the composition of spider assemblages and population dynamics (Weyman et al. 1994; Harwood et al. 2003). Measuring the impact of prey supply on spider dispersal was unfeasible with field experiments in the grove. Hence, we selected two spider species that are common in agroecosystems and performed experiments in semi-field or laboratory conditions during two research stays, in collaboration with other researchers.

Fig. 1.1. General appearance of clementine trees in the study system (December 2009).

Objectives of the thesis

In the first place, this PhD thesis focuses on the interactions between spiders and their competitors and intraguild predators in the grove, namely ants and birds. To examine which consequences ant and bird presence had on spiders, we conducted a series of field experiments in which we excluded ants from the canopies with glue rings and birds from the canopies and from the ground with large net cages enclosing groups of trees. We sampled spiders with different sampling methods, but mainly with beating trays and pitfall traps. Since we aimed at a comprehensive study of the changes on the spider assemblage composition caused by ants and birds, we identified all spiders to species. In the second place, once we identified the most representative spiders in the grove, we wanted to determine their trophic positions within the arthropod food web analysing stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of different species of spiders and other arthropods. Finally, we tested the influence of perceived food availability and of actual food intake on the dispersal of two spiders common in arable land to gain understanding of the role that lower trophic levels play in spider population dynamics.

Below follows an outline of the specific objectives addressed in the thesis. Chapters 2-4 address the effects of ants and birds on the spider assemblage of the grove, chapter 5 deals with the trophic ecology of the main spider species and insects; chapters 6-7 go on to examine the effect of food availability on spider emigration and site-selection behaviour.

Chapter 2: to compare the relative effect of birds and ants on the spider assemblage.

Piñol et al. (2010) had conducted a one-way exclusion experiment in 2006 to compare the individual effects of ants and birds on arthropods, and they found a negative effect of ants on some spider families but no effect of birds. We now designed a crossed experiment to test for the combined impact of both ants and birds and potential non-additive effects, not only on canopy spiders but also on ground spiders and over a longer time period (2008-2009). Moreover, we analysed the impacts on the spider assemblage at species level, which to our knowledge had not been done before.

Chapter 3: to test the differential impact of bird predation on diurnal and nocturnal canopy spiders.

Although in the previous chapter we had not detected any effect of birds on spiders, anecdotal observations made us suspect that this negative result could be due to the use of beating trays as a sampling method. We thus switched to visual searches to sample spiders in the canopies and cardboard bands on the trunks. Because bird predation is thought to have promoted the evolution of nocturnal activity in spiders, we focused on the differential effects of birds on nocturnal and diurnal web-weaving spiders to test this hypothesis.

Chapter 4: to study the long-term effects of canopy-foraging ants on the spider assemblage.

Because ants had a great influence on nearly all arthropod groups in the canopies (Piñol et al. 2012a), we decided to study their impact on the spider assemblage over an 8-year period. We tested which spider species were positively or negatively affected by ant activity in the canopies and whether the effect of ants changed over time. We were also interested in testing whether the patterns detected with species-level data were retrieved with family-level identifications (taxonomic sufficiency).

Chapter 5: to unravel the trophic structure of the arthropod food web of the grove with stable isotope analyses.

We aimed at exploring the trophic structure of the spider assemblage, from both the canopies and the ground. We analysed the stable isotopes of carbon and nitrogen to determine the trophic positions of the most common spiders relative to other predators and potential prey at different times of the year. Because in the previous chapter we found ants to change the abundances of some spider species in the canopies, we tested whether ants also modified their stable isotope ratios, which would suggest that the spiders shifted diets.

Chapter 6: to test the effect of cues of food availability on site-selection and of prey supply on emigration decisions of the colonial spider *Cytrophora citricola*.

C. citricola is a web-weaving spider very common in Mediterranean agroecosystems that aggregates in colonies in the tree canopies. However, the exact causes of coloniality are not known. We manipulated information of prey availability by placing different numbers of dead prey on the webs of established colonies and tested the settling decisions of immigrant spiders released onto these colonies. We then tested the emigration propensity of established spiders when given different amounts of prey. These experiments, together with field surveys, allowed us to gather evidence in favour of a parasocial pathway driving the evolution of spider coloniality.

Chapter 7: to test the importance of direct and maternal food supply on long- and short-distance emigration decisions of *Erigone dentipalpis*.

Like many linyphiids, *Erigone* spiders are common residents of agricultural landscapes and have a great capacity to disperse long distances (by ballooning) and short distances (by rappelling). We used *E. dentipalpis* as a model organism to study the probability of these dispersal modes in reaction to food supply as an indicator of habitat quality with a crossed experimental design to test the effect of both immediate and maternal food supply. Thus, we tested for the existence of maternal effects providing information to offspring about past food availability and also if offspring were able to integrate current and maternal information to reach an emigration decision. This would indicate that maternal effects play a role in the spatial dynamics of populations in fragmented landscapes.

2

Effects of ant competition and bird predation on the spider assemblage of a citrus grove


P. García

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ABSTRACT

Characterizing intraguild interactions is key to improving understanding of food webs because they are major forces in the structuring of communities. Spiders are generalist predators with intermediate positions in the food web that establish intraguild interactions with ants and birds, which respectively compete with and prey on them. Research has also found interactions between birds and ants, potentially resulting in non-additive effects of both groups on arthropod assemblages, although studies of their combined impacts with tests for multiple-predator effects are scarce. We thus aimed to discern the relative effect of ants and birds on the spider assemblage of a citrus grove. We used a split-plot design to factorially exclude these groups over 2 years, preventing ants reaching the canopies by placing sticky bands around tree trunks, and birds by enclosing groups of trees in cages. We sampled spiders from the canopies (beating) and the ground (pitfalls) every 3 months, and we identified them to species. We found a strong influence of ants on the canopy spider assemblage, mainly through a negative effect on the families Araneidae and Theridiidae. Since spiders' weights from ant-excluded and control trees were similar, these results suggest interference competition of ants on spiders rather than competitive exploitation. Bird exclusion did not affect the spider assemblage, contrasting with other studies reporting a marked predatory pressure of birds on spiders; nor were there any non-additive effects of ants and birds. Our findings show that spider assemblages are not uniformly affected by intraguild competitors.

Keywords: agroecosystem; Araneae; interference competition; intraguild interactions; multiple exclusion; non-additive effects.

Introduction

Intraguild interactions (e.g. competition and intraguild predation) are major factors in the structuring of terrestrial communities (Polis et al. 1989; Wise 1993). Intraguild predation is nowadays well acknowledged as having far-reaching effects on food-webs, for example, by modifying the strength of trophic cascades and interfering with herbivore suppression in biological control (Cardinale et al. 2003; Finke & Denno 2005). Characterizing intraguild interactions is therefore crucial to our understanding of terrestrial food webs.

Spiders are ubiquitous generalist predators in terrestrial ecosystems (Buddle et al. 2000; Entling et al. 2007), where they have intermediate positions in the food web and establish intraguild interactions with ants and birds. Ants on the forest floor climb in groups to forage on tree canopies and, as generalist predators, compete with spiders for prey (Halaj et al. 1997), although some families of spiders benefit from the presence of ants (McIver & Stonedahl 1993; Schuch et al. 2008). Additionally, many ant species have a mutualistic relationship with aphids, feeding on their sugary secretions and defending them from predators and parasitoids (Buckley 1987). Both foraging modes lead to negative consequences for densities of spiders and other tree-living arthropods (Vandermeer et al. 2002; Piñol et al. 2012a).

Insectivorous birds are predators that require large quantities of insects to meet their energy demands, especially in the breeding season (Hogstad 1984; Gunnarsson 2007). Several studies show that birds reduce insect abundance in trees and that predation on spiders usually results in a substantial reduction in numbers (Evelegh et al. 2001; Recher & Majer 2006). Nevertheless, different foraging methods and diets mean that the impacts of birds and ants on a shared arthropod assemblage are likely to differ, and the few works comparing the simultaneous effect of these groups on arthropods report contrasting results, with either birds having a higher impact than ants (Philpott et al. 2004) or ants having a higher impact than birds (Mooney 2006, 2007; Piñol et al. 2010).

Moreover, research has revealed notable intraguild interactions between ants and birds: whereas bird predation sometimes reduces ant numbers in trees (Haemig 1997; Mooney & Linhardt 2006), ants can diminish bird foraging activity (Haemig 1996; Philpott et al. 2005). These interactions between the two groups could result in non-additive effects, whether antagonistic or synergistic, on arthropods (Vance-Chalcraft & Soluk 2005). However, there are almost no studies looking at the combined impact of ants and birds to test for multiple-predator effects (but see Mooney 2006, 2007).

In the present study, we investigated the impact of ants and birds on the spider community of a Mediterranean citrus grove. Groves have the advantage of being simpler than natural systems, favouring the detection of functional relationships that might be obscured by the more complex interactions occurring in nature. On the same site, Piñol et al. (2010) conducted a one-way exclusion experiment to compare the individual effects of ants and birds on the arthropod assemblage in the canopies throughout 10 months. The study found a negative effect of ants on some spider families but did not find any effect of birds. Moreover, the experimental design did not allow to test for an interaction between ants and birds. As reports of absence of an effect of birds on the arthropod community are uncommon in the literature, we built upon the work of Piñol et al. (2010) by setting up a factorial exclusion of ants and birds for a longer period of time (21 months) to examine their individual and combined effects on the spider assemblages in the canopies and on the ground for a larger set of trees. This time we favoured multiple-tree enclosures over single-tree cages because movements of arthropods between neighbouring trees could have weakened the effect of bird predation. Moreover, we sampled ground-dwelling arthropods, which we had ignored in the previous study.

Specifically, we wanted to answer the following questions. First, did spider assemblages change due to ant or bird presence? Second, were the effects of ants and birds on spider assemblages independent of each other or did they interact? Third, in the event that we found spider assemblages to differ between treatments, which spider species showed greatest changes in abundance between treatments?

Materials and methods

Study site

The grove is located at La Selva del Camp (Catalonia, NE Spain; 41º 13' 07″N, 1º 8' 35″E). The climate is Mediterranean, with a rainy spring and autumn and a dry winter and summer. The grove consists of ca. 300 Clementine trees (*Citrus clementina* var. *clemenules*) grafted on the hybrid rootstock Carrizo citrange (*Poncirus trifoliata* (L.) Raf. x *Citrus sinensis* (L.) Osb.). The trees are watered during dry periods. The grove complied with all organic agriculture standards, i.e. no pesticides, fungicides or herbicides were applied, and only organic manure was used as fertilizer. Grasses and other weeds that form a permanent ground cover were mowed 3-4 times per year between rows and 5-6 times per year beneath trees.

Experimental design

We set up a split-plot design to exclude birds at the plot level and ants at the subplot level. The experimental area consisted of 4 rows of 16 trees planted in 2001, and each row was divided into 2 blocks of 7 trees separated by 2 non-experimental trees. For the bird exclusion, the 8 blocks were divided into 2 plots of 3 trees each, generally separated by 1 non-experimental tree. The 2 plots in each block were randomly assigned to either a "cage" or a "no cage" treatment so that the two treatments were present in each of the 8 blocks. To preclude birds' access to the trees, net cages of ca. 10.5 x 3 x 2 m with a plastic mesh of 30 x 30 mm were built around the plots assigned to the "cage" treatment (see Fig. s2.1). The mesh size allowed large insects such as butterflies and grasshoppers to enter the cages. For the ant exclusion, 2 of the 3 trees in each plot were randomly assigned to either a "band" or a "no band" treatment and thus the two treatments were present in each plot. Therefore, the split-plot design resulted in N=8 trees for each of the 4 possible combinations of treatments. The band was a sticky ring placed on the trunk to prevent ants climbing up to the canopy and was made by spreading a polybutene-based glue (Rata Stop ®) on a sheet of plastic film tightly attached to a foam padding that encircled the trunk. However, some ants would reach the canopy via tall weeds or overlapping branches between adjacent trees, or by crossing the glue barrier using dead insects as stepping stones. We therefore inspected trees on a weekly basis and when any of these problems was detected we addressed it by cutting tall weeds, pruning those branches or adding glue to the sticky band. The treatments were operative between February 2008 and October 2009.

Sampling methodology

Samplings were conducted at 3-month intervals from February 2008 to September 2009, resulting in 7 sampling dates in different seasons of the year. Beating trays were used to sample spiders and other arthropods from the canopies. They were dislodged with six strikes to the tree crowns (three strikes on each of two opposite sides), captured with entomological aspirators and preserved in 70% ethanol. Each tree represented one sample.

To sample the ground, 3 pairs of pitfall traps were placed on each plot, each pair on different sides, 75 cm away from the base of a tree. The pitfall traps were plastic cups (7 cm depth and 5.5 cm diameter). They were opened on each sampling date, filled with 20 mL of water mixed with detergent, and left open for 48 hours. After collection, all arthropods were preserved in 70% ethanol. The contents of the 6 pitfall traps of each plot were pooled into one sample.

In the laboratory, the collected arthropods were separated into orders and adult spiders were identified to species using different keys (Roberts 1985a,b; Heimer & Nentwig 1991), following nomenclature by Platnick (2011). Some juveniles could only be identified to genus level. However, taking a conservative approach, juveniles from a given genus were assigned to the same species as adults if that species was the sole representative of that genus in the grove. Most juvenile Linyphiidae could only be assigned to family. Ants were identified to species using Collingwood (1978).

We had some knowledge of the bird community of the grove area from censuses conducted in 2006 (Piñol et al. 2010). To complement this information, we estimated the abundance of insectivorous and omnivorous birds in the grove (Cramp & Simmons 2004) by conducting monthly censuses from July to September 2009. Each census consisted of two 10-minute point counts (IPAs; Bibby et al. 2000) conducted on 2 consecutive days. More details can be found in Piñol et al. (2010).

Statistical analyses

As a measure of abundance, we used the numbers of individuals combined from all sampling dates. To test for differences between treatments in the species composition of the canopy spider assemblage, we conducted a permutational multivariate ANOVA (PERMANOVA) on the square-root transformed abundance using the Bray-Curtis index of similarity, with "bird exclusion" (cage, no cage), and "ant exclusion" (band, no band) as fixed factors, and "block" as a random factor (split-plot design). The interaction term "ant exclusion" x "bird exclusion" in this analysis served as a test for the existence of non-additive effects of ants and birds. We likewise compared the ground spider assemblage between bird-excluded and control plots using a PERMANOVA with the fixed factor "bird exclusion" and the random factor "block" (randomized complete block design). To compare ground and canopy spider assemblages, we standardized the samples to obtain species percentages from the species counts and we then conducted a PERMANOVA with "stratum" (canopy, ground) as a fixed factor, and "block" as a random factor.

We were also interested in quantifying the effects of ants and birds on potential spider prey. Whereas the most numerous groups in the canopies, other than ants, were Aphididae, Coleoptera and Psocoptera, in the pitfall traps there were very low numbers of insects, apart from Coleoptera and Diptera. All these groups are common prey of spiders (Halaj et al. 1997; Foelix 2010). Thus, we ran univariate permutational ANOVAs on the square-root transformed abundance of each group using the Euclidean distance, resulting in a permutational equivalent of classical ANOVAs (Anderson et al. 2008). We likewise conducted univariate permutational

ANOVAs on the abundance of ants in the canopies to test the effectiveness of the band treatment and the effect of bird exclusion.

When the PERMANOVA analyses were significant, we subsequently ran univariate permutational ANOVAs on the square-root transformed abundance of the most abundant spider species using Euclidean distance. These univariate analyses allowed us to detect which spiders were behind the changes in species assemblages.

If the analysis of the abundance of a given species was significant, we obtained the total dry weight per sample for that species by drying all the individuals (both juveniles and adults) from each sample at 60 ºC for 72 hours. We then calculated the average dry weight per individual in each sample and tested for differences between treatments with univariate permutational ANOVAs. This would allow us to know whether ants or birds were also influencing the weight of spiders through effects on resource abundance. For these analyses we used the average biomass for the two summer samples of 2008 and 2009, when ants and birds were active and the abundance of spiders and their insect prey was highest.

Finally, differences in spider diversity between treatments were analysed with univariate permutational ANOVAs on species richness (S) using the Euclidean distance. The response variable was the mean spider richness over all sampling dates. The estimate of S was conservative, since not all spiders could be identified to species. All analyses were conducted with the software PERMANOVA+ for PRIMER v.6 (Anderson et al. 2008).

Results

Ant and bird assemblages

The glue band was an effective barrier against ants, as their abundance was significantly higher on control trees (mean ± SE = 89.8 ± 12.4) than on banded trees (6.3 ± 2.8; pseudo-$F_{1,23}$ = 96.90, $P < 0.0001$). The most abundant ants in the canopies were the aphid-tending species *Lasius grandis* (46% of all sampled individuals) and *Formica rufibarbis* (26%). The sticky barrier also excluded earwigs *Forficula* spp. (Dermaptera: Forficulidae) from the tree canopies. For clarity, however, we will use the term "ant exclusion" for the remainder of the paper. Birds did not affect ant (pseudo-$F_{1,7}$ = 1.94, P = 0.21) or earwig (pseudo-$F_{1,7}$ = 1.37, P = 0.27) numbers in the canopies.

Insectivorous and omnivorous birds were common in the grove, with about 100 individuals detected over the summer of 2009, decreasing to 50 in September. Of the 16 species recorded, the most common were the House Sparrow (*Passer domesticus*; Passeridae), the Tree Sparrow (*Passer montanus*; Passeridae) and the Starling (*Sturnus* sp.; Sturnidae). Together, these 3 species accounted for 82% of all individuals (see Table s2.1 for a complete list of species).

Spider assemblage

Around 2,500 spiders were sampled from the canopies. Fifty-three species from 15 families were recorded, the most abundant being Theridiidae (35%), Philodromidae (16%), Araneidae (12%), Salticidae (8%) and Clubionidae (8%). Each individual family was clearly dominated by a single species (Philodromidae: 82% *Philodromus cespitum*; Araneidae: 62% *Neoscona subfusca*; Salticidae: 76% *Icius hamatus*) or genus (Theridiidae: 58% *Theridion* spp.). *Clubiona leucaspis* was the only Clubionidae species found in the grove.

The pitfall traps captured 844 spiders from 54 species and 14 families. The most abundant families were Lycosidae (35%), Linyphiidae (24%), Gnaphosidae (13%) and Dysderidae (9%). Lycosidae were dominated by *Pardosa proxima* (74%), Linyphiidae by *Pelecopsis parallela* (35%), and *Dysdera crocata* was the only Dysderidae species. Gnaphosidae were more diverse, *Nomisia* sp., *Zelotes* spp. and *Trachyzelotes holosericeus* being the most abundant. (See Figs. s2.2 and s2.3 for temporal variation in the abundances the most common spider families, and Tables s2.2 and s2.3 for lists of species).

As expected, the canopy and the ground spider assemblages differed (pseudo-$F_{1,55}$ = 74.73, P < 0.0001), with only 6 species shared out of a total of 101: *Aphantaulax trifasciata* (Gnaphosidae), *Chalcoscirtus infimus* (Salticidae), *Euryopis episinoides* (Theridiidae), *Oxyopes lineatus* (Oxyopidae), *Pelecopsis mengei* (Linyphiidae) and *Thanatus vulgaris* (Philodromidae).

Effects of ant and bird exclusion

Effects of ants and birds in the canopy

The canopy spider assemblage was affected by ant exclusion (P = 0.0015; Table 2.1) but not by bird exclusion (P = 0.29) nor by the interaction between the 2 factors (P = 0.60). Univariate permutational ANOVAs showed that the species *N. subfusca* (Araneidae; P = 0.0057; see Table s2.4), *Anelosimus vittatus* (Theridiidae; P = 0.0085), *Platnickina tincta* (Theridiidae; P = 0.0052) and *Theridion* spp. (Theridiidae; P = 0.0096) were more abundant in trees without ants; all these are web-building species. Abundances of the remaining common spider species were similar between treatments (pseudo-$F_{1,23}$ < 0.49, P > 0.56 in all the species tested; Fig. 2.1A).

Insect prey such as Psocoptera and Coleoptera were more abundant in ant-excluded than in ant-frequented trees (pseudo-F > 23.75, $P < 0.0004$), in contrast with Aphididae (pseudo-F = 2.55, $P = 0.14$; see Fig. s2.4A). Neither bird exclusion nor the interaction between ant exclusion and bird exclusion affected insect abundances in the canopies (pseudo-F < 1.69, $P > 0.23$). The average dry body weight of *N. subfusca* (N = 8, control: 0.12 ± 0.01 mg; ant-excluded: 0.09 ± 0.02 mg; pseudo-$F_{1,15}$ = 1.17, $P = 0.30$) and *Theridion* spp. individuals (N = 7, control: 0.09 ± 0.02 mg; ant-excluded: 0.08 ± 0.02 mg; pseudo-$F_{1,14}$ = 0.34, $P = 0.57$) was not influenced by ant exclusion. We did not analyse the mean body weight of the remaining Theridiidae because the sample size (number of trees with individuals) for these species was low. We did not weigh individuals of hunting spider species because the abundances of these species were not affected by ant presence. Spider richness was only marginally influenced by ant exclusion (pseudo-$F_{1,14}$ = 4.67, $P = 0.051$), but not by bird exclusion (pseudo-$F_{1,7}$ = 0.023, $P = 0.88$; Fig. 2.2).

Effects of birds on the ground

The ground spider assemblage was similar between bird-excluded and control plots (pseudo-$F_{1,7}$ = 1.14, $P = 0.35$; Fig. 2.1B, Table 2.2) and spider species richness was not affected by bird exclusion (pseudo-$F_{1,7}$ = 0.92, $P = 0.37$; Fig. 2.2). Bird presence did not influence either Coleoptera or Diptera numbers in the pitfall traps (pseudo-F < 1.82, $P > 0.21$; see Fig s2.4B).

Discussion

The field experiments described above revealed that ants exerted a strong negative effect on the abundance of canopy spiders due to a reduction in the numbers of web-building Araneidae and Theridiidae species in ant-frequented trees. In contrast, birds had no detectable influence on either the canopy or the ground spider assemblages, nor did we find any non-additive effects of ants and birds on spiders. Our study shows that the impact of ants on this system is pervasive and clearly greater than that of birds.

Ants had a negative influence on spider abundance in the canopies but only a slight effect on spider richness. A more detailed analysis revealed that the decrease in spider numbers was caused by the web-building species *N. subfusca*, *A. vittatus*, *P. tincta* and *Theridion* spp., which were between 1.5 and 3 times more numerous in ant-free than in ant-frequented trees. Previous studies on the effects of ant foraging on canopy spiders have also reported a negative association between ants and spiders (Buckley 1990; Vandermeer et al. 2002; Vanek & Potter 2010), but research on the effect of ants on different spider groups is scarce (Halaj et al. 1997; Sanders & Platner 2007). Piñol et al. (2010) found a negative effect of ants on the spider families Theridiidae and Thomisidae. Though spiders were not analysed to the species level, the effect of ants on Thomisidae was assumed to take place mostly on *Xysticus* sp., the most abundant Thomisidae in the grove. By contrast, abundance of *Xysticus* sp. in the present study was lower and there was a non-significant trend toward a higher abundance of *Xysticus* sp. in ant-free trees.

Exploitative competition and interference competition are possible causes of the negative effect of ants on Araneidae and Theridiidae species, as predation of ants on spiders has been found to be irrelevant (Brüning 1991; Halaj et al. 1997). There was some evidence of exploitative competition because ants decreased the numbers of Psocoptera and Coleoptera in the canopies, which could limit the availability of prey to web-building spiders and reduce their abundance in control trees. Web builders would therefore settle in a tree or leave it, according to the abundance of prey (Weyman et al. 2002; Mestre & Lubin 2011), and larger spiders, with higher energy needs, would mostly be found on banded trees, increasing the average individual weight of spiders in ant-free canopies. However, the lack of differences in the body weights of *N. subfusca* and *Theridion* spp. from banded and non-banded trees did not support this explanation. These species were very abundant in the grove, comprising roughly 60% of the Araneidae and Theridiidae individuals. As web builders, they were particularly exposed to the foraging activity of ants, because their sedentary lifestyles involve spending most of their time in the canopy in their webs or retreats (Foelix 2010). Therefore, our results suggest that these species might suffer from interference competition with ants.

Birds did not affect the canopy spider assemblage in our experimental setting, confirming earlier findings (Piñol et al. 2010), nor did they affect the ground spider assemblage. We did not find any evidence of non-additive effects of birds and ants, since the bird and ant exclusions did not interact in influencing the abundances of insects or spiders, and the number of ants in the canopies did not increase with the exclusion of birds. A strong negative influence of bird predation on canopy arthropods has been detected in other systems (Evelegh et al. 2001; Gunnarsson et al. 2009). Some studies that take into account spider size have found that bird predation affects negatively only large spiders (Askenmo et al. 1977; Greenberg et al. 2000), but other works report a negative effect of birds on both large and small spiders (Van Bael et al. 2003; Philpott et al. 2004; Recher & Majer 2006; Johnson et al. 2009). In a previous experiment (Piñol et al. 2010), we measured the spiders in the grove and segregated them into two size classes, large (>2mm) and small (<2mm), but we found no effect of bird predation on large spiders (Piñol et al. unpublished). In our Mediterranean citrus grove, canopy-foraging ants had a major influence on spiders and their insect prey, whereas predation by birds did not produce any significant effects.

Very few studies have set up a factorial exclusion of predators to test for intraguild interactions that potentially interfere with their top-down effects on arthropods. In two studies conducted in a ponderosa pine stand in Colorado, the effects of ants and birds on spiders were also found to be additive, even if birds reduced the abundance of ants in the canopies (Mooney 2006, 2007). Birds had a small negative impact on the abundance of hunting spiders in Mooney (2007), but in both studies ants had a much greater effect on spiders than birds, a result that resembles our findings. On the other hand, factorial exclusions of vertebrates in neotropical systems have revealed that birds and lizards (Borkhataria et al. 2006), and bats and birds (Kalka et al. 2008; Williams-Guillén et al. 2008) reduce arthropod populations in these settings.

The 2-year exclusion experiment revealed a marked effect of ants on the canopy spider assemblage, probably through interference competition with the web-building families Araneidae and Theridiidae. The influences of ants and birds on insects and spiders were independent of each other, and bird predation proved not to have any detectable effects on arthropods. Our findings highlight the fact that spider assemblages were not uniformly affected by intraguild competitors.

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Tables

Table 2.1. Complete PERMANOVA table of the split-plot design used to test the effects of ant exclusion and bird exclusion on the species composition of the canopy spider assemblage over the 2 years of study.

Source	df	SS	MS	Pseudo-F	*P* (perm)
Block	7	7346.80	1049.54	1.57	0.02
Bird exclusion	1	848.40	848.40	1.27	0.29
Plot error	7	4692	670.28		
Plot total	15	12887	859.14	1.40	0.005
Ant exclusion	1	2260.60	2260.60	3.69	0.0015
Bird x ant exclusion	1	525.79	525.79	0.86	0.60
Subplot error	14	8583.20	613.09		
Total	31	24257			

Table 2.2. Complete PERMANOVA table of the randomized block design used to test the effect of bird exclusion on the species composition of the ground spider assemblage over the 2 years of study.

Source	df	SS	MS	Pseudo-F	*P* (perm)
Block	7	19491	2784.40	1.25	0.10
Bird exclusion	1	2532	2532	1.14	0.35
Plot error	7	15619.60	2231.40		
Total	15	37642			

Figures

Fig. 2.1. Abundance of the most common spider species over the 2 years of study. (A) Comparison between spider abundance in the canopy of banded (No ants) and non-banded (Ants) trees (Table 2.1). (B) Comparison between spider abundance in pitfall trap catches in caged (No birds) and non-caged (Birds) plots (Table 2.2). Means ± SE are shown. Asterisks indicate a significant difference (***P* < 0.01). Codes: Nsub (*Neoscona subfusca*), Avitt (*Anelosimus vittatus*), Ptin (*Platnickina tincta*), Ther (*Theridion* spp.), Iham (*Icius hamatus*), Xyst (*Xysticus* sp.), Pces (*Philodromus cespitum*), Cleu (*Clubiona leucaspis*). Dcro (*Dysdera crocata*), Ppro (*Pardosa proxima*), Ppar (*Pelecopsis parallela*).

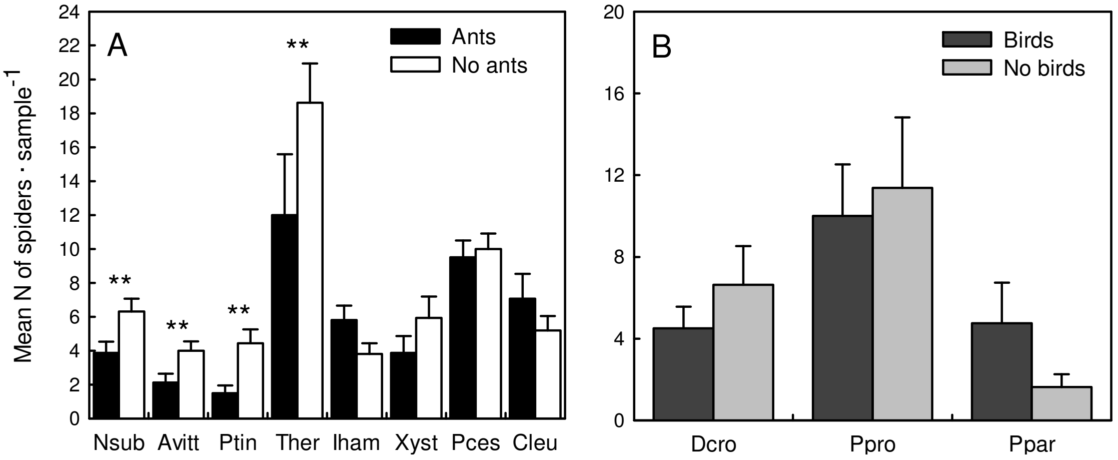
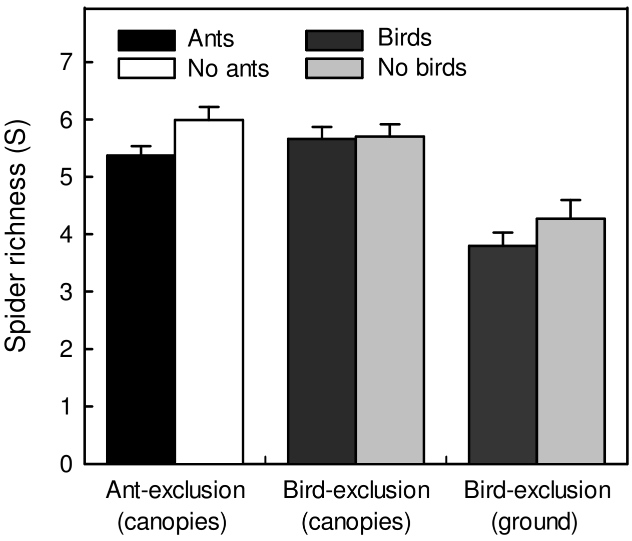


Fig. 2.2. Mean species richness of spiders over the 2 years of study. Comparison between spider richness in the canopy of banded (No ants) and non-banded (Ants) trees, and of caged (No birds) and non-caged (Birds) trees, and comparison between spider richness in pitfall trap catches of caged-and non-caged plots. Means ± SE are shown. There were no significant differences between the treatments.



Supplementary material

Table s2.1. Average number of birds detected in the monthly censuses (IPAs) over the summer of 2009, inside the citrus grove (or flying over it) and outside the grove. Only foliage- or ground-gleaning species (Cramp & Simmons 2004) are reported.

		July		August		September	
Species	Common name	In	Out	In	Out	In	Out
Athene noctua (Scopoli, 1769)	Little Owl	0	0	0	1	0	0
Picus viridis (Linnaeus, 1758)	Green Woodpecker	0	0	0	0.5	0	0.5
Motacilla alba (Linnaeus, 1758)	White Wagtail	0	0	0	0.5	0	0.5
Turdus viscivorus (C L Brehm, 1831)	Mistle Thrush	0	0	0	0	0	1.5
Turdus merula (Linnaeus, 1758)	Blackbird	0.5	0	0	0.5	0	0
Sylvia melanocephala (Gmelin, 1789)	Sardinian Warbler	4.5	0	2.5	1	1	2
Cisticola juncidis (Rafinesque, 1810)	Fan-tailed Warbler	0	0.5	0	0	0	0
Pica pica (Linnaeus, 1758)	Magpie	1.5	2	0.5	0.5	2.5	1
Sturnus sp.	Starling	12.5	0.5	40.5	16.5	22	4.5
Passer domesticus (Linnaeus, 1758)	House Sparrow	8	55	11	17.5	0	0.5
Passer montanus (Linnaeus, 1758)	Tree Sparrow	5.5	7.5	0	0	7	0.5
Fringilla coelebs (Linnaeus, 1758)	Chaffinch	0	0	0	0	0	0.5
Serinus serinus (Linnaeus, 1766)	Serin	0	1	2	0	1	0
Carduelis cannabina (Linnaeus, 1758)	Linnet	0	0	1.5	0	0	0
Carduelis chloris (Linnaeus, 1758)	Greenfinch	2.5	2.5	3.5	0	0.5	0
Carduelis carduelis (Linnaeus, 1758)	Goldfinch	2	0	0	0	3.5	0
	Total In/Out	37	69	61.5	38	37.5	11.5
	Total month		106		99.5		49

Table s2.2. Complete list of spider species collected in the canopies of 32 citrus trees by beating trays. Nomenclature follows Platnick (2011).

Family	Species	# individuals
Araneidae	*Araniella cucurbitina* (Clerck, 1757)	9
	Cyclosa oculata (Walckenaer, 1802)	3
	Cyrtarachne ixoides (Simon, 1870)	3
	Cyrtophora citricola (Forsskål, 1775)	26
	Gibbaranea sp. (Archer, 1951)	1
	Mangora acalypha (Walckenaer, 1802)	47
	Neoscona subfusca (C. L. Koch, 1837)	175
	Zilla diodia (Walckenaer, 1802)	1
	Zygiella x-notata (Clerck, 1757)	13
Clubionidae	*Clubiona leucaspis* Simon, 1932	196
Dictynidae	*Lathys* sp. Simon, 1884	2
	Marilynia bicolor (Simon, 1870)	1
	Nigma walckenaeri (Roewer, 1951)	56
Gnaphosidae	*Aphantaulax trifasciata* (O. P.-Cambridge, 1872)	40
Linyphiidae	*Pelecopsis mengei* (Simon, 1884)	60
	Styloctetor romanus (O. P.-Cambridge, 1872)	4
	Undetermined Linyphiidae	37
Mimetidae	*Ero aphana* (Walckenaer, 1802)	5
Miturgidae	*Cheiracanthium mildei* L. Koch, 1864	55
Oxyopidae	*Oxyopes lineatus* Latreille, 1806	41
Philodromidae	*Philodromus cespitum* (Walckenaer, 1802)	312
	Philodromus rufus Walckenaer, 1826	66
	Philodromus sp. Walckenaer, 1826	1
	Thanatus vulgaris Walckenaer, 1826	3
Pisauridae	*Pisaura mirabilis* (Clerck, 1757)	3
Salticidae	*Ballus chalybeius* (Walckenaer, 1802)	40
	Chalcoscirtus infimus (Simon, 1868)	1
	Heliophanus apiatus Simon, 1868	2
	Icius hamatus (C. L. Koch, 1846)	154
	Salticus scenicus (Clerck, 1757)	6
Sparassidae	*Olios argelasius* (Walckenaer, 1805)	37
Theridiidae	*Anelosimus vittatus* (C. L. Koch, 1836)	98
	Dipoena melanogaster (C. L. Koch, 1837)	66
	Euryopis episinoides (Walckenaer, 1847)	4
	Neottiura uncinata (Lucas, 1846)	1
	Paidiscura pallens (Blackwall, 1834)	14
	Parasteatoda sp. Archer, 1946	5
	Phycosoma inornatum (O. P.-Cambridge, 1861)	6

Table s2.2 (continued). Complete list of spider species collected in the canopies of 32 citrus trees by beating trays. Nomenclature follows Platnick (2011).

Family	Species	# individuals
Theridiidae	*Phylloneta* sp. Archer, 1950	11
	Platnickina tincta (Walckenaer, 1802)	95
	Simitidion simile (C. L. Koch, 1836)	14
	Steatoda nobilis (Thorell, 1875)	11
	Theonoe minutissima (O. P.-Cambridge, 1879)	1
	Theridion mystaceum L. Koch, 1870	6
	Theridion pinastri L. Koch, 1872	7
	Theridion varians Hahn, 1833	8
	Theridion spp. Walckenaer, 1805	490
	Undetermined Theridiidae	2
Thomisidae	*Runcinia grammica* (C. L. Koch, 1837)	11
	Synema globosum (Fabricius, 1775)	9
	Thomisus onustus Walckenaer, 1805	1
	Tmarus sp. Simon, 1875	3
	Xysticus sp. C. L. Koch, 1835	157
Uloboridae	*Uloborus walckenaerius* Latreille, 1806	1
Undetermined	Undetermined	1
TOTALS		2422

Table s2.3. Complete list of spider species collected in the ground from 16 plots with pitfall traps. Nomenclature follows Platnick (2011).

Family	Species	# individuals
Agelenidae	*Textrix* sp. Sundevall, 1833	1
Araneidae	Undetermined Araneidae	2
Dysderidae	*Dysdera crocata* C. L. Koch, 1838	76
Gnaphosidae	*Aphantaulax trifasciata* (O. P.-Cambridge, 1872)	1
	Haplodrassus dalmatensis (L. Koch, 1866)	4
	Haplodrassus signifer (C. L. Koch, 1839)	4
	Haplodrassus spp. Chamberlin, 1922	12
	Micaria sp. Westring, 1851	2
	Nomisia celerrima (Simon, 1914)	2
	Nomisia exornata (C. L. Koch, 1839)	2
	Nomisia spp. Dalmas, 1921	23
	Setaphis carmeli (O. P.-Cambridge, 1872)	4
	Trachyzelotes fuscipes (L. Koch, 1866)	8
	Trachyzelotes holosericeus (Simon, 1878)	16
	Zelotes civicus (Simon, 1878)	1
	Zelotes nilicola (O. P.-Cambridge, 1874)	1
	Zelotes petrensis (C. L. Koch, 1839)	4
	Zelotes spp. Gistel, 1848	24
Linyphiidae	*Bathyphantes* sp. Menge, 1866	1
	Meioneta rurestris (C. L. Koch, 1836)	7
	Monocephalus castaneipes (Simon, 1884)	2
	Palliduphantes ericaeus (Blackwall, 1853)	3
	Pelecopsis bucephala (O. P.-Cambridge, 1875)	24
	Pelecopsis mengei (Simon, 1884)	35
	Pelecopsis parallela (Wider, 1834)	70
	Silometopus ambiguus (O. P.-Cambridge, 1905)	5
	Tapinocyba sp. Simon, 1884	2
	Tenuiphantes tenuis (Blackwall, 1852)	4
	Typhocrestus bogarti Bosmans, 1990	10
	Undetermined Linyphiidae	38
Lycosidae	*Alopecosa albofasciata* (Brullé, 1832)	19
	Hogna radiata (Latreille, 1817)	2
	Pardosa hortensis (Thorell, 1872)	56
	Pardosa proxima (C. L. Koch, 1847)	220
	Pardosa sp. C. L. Koch, 1847	2
Nemesiidae	*Nemesia dubia* (Karsch, 1878)	5
Oxyopidae	*Oxyopes lineatus* Latreille, 1806	2
Philodromidae	*Thanatus vulgaris* Walckenaer, 1826	5

Table s2.3 (continued). Complete list of spider species collected in the ground from 16 plots with pitfall traps. Nomenclature follows Platnick (2011).

Family	Species	# individuals
Salticidae	*Aelurillus v-insignitus* (Clerck, 1757)	5
	Chalcoscirtus infimus (Simon, 1868)	24
	Euophrys herbigrada (Simon, 1871)	4
	Evarcha jucunda (Lucas, 1846)	2
	Icius hamatus (C. L. Koch, 1846)	1
	Menemerus semilimbatus (Hahn, 1829)	2
	Phlegra bresnieri (Lucas, 1846)	1
	Talavera aequipes (O. P.-Cambridge, 1871)	5
Theridiidae	*Asagena phalerata* (Panzer, 1801)	1
	Euryopis episinoides (Walckenaer, 1847)	4
	Undetermined Theridiidae	1
Thomisidae	*Ozyptila pauxilla* (Simon, 1870)	9
	Xysticus bliteus (Simon, 1875)	8
	Xysticus kochi Thorell, 1872	11
Titanoecidae	*Nurscia albomaculata* (Lucas, 1846)	5
Zodariidae	*Zodarion pseudoelegans* Denis, 1933	19
	Zodarion styliferum (Simon, 1870)	40
Undetermined	Undetermined	3
TOTALS		844

Table s2.4. Summary of the PERMANOVA table of the effect of ant exclusion on the abundances of the most common spider species in the canopy over the 2 years of study.

Spider species	Pseudo-F	*P* (perm)
Neoscona subfusca	8.60	0.0057
Anelosimus vittatus	4.09	0.0085
Platnickina tincta	8.56	0.0052
Theridion spp.	3.68	0.0096
Icius hamatus	2.92	0.089
Xysticus sp.	1.69	0.17
Philodromus cespitum	0.49	0.56
Clubiona leucaspis	0.86	0.41

Fig. s2.1. Split-plot design of the concurrent exclusion of birds (plot level) and ants (subplot level). Each coloured square represents a tree. There were 8 blocks (thick-lined rectangles) and each of them had 2 plots (fine-lined rectangles), one with a "cage" treatment and other with a "no cage" treatment, both comprising 3 trees. Within each plot, 2 of the 3 trees were assigned to either a "band" or a "no band" treatment.

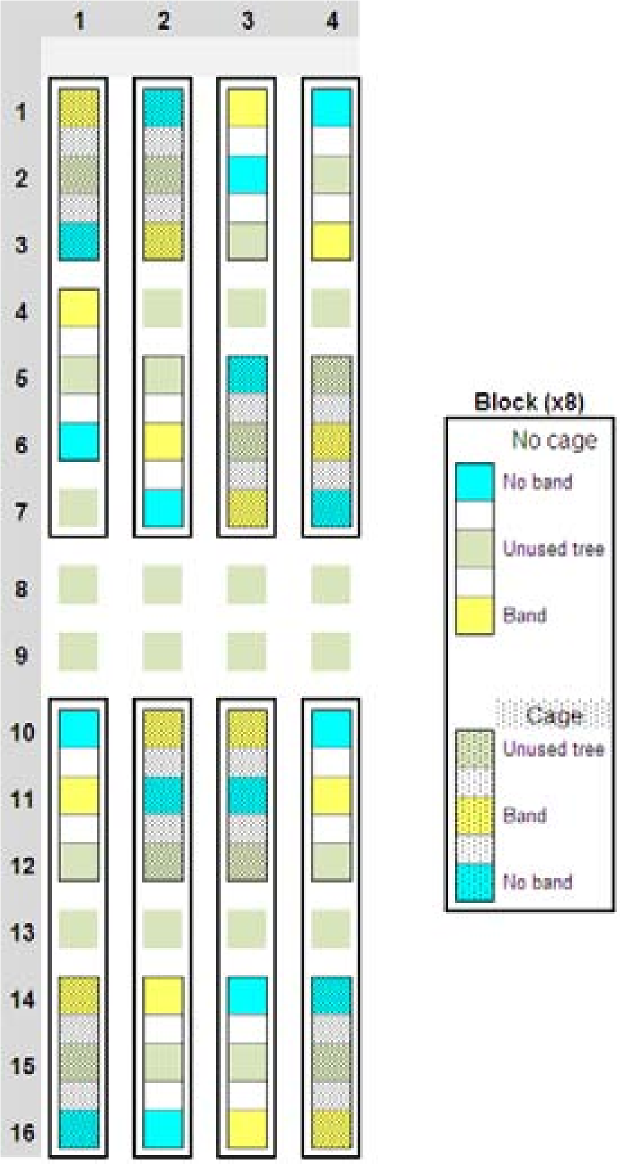


Fig. s2.2. Number of individuals of the most common spider families in the canopy of banded trees (No ants) and non-banded trees (Ants) at each sampling date. Means ± SE are shown.

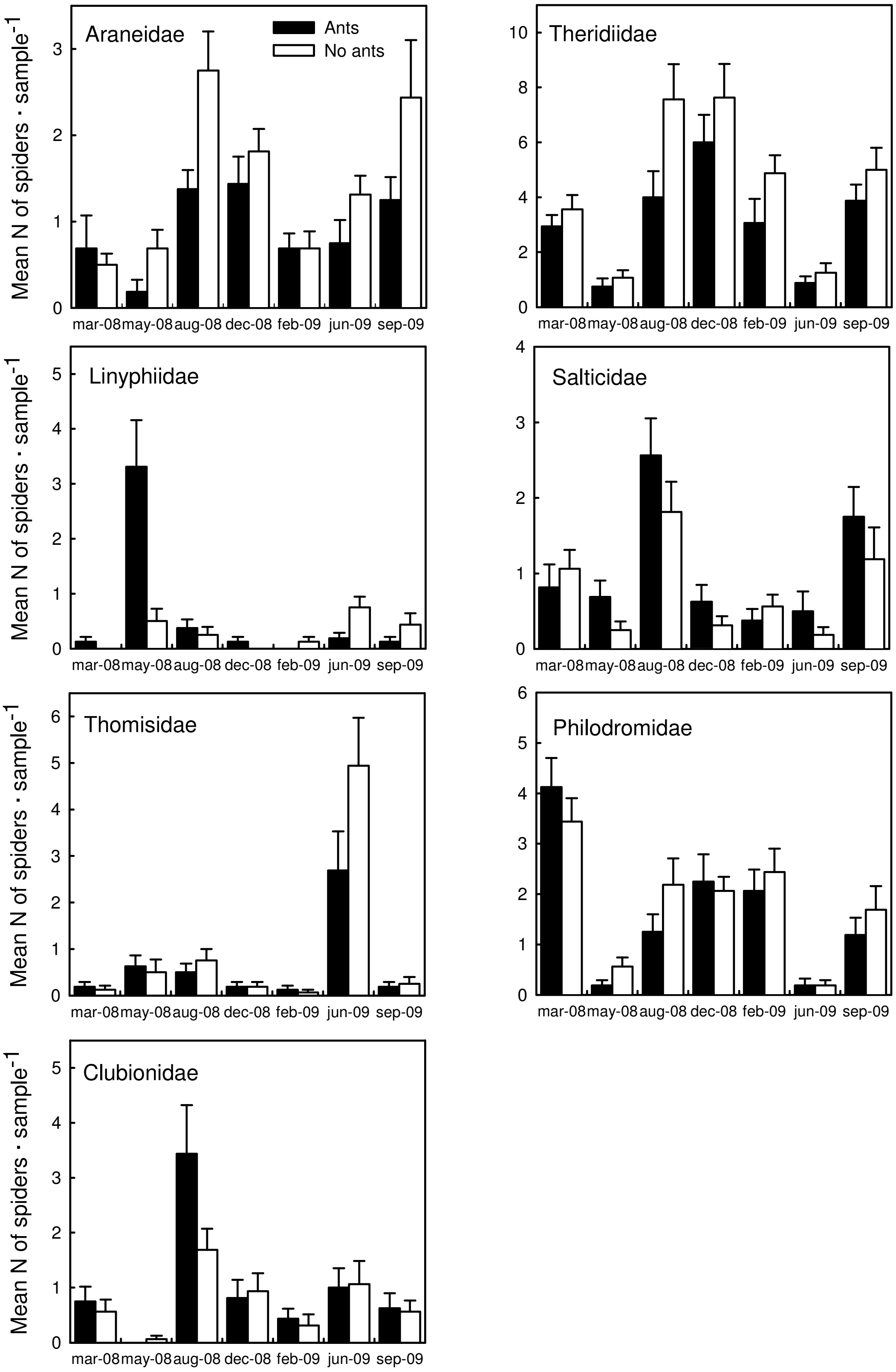


Fig. s2.3. Number of individuals of the most common spider families in pitfall trap catches in caged plots (No birds) and non-caged plots (Birds) at each sampling date. Means ± SE are shown.

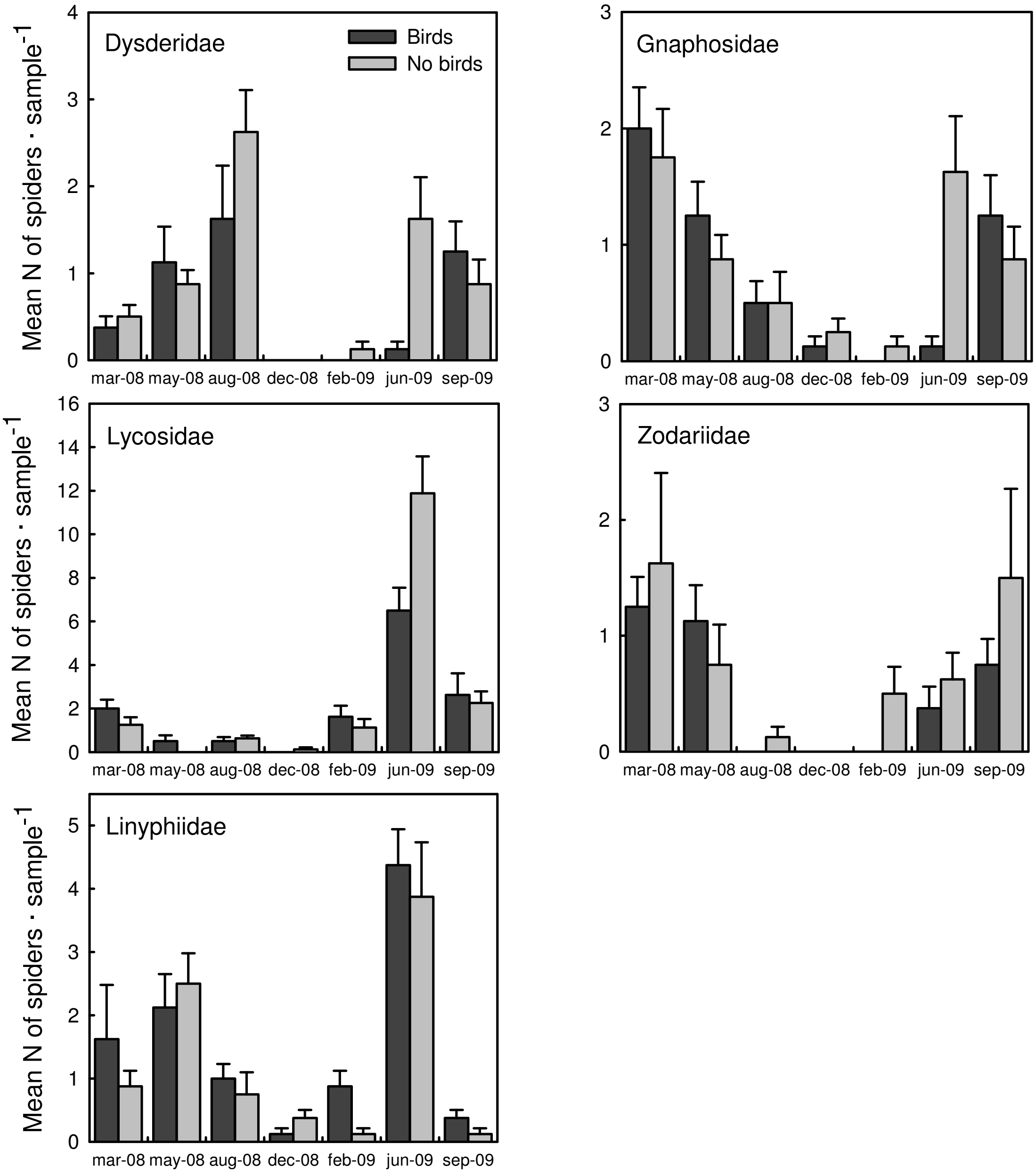
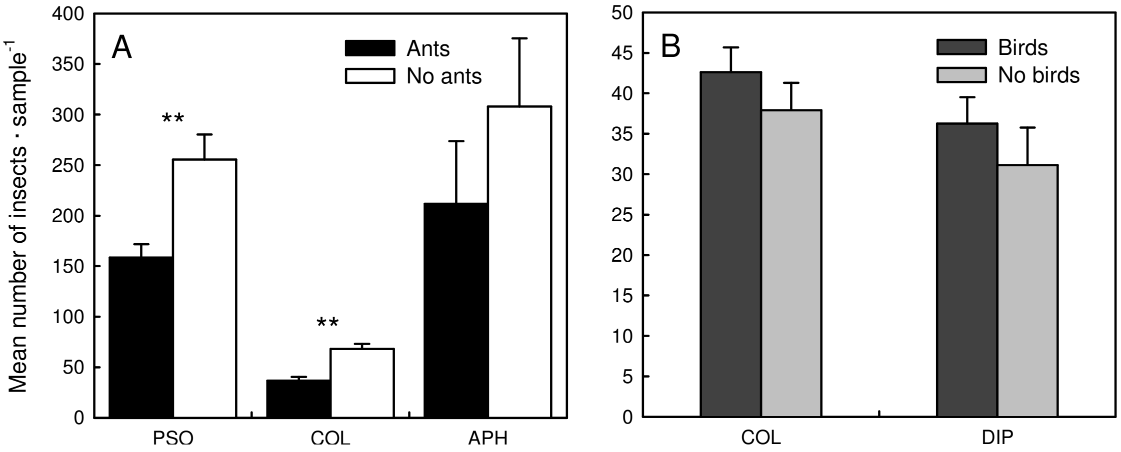


Fig. s2.4. Abundance of some insect groups over the 2 years of study. (A) Comparison between insect abundance in the canopy of banded (No ants) and non-banded trees (Ants). (B) Comparison between insect abundance in pitfall trap catches in caged (No birds) and non-caged plots (Birds). Means ± SE are shown. Asterisks indicate a significant difference (**: P < 0.01). Codes: PSO (Psocoptera), COL (Coleoptera), APH (Aphididae), DIP (Diptera).



3

Bird predation affects diurnal and nocturnal web-building spiders in a Mediterranean citrus grove

Mestre, L.; Garcia, N.; Barrientos, J. A.; Espadaler, X; Piñol, J. Submittted to Acta Oecologica.

ABSTRACT

Spiders and birds can greatly decrease insect populations, but birds also limit spider densities in some habitats. Although many spiders are nocturnal, studies of bird predation rely mostly on day samplings. Bird predation is thought to have promoted the evolution of nocturnal activity in spiders, so night-active spiders that hide in retreats during the day might be less affected by bird foraging than day-active spiders. We investigated the importance of bird predation on the spider community of a Mediterranean organic citrus grove. We excluded birds by placing net cages over the trees and we conducted visual searches in the canopies to sample web-building spiders. As there are many nocturnal species in the family Araneidae, we conducted searches both by day and by night to compare the abundance of active araneids in these 2 time periods. We sampled the tree trunks with cardboard bands to collect hunting spiders. In bird-excluded canopies there were more araneids and theridiids. There were higher numbers of active araneids at night, but these were just as negatively affected by bird predation as day-active araneids, so there was no evidence of nocturnal activity serving as an anti-predator strategy. We did not find any negative effect of birds on hunting spiders. Our results contrast with other studies reporting a negative effect of birds on hunting but not on web-building spiders.

Keywords: Araneidae; diel activity; hunting spider; night; Theridiidae; web-building spider.

Introduction

Spiders and birds are abundant predators that can reduce insect pest populations in terrestrial habitats (Buddle et al. 2000; Gruner 2004) and even curtail plant damage by lowering the numbers of herbivores (Mols & Visser 2002; Van Bael et al. 2003; Sanders et al. 2011). Some experimental studies, however, have shown that birds can sometimes limit spider populations (Wiens et al. 1991; Philpott et al. 2004; reviewed by Gunnarsson 2007).

Although many spider species are nocturnal, remaining inactive and hidden in retreats during the day, studies of bird predation are based on daytime samplings and thus greatly underestimate the abundance of nocturnal species (Coddington et al. 1996; Cardoso et al. 2008; Richardson & Hanks 2009). As birds forage during the day, their predation is thought to have promoted the evolution of nocturnal activity in spiders (Foelix 2010; Jones et al. 2011); accordingly, night-active spiders should be less affected by bird foraging than day-active spiders. However, this possibility has received very little attention (but see Rypstra 1984).

Our aim was to investigate the importance of bird predation on the spider community of a Mediterranean organic citrus grove. Mestre et al. (2012) had already excluded birds (and ants) from trees on the same site and sampled arthropods with beating trays. Although spiders were not found to be affected by bird predation, visual inspection of the canopies suggested that this negative result could be due to the chosen sampling method, particularly as beating trays under-represent some groups of spiders, such as web-builders (Costello & Daane 1995).

In the present work we study the effect of birds on the spider assemblage, using different sampling methods, both by day and by night, to confirm or refute our previous findings. We wanted to answer the following questions. First, did bird predation affect the spider assemblage of the grove? If so, which spiders were involved in these changes? Third, was the effect of bird predation lower in night-active spiders?

Material and methods

Study site

The grove is located at La Selva del Camp (Catalonia, NE Spain; 41º 13' 07″N, 1º 8' 35″E). The climate is Mediterranean, with a rainy spring and autumn and a dry winter and summer. There are ca. 300 Clementine trees (*Citrus clementina* var. *clemenules*) grafted on the hybrid rootstock Carrizo citrange (*Poncirus trifoliata* (L.) Raf. x *Citrus sinensis* (L.) Osb.), which are watered during dry periods. The grove complies with all organic agriculture standards, i.e. no pesticides, fungicides or herbicides are applied, and only organic manure is used as fertilizer. Grasses and other ruderal vegetation form a permanent ground cover, which is mowed 3-4 times per year between rows and 5-6 times per year beneath trees.

Experimental design

We set up a randomized complete block design (RCBD) to exclude birds from the tree canopies. The experimental area consisted of 4 tree rows of 16 trees planted in 2001, each row being divided into 2 blocks of 7 trees separated by 2-3 non-experimental trees. These blocks were divided into 2 plots of 3 trees each, generally separated by 1 non-experimental tree. The plots were randomly assigned to either a "cage" or a "no cage" treatment so that the two treatments were present in each of the 8 blocks (thus N = 8 plots). Net cages of ca. 10.5 x 3 x 2 m, with a plastic mesh of 30 x 30 mm, were built around the multiple-tree plots to prevent birds accessing the canopies; the mesh size allowed large insects such as butterflies and grasshoppers to enter the cages. The treatments were operative between February 2008 and October 2009.

Sampling methodology

We randomly assigned 2 of the 3 trees in each plot to a sampling method: (1) visual searches in the canopies, and (2) cardboard bands on the trunks. In this way, we prevented any potential interference between different sampling methods conducted in the same tree. Visual searches in the canopies were undertaken twice, in June and September 2009. Samples were taken from the trunks at 2-week intervals from mid-June to mid-October 2009, resulting in 8 sampling dates over a 4-month period.

Visual searches

We sampled web-building spiders in the tree canopies twice on a given day (noon, midnight) with non-intrusive visual searches, so that nocturnal searches in a given tree would not be influenced by the diurnal searches conducted a few hours earlier. As we did not collect spiders, we had to identify individuals in the field and thus could only reliably assign them to families, although we could identify a few individuals to species, on the basis of their shape and colour markings. Searches were conducted by two trained observers (LM and NG) and took an average time of 15 minutes per tree.

Diurnal searches

At noon (12-14h) we looked for individuals belonging to all web-building spider families. The most abundant families of web-builders in the grove are Araneidae, Theridiidae, and Linyphiidae

(Piñol et al. 2010). We included occupied as well as empty but intact webs of Linyphiidae, Theridiidae and Araneidae because abandoned webs degenerate in a few days (Toft et al. 1995), and we assumed intact empty webs of Araneidae to belong to a spider hidden in a retreat in the canopy (Foelix 2010).

Nocturnal searches

Because most araneid species are nocturnal (Scharff & Coddington 1997), a second visual search for araneid spiders was performed at midnight (24-02h) with headlamps. We only found a few individuals from species that have no distinct day-night activity patterns but sit permanently on their webs (*Argiope bruennichi*, *Cyclosa oculata*, and *Cyrtophora citricola*; Blanke 1972; Scharff & Coddington 1997).

In order to quantify differences in the activity of araneid spiders by day and by night, we defined a spider as "active" if it was sitting in its web rather than hiding in the canopy. We therefore only took into account occupied webs when making comparisons between daytime and night-time activity.

Cardboard bands

Fifteen days before the first sampling date, one half-corrugated cardboard band was wrapped around the tree trunks. The band was 15 cm wide and had 4 mm-wide corrugations, which were put in contact with the trunk. Cardboard bands are used as temporary shelters by hunting spiders, and they can hide either among the corrugations or between the trunk and the band (Isaia et al. 2006).

At each sampling date, the bands were collected and replaced with new ones. Before removing a band, a plastic collar was placed around the tree trunk just below the band to intercept spiders that were escaping, which were then captured and preserved in 70% alcohol. The removed bands were put in plastic bags with a piece of cotton damped with ethyl acetate to kill the remaining spiders. These were also put in alcohol in the laboratory within 24 hours of collection, to prevent any shrinkage of their soft structures. The spiders were identified to species level following the nomenclature given in Platnick (2012), using different keys (Roberts 1985a,b; Heimer & Nentwig 1991). Since juveniles lack distinctive genitalia, some spiders could only be identified to genus or, in the case of Linyphiidae, to family. However, juveniles from a given genus were assigned to the same species as adults if that species was the only representative of that genus in the grove.

Statistical analyses

Response variables were cumulative abundances of individuals over all dates (2 for visual searches, 8 for cardboard bands). To test for differences between treatments in the spider assemblage for each sampling method, we conducted permutational multivariate ANOVAs (PERMANOVA) on the square-root transformed abundances using the Bray-Curtis index of similarity, with "bird exclusion" (cage, no cage) as a fixed factor and "block" as a random factor (RCBD). We conducted the analyses of visual searches at the family level, and the analyses of cardboard bands at the species level.

When PERMANOVA analyses were significant, we ran univariate permutational ANOVAs on the square-root transformed abundance of the most abundant spider species or families with the Euclidean distance (mean ≥ 4 individuals per sample in at least one treatment), resulting in a permutational equivalent of classical ANOVAs (Anderson et al. 2008). The purpose of these univariate analyses was to detect which spiders were behind the differences in assemblage composition between treatments.

Abundances of active araneids were also compared between day and night with a split-plot design, in order to deal with the time-dependent structure of the data. We used permutational ANOVAs on the square-root transformed abundance, with "bird exclusion" as a plot factor and "time" (day, night) as a subplot factor (both fixed factors), and "block" as random factor (Anderson et al. 2008). For these analyses we only considered occupied webs. Analyses were conducted with the software PERMANOVA+ for PRIMER v.6 (Anderson et al. 2008).

Results

Visual searches

In June and in September we found 256 web-building spiders by day. The most abundant families were Araneidae (73.4%) and Theridiidae (21.1%), whereas Linyphiidae, Dictynidae (all *Nigma walckenaeri*) and Uloboridae (all *Uloborus walckenaerius*) only comprised 5% of the detected individuals. The spider assemblage was significantly different in bird-excluded and control trees (pseudo $F_{1,7}$ = 6.54, P = 0.012). Univariate permutational ANOVAs showed that the families Araneidae (pseudo-$F_{1,7}$ = 11.29, P = 0.0028) and Theridiidae (pseudo $F_{1,7}$ = 6.12, P = 0.034; Fig. 3.1A) were more abundant in caged trees.

Abundances of active araneid spiders were higher in bird-excluded than in control trees (pseudo-$F_{1,7}$ = 6.94, P = 0.034), and they were also higher by night than by day (pseudo-$F_{1,14}$

= 29.14, $P < 0.0002$). There was no interaction between the time of the visual search and the bird-exclusion treatment (pseudo-$F_{1,14} = 0.38$, $P = 0.55$; Fig. 3.2).

Cardboard bands

In the trunks, we found 1,406 spiders belonging to 16 families; these were mainly Theridiidae (36.3%), Miturgidae (17.5%), Gnaphosidae (11.6%), Salticidae (11.4%), and Clubionidae (11.2%). Each family was dominated by a single species (Theridiidae: 99.4% *Euryopis episinoides*; Salticidae: 82.5% *Icius hamatus*; Gnaphosidae: 70% *Nomisia exornata*). *Clubiona leucaspis*, *Cheiracanthium mildei*, and *Zodarion* spp. were the only Clubionidae, Miturgidae and Zodariidae in the grove, respectively (see Table s3.1 for a complete list of species). Bird exclusion did not affect the spider assemblage in the trunks (pseudo $F_{1,7} = 0.67$, $P = 0.69$; Fig. 3.1B).

Discussion

Our results show that bird predation changed the spider assemblage of the grove due to a negative effect on the most abundant families of web-builders. In the canopies, birds reduced the numbers of web-building spiders belonging to the families Araneidae and Theridiidae. By contrast, in two independent studies in which we used the method of beating trays to sample spiders, we observed no difference between bird-excluded and control trees, and the number of spiders in the samples was much lower (Piñol et al. 2010; Mestre et al. 2012). Visual searches may therefore have allowed us to detect an effect of bird predation because they sampled a different part of the spider community living in the tree canopies.

Hunting spiders, sampled in the trunks, were not affected by bird presence. These species constituted an overlap of common canopy (*C. leucaspis*, *C. mildei*, *I. hamatus*) and ground spiders (*E. episionides*, *N. exornata*, *Zodarion* spp.) in this grove, but with different relative proportions of species (Mestre et al. 2012; see Table s3.1 for a comparison of different sampling methods).

Most works on bird predation have considered spiders as a single group, so to date there is no evidence as to whether birds affect all spider families equally. Mooney & Linhart (2006) and Mooney (2007) reported that birds slightly reduced the density of hunting spiders in a Colorado pine stand. Our system found that the web-building families Araneidae and Theridiidae were negatively affected by birds, whereas hunting spiders were not.

As expected, there were more active araneids by night than by day. We found no evidence, however, that nocturnal activity serves as an anti-predator strategy: nocturnal araneids were as negatively affected by birds as day-active araneids, suggesting that foliage-gleaning birds search for spiders hidden in their retreats during the day. A study conducted in a tropical system reported that the impact of birds on web-building spiders was stronger in the daytime, but no distinction was made between nocturnal and diurnal spiders (Rypstra 1984).

In conclusion, visual searches enabled us to track spider abundance non-intrusively at different times of the day and night, allowing us to find a strong negative effect of bird predation on web-building spiders that we would have overlooked with other sampling methods.

ACKNOWLEDGMENTS

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Figures

Fig. 3.1. Number of individuals per tree in caged and non-caged trees over the study period, sampled by (A) visual searches in the canopies and (B) cardboard bands on the trunks. Means ± SE are shown. Asterisks indicate a significant difference (**P* < 0.05; ***P* < 0.01). Family codes: ARA (Araneidae), THE (Theridiidae), LIN (Linyphiidae), DIC (Dictynidae), ULO (Uloboridae). Species codes: Eepi (*Euryopis episinoides*), Cmil (*Cheiracanthium mildei*), Cleu (*Clubiona leucaspis*), Iham (*Icius hamatus*), Nexo (*Nomisia exornata*), Zod (*Zodarion* spp.).

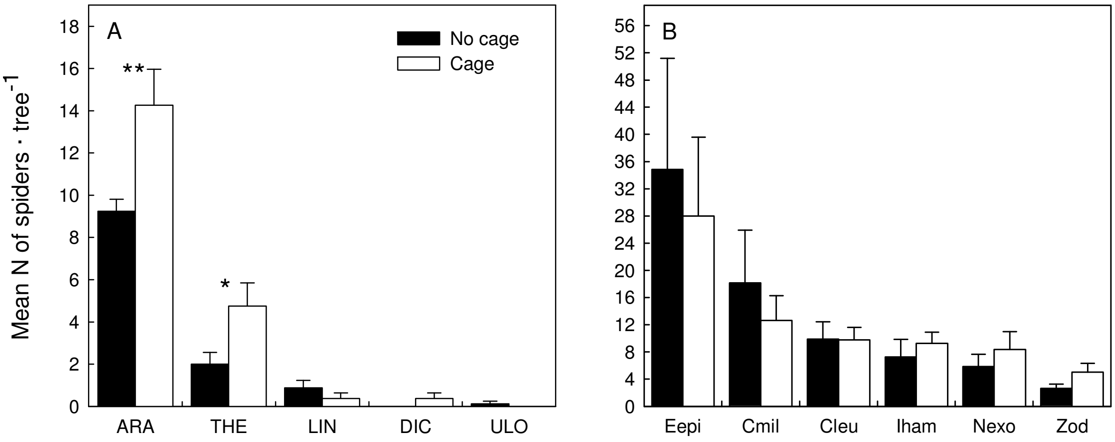
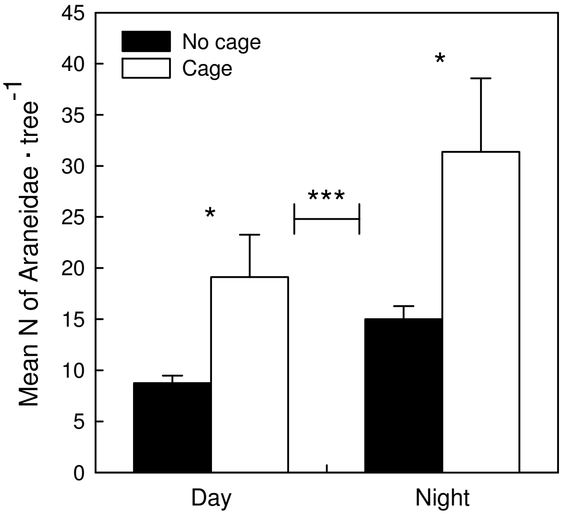


Fig. 3.2. Number of araneids per tree in caged and non-caged trees between day (12-14h) and night (24-02h), over the study period. Means ± SE are shown. Asterisks indicate a significant difference (**P* < 0.05; ****P* < 0.001).



Supplementary material

Table s3.1. Complete list of spider species collected in the trunks of 16 citrus trees with cardboard bands. Complete lists of species collected by beating trays and pitfall traps (Mestre et al. 2012) are also reported for a comparison of the relative proportions (in %) of collected species with the three sampling methods (white: 0%, light grey: 1-5%, dark grey: 6-10%, black: > 10%). Nomenclature follows Platnick (2012).

Family	Species	Canopy	Trunk	Ground
Agelenidae	*Textrix* sp. Sundevall, 1833		░	░
Araneidae	*Araniella cucurbitina* (Clerck, 1757)	░		
	Cyclosa oculata (Walckenaer, 1802)	░		
	Cyrtarachne ixoides (Simon, 1870)	░		
	Cyrtophora citricola (Forsskål, 1775)	░		
	Gibbaranea sp. (Archer, 1951)	░		
	Mangora acalypha (Walckenaer, 1802)	░		
	Neoscona subfusca (C. L. Koch, 1837)	▒		
	Zilla diodia (Walckenaer, 1802)	░		
	Zygiella x-notata (Clerck, 1757)	░		
	Undetermined Araneidae			░
Clubionidae	*Clubiona leucaspis* Simon, 1932	▒	█	
Dictynidae	*Lathys* sp. Simon, 1884	░		
	Marilynia bicolor (Simon, 1870)	░	░	
	Nigma walckenaeri (Roewer, 1951)	░	░	
Dysderidae	*Dysdera crocata* C. L. Koch, 1838		░	▒
Gnaphosidae	*Aphantaulax trifasciata* (O. P.-Cambridge, 1872)	░	░	░
	Haplodrassus dalmatensis (L. Koch, 1866)			░
	Haplodrassus signifer (C. L. Koch, 1839)			░
	Haplodrassus spp. Chamberlin, 1922			░
	Leptodrassus sp. Simon, 1878		░	
	Micaria sp. Westring, 1851		░	░
	Nomisia celerrima (Simon, 1914)			░
	Nomisia exornata (C. L. Koch, 1839)		▒	░
	Nomisia spp. Dalmas, 1921			░
	Setaphis carmeli (O. P.-Cambridge, 1872)		░	░
	Trachyzelotes fuscipes (L. Koch, 1866)			░
	Trachyzelotes holosericeus (Simon, 1878)			░
	Zelotes civicus (Simon, 1878)			░
	Zelotes nilicola (O. P.-Cambridge, 1874)			░

Table s3.1 (continued). Complete list of spider species collected in the trunks of 16 citrus trees with cardboard bands. Complete lists of species collected by beating trays and pitfall traps (Mestre et al. 2012) are also reported for a comparison of the relative proportions (in %) of collected species with the three sampling methods (white: 0%, light grey: 1-5%, dark grey: 6-10%, black: > 10%). Nomenclature follows Platnick (2012).

Family	Species	Canopy	Trunk	Ground
Gnaphosidae	*Zelotes petrensis* (C. L. Koch, 1839)			░
	Zelotes spp. Gistel, 1848		░	░
	Undetermined Gnaphosidae		░	
Linyphiidae	*Bathyphantes* sp. Menge, 1866			░
	Meioneta rurestris (C. L. Koch, 1836)			░
	Monocephalus castaneipes (Simon, 1884)			░
	Ostearius melanopygius (O. P.-Cambridge, 1879)		░	
	Palliduphantes ericaeus (Blackwall, 1853)			░
	Pelecopsis bucephala (O. P.-Cambridge, 1875)		░	░
	Pelecopsis mengei (Simon, 1884)	░		░
	Pelecopsis parallela (Wider, 1834)			▓
	Silometopus ambiguus (O. P.-Cambridge, 1905)			░
	Styloctetor romanus (O. P.-Cambridge, 1872)	░		
	Tapinocyba sp. Simon, 1884			░
	Tenuiphantes tenuis (Blackwall, 1852)			░
	Typhocrestus bogarti Bosmans, 1990			░
	Undetermined Linyphiidae	░	░	░
Lycosidae	*Alopecosa albofasciata* (Brullé, 1832)			░
	Hogna radiata (Latreille, 1817)			░
	Pardosa hortensis (Thorell, 1872)			▓
	Pardosa proxima (C. L. Koch, 1847)			█
	Pardosa sp. C. L. Koch, 1847			░
Mimetidae	*Ero aphana* (Walckenaer, 1802)	░		
Miturgidae	*Cheiracanthium mildei* L. Koch, 1864	░	█	
Nemesiidae	*Nemesia dubia* (Karsch, 1878)			░
Oonopidae	*Silhouettella loricatula* (Roewer, 1942)		░	
Oxyopidae	*Oxyopes lineatus* Latreille, 1806	░		░
Philodromidae	*Philodromus cespitum* (Walckenaer, 1802)	█	░	
	Philodromus rufus Walckenaer, 1826	░		
	Philodromus sp. Walckenaer, 1826	░		
	Thanatus vulgaris Walckenaer, 1826	░		░
Pisauridae	*Pisaura mirabilis* (Clerck, 1757)	░		

Table s3.1 (continued). Complete list of spider species collected in the trunks of 16 citrus trees with cardboard bands. Complete lists of species collected by beating trays and pitfall traps (Mestre et al. 2012) are also reported for a comparison of the relative proportions (in %) of collected species with the three sampling methods (white: 0%, light grey: 1-5%, dark grey: 6-10%, black: > 10%). Nomenclature follows Platnick (2012).

Family	Species	Canopy	Trunk	Ground
Salticidae	*Aelurillus v-insignitus* (Clerck, 1757)			░
	Ballus chalybeius (Walckenaer, 1802)	░		
	Chalcoscirtus infimus (Simon, 1868)	░		░
	Euophrys herbigrada (Simon, 1871)			░
	Evarcha jucunda (Lucas, 1846)			░
	Heliophanus apiatus Simon, 1868	░	░	
	Icius hamatus (C. L. Koch, 1846)	▓	▓	░
	Menemerus semilimbatus (Hahn, 1829)			░
	Phlegra bresnieri (Lucas, 1846)			░
	Salticus scenicus (Clerck, 1757)	░	░	
	Talavera aequipes (O. P.-Cambridge, 1871)			░
	Undetermined Salticidae		░	
Segestridae	*Segestria senoculata* (Linnaeus, 1758)		░	
Sparassidae	*Olios argelasius* (Walckenaer, 1805)	░	░	
Theridiidae	*Anelosimus vittatus* (C. L. Koch, 1836)	░		
	Asagena phalerata (Panzer, 1801)			░
	Dipoena melanogaster (C. L. Koch, 1837)	░		
	Euryopis episinoides (Walckenaer, 1847)	░	█	░
	Neottiura uncinata (Lucas, 1846)	░		
	Paidiscura pallens (Blackwall, 1834)	░		
	Parasteatoda sp. Archer, 1946	░		
	Phycosoma inornatum (O. P.-Cambridge, 1861)	░		
	Phylloneta sp. Archer, 1950	░		
	Platnickina tincta (Walckenaer, 1802)	░		
	Simitidion simile (C. L. Koch, 1836)	░		
	Steatoda nobilis (Thorell, 1875)	░	░	
	Theonoe minutissima (O. P.-Cambridge, 1879)	░		
	Theridion mystaceum L. Koch, 1870	░	░	
	Theridion pinastri L. Koch, 1872	░		
	Theridion spp. Walckenaer, 1805	█		
	Theridion varians Hahn, 1833	░		
	Undetermined Theridiidae	░		░

Table s3.1 (continued). Complete list of spider species collected in the trunks of 16 citrus trees with cardboard bands. Complete lists of species collected by beating trays and pitfall traps (Mestre et al. 2012) are also reported for a comparison of the relative proportions (in %) of collected species with the three sampling methods (white: 0%, light grey: 1-5%, dark grey: 6-10%, black: > 10%). Nomenclature follows Platnick (2012).

Family	Species	Canopy	Trunk	Ground
Thomisidae	*Ozyptila pauxilla* (Simon, 1870)			░
	Runcinia grammica (C. L. Koch, 1837)	░		
	Synema globosum (Fabricius, 1775)	░		
	Thomisus onustus Walckenaer, 1805	░		
	Tmarus sp. Simon, 1875	░		
	Xysticus bliteus (Simon, 1875)			░
	Xysticus kochi Thorell, 1872			░
	Xysticus sp. C. L. Koch, 1835	▒	░	
Titanoecidae	*Nurscia albomaculata* (Lucas, 1846)		░	░
Uloboridae	*Uloborus walckenaerius* Latreille, 1806	░		
Zodariidae	*Zodarion pseudoelegans* Denis, 1933			░
	Zodarion styliferum (Simon, 1870)			░
	Zodarion spp. Walckenaer, 1826		░	
Undetermined	Undetermined	░	░	░

4

Eight-year experiment in citrus trees reveals a pervasive yet changing effect of ants on a Mediterranean spider assemblage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ABSTRACT

Ants and spiders are ubiquitous generalist predators that exert top-down control on herbivore populations. Research shows that intraguild interactions between ants and spiders can negatively affect spider populations but there is a lack of long-term experiments documenting the strength of such interactions and the potential differential effects of ants on the diverse array of species in a spider assemblage. Similarly, the suitability of family-level surrogates for finding patterns revealed by species-level data (taxonomic sufficiency) has almost never been tested in spider assemblages. In this study, we excluded ants from trees over an 8-year period to test their impact on the spider assemblage of a Mediterranean citrus grove. Ants had a widespread influence on the spider assemblage, although the effect was only evident in the last 5 years of the study. During those years, ants negatively affected many spiders; effects were especially strong for sedentary spiders. Analyses at the family level also found differences in the spider assemblage between treatments but failed to retrieve contrasting responses to ant exclusion in related species. Our findings show that the effects of experimental manipulations in ecology can vary greatly over time and highlight the need for long-term studies to document species interactions.

Keywords: agroecosystem; ant exclusion; competition; intraguild interactions; taxonomic resolution.

Introduction

Ants and spiders are ubiquitous generalist predators in terrestrial arthropod communities, exerting top-down control on herbivore populations (Buddle et al. 2000; Schmidt et al. 2003; Sanders et al. 2008) that can potentially cascade down to plants (Snyder & Wise 2001; Sanders et al. 2011). Ants engage in mutualistic relationships with hemipterans, protecting them against their enemies in exchange for honeydew (Styrsky & Eubanks 2007); they also compete against spiders (Halaj et al. 1997). Intraguild interactions between ants and spiders can thus negatively affect spider populations (James et al. 1999; Del-Claro & Oliveira 2000) and even reduce the strength of top-down control (Sanders et al. 2011; but see Karhu 1998; Philpott et al. 2008). Unfortunately, most of the evidence on the importance of ants in communities comes from short-term experiments (less than 2 years), although effects of ecological manipulations have been shown to vary over much longer periods of time (Carson & Root 2000; Allan & Crawley 2011).

Spiders show a striking variety of activity patterns and foraging styles (Jocqué & Dippenaar-Schoeman 2006) but few works go beyond the classification of spiders into broad functional groups to consider how the effects of competitors vary according to the identity of the spiders involved (Sanders & Platner 2007; Piñol et al. 2010). These potentially differential effects could, however, modify the taxonomic composition of spider assemblages in the presence of competitors. Furthermore, species-level identification of large data sets is costly and time-consuming, leading many studies on the ecology of arthropod communities to adopt a taxonomic sufficiency approach. Taxonomic sufficiency involves identifying organisms to a level of taxonomic resolution sufficient to meet established goals, i.e. finding the patterns revealed by species-level data. Family-level identifications have proved to retain enough information to detect differences between assemblages and are therefore useful surrogates for identification at species level (Bertasi et al. 2009; Groc et al. 2010). Nevertheless, the suitability of higher taxa surrogates in spider assemblages has largely been ignored (Cardoso et al. 2004).

We excluded ants from tree canopies over 8 years to test their impact on the spider assemblage of a Mediterranean organic citrus grove. We already know from a long-term experiment in the same setting by Piñol et al. (2012a) that ants have had a strong influence on the abundance of different arthropod groups, including spiders. In the present study we tested (1) whether ants changed the taxonomic composition of the canopy spider assemblage and subsequently investigated (2) which spider species were most affected by ants. We also looked for (3) potential changes over time in the impact of ant exclusion on the spider assemblage and tested (4) whether identification at the family level was an adequate surrogate for effects detected with species-level data.

Material and methods

Study site

The grove is located at La Selva del Camp (Catalonia, NE Spain; 41º 13' 07″N, 1º 8' 35″E). The climate is Mediterranean, with a rainy spring and autumn and a dry winter and summer. The grove consists of ca. 300 Clementine trees (*Citrus clementina* var. *clemenules*) grafted on to the hybrid rootstock Carrizo citrange (*Poncirus trifoliata* (L.) Raf. x *Citrus sinensis* (L.) Osb.). The trees are watered during dry periods. Grasses and other weeds form a permanent ground cover that is mowed regularly. The grove was converted from conventional to organic agriculture in 2004, but pesticides and herbicides ceased to be applied in 2001 and 2002, respectively. For more details see Piñol et al. (2012a).

Experimental design

Experimental trees were randomly selected from an area with 69 trees and randomly assigned to two groups: there were 8 control trees (nine in 2009) and 8 banded trees (seven in 2002, nine in 2009) to which a glue band was applied on the trunk to prevent ants climbing up to the canopies. The band consisted of a polybutene-based sticky ring applied on plastic film tightly attached over a padded cylinder in contact with the trunk (Samways & Tate 1985). Trees were inspected weekly, and if ants were detected in the canopy, tall weeds were cut down or more glue was added to the barrier. The trunk barrier effectively excluded ants from the canopies most of the time (Piñol et al. 2012a). Treatments were established in January (February in 2002) and trees were sampled every month until December. The experiment was repeated for 8 years (2002-2009), using a different set of experimental trees each year.

The sticky barrier was also effective against other crawling insects in the grove, such as earwigs *Forficula* spp. (Piñol et al. 2009). This ant-exclusion experiment therefore has to be interpreted as one involving the exclusion of both ants and earwigs. For the sake of brevity, the term ant exclusion is used throughout the paper.

Sampling methodology

Arthropods from the canopy were sampled every month using beating trays (0.5 m^2), with three blows in opposite directions on the tree crowns; they were then captured with entomological aspirators and preserved in 70% ethanol. Sampling was comparable throughout the 8 years because the area covered by each of the sampled canopies was sufficiently large, from the start of the experiment, to contain all the beating trays (mean ± SE canopy area: 2.3 ± 0.1 m^2 in 2002).

Taxonomic identifications

Spiders were identified to species, using mainly the keys of Roberts (1985a,b) and Heimer & Nentwig (1991). We used additional keys to determine individuals belonging to the families Anyphaenidae (Urones et al. 1995), Corinnidae (Bosselaers et al. 2009), Linyphiidae (Wunderlich 1980; Bosmans & Abrous 1990) and Salticidae (Alicata & Cantarella 1994). Some juveniles could only be identified to the genus level. Nevertheless, juveniles from a given genus were assigned to the same species as adults if that species was the sole representative of that genus in the grove, but not all juvenile linyphiids could be classified. We followed the nomenclature given in Platnick (2011). Ants were also identified to species using Collingwood (1978) and Seifert (1992). The most common ants in the trees were the aphid-tending species *Lasius grandis* Forel (60% of the individuals) and *Formica rufibarbis* Fabricius (15%), followed by the nectarivorous *Plagiolepis pygmaea* (Latreille) (9%). A general overview of the remaining arthropod orders sampled from the canopies is given in Piñol et al. (2012a).

Statistical analyses

The response variable was the average number of spiders in each tree from February (March in 2002) to December of each year. We did not use data from the January samples (February in 2002) because the experimental exclusion of ants started the following month.

For each year, we tested for differences between treatments on the taxonomic composition of the canopy spider assemblage with permutational multivariate ANOVAs (PERMANOVA) on the square-root-transformed averages, using the Bray-Curtis index of similarity, with "ant exclusion" (control, band) as a fixed factor. PERMANOVA is a non-parametric analogue to MANOVA that does not require multivariate data to be normality distributed. PERMANOVA is thus particularly suitable for analysing data on assemblage species composition, which rarely satisfy multivariate normality. We conducted the analyses at species and family levels to test the influence of taxonomic resolution on the detection of effects.

When the PERMANOVA analysis for a given year was significant, we ran univariate permutational ANOVAs on the square-root-transformed abundances of the most common spider species or families in that year using the Euclidean distance, resulting in a permutational equivalent of classical ANOVAs (Anderson et al. 2008). These univariate analyses served as *a* *posteriori* statistical tests that allowed us to detect which species were causing the differences in assemblage composition between ant-excluded and control trees. To adjust the level of significance we used the step-up false discovery rate (FDR) by Benjamini & Hochberg (1995). We considered that the set of univariate analyses derived from each significant PERMANOVA analysis constituted a family of tests (García 2004).

We analysed differences in species richness (S) between treatments for each year with univariate permutational ANOVAs on S, using the Euclidean distance. The response variable was the average spider richness in each tree from February (March in 2002) to December of each year. Since we could not identify all the spiders to species, the estimate of S was conservative.

To test whether the spider assemblage in the control trees changed gradually over the years, we conducted a RELATE analysis —a multivariate analogue to simple regression— on the square-root-transformed averages, with the Bray-Curtis index of similarity. We used the Spearman correlation (statistic ρ). We previously standardized the samples to obtain species-relative percentages from species counts. Thus, a significant result would indicate that a change in the composition of spider assemblage was caused by a shift in the species' relative proportions, rather than a mere change in spider abundance over time. We conducted a second RELATE analysis to test the relationship between the spider and the ant assemblages, using the total yearly abundances of all the spider and ant species. Finally, we repeated this analysis without the ant *Lasius grandis*, to test its influence on the spider assemblage, as this species seemed to play a major role in determining the abundances of arthropods in the tree canopies (Piñol et al. 2012a). We conducted the three RELATE analyses at species and family levels to test again the influence of taxonomic resolution on the detection of effects. We also analysed the relationship between S and the year of study: considering a potential covariation of S with total spider abundance each year, we conducted a multiple regression of S with a permutational distance-based linear model (DISTLM), taking the explanatory variables "spider abundance" and "year" (2002-2009), using only control trees. All analyses were conducted with the software PERMANOVA+ for PRIMER v.6 (Anderson et al. 2008).

Results

The spider assemblage

A total of 13,460 spiders were captured from the canopies with beating trays. Seventy-seven species from 21 families were sampled (see Table s4.1 for a complete list), the most abundant being Theridiidae (34% of all individuals), Philodromidae (21.6%), Araneidae (13.4%), Salticidae (8.3%), Clubionidae (6.1%), and Thomisidae (3.9%). Each of these families was dominated by one species (Philodromidae: 83.3% *Philodromus cespitum*; Araneidae: 80.8% *Neoscona subfusca*; Salticidae: 62.2% *Icius hamatus*; Thomisidae: 66.4% *Xysticus* sp.) or genus (Theridiidae: 41.8% *Theridion* spp., 26.1% *Anelosimus vittatus*). *Clubiona leucaspis* was the only clubionid species in the grove. The genus *Theridion* comprised 3 species, namely *T. mystaceum*, *T. pinastri* and *T. varians*, but the majority of individuals were juveniles and we thus assigned them to genus. However, we analysed *Theridion* spp. as a single species because the 3 species share similar lifestyles. The most diverse families were Theridiidae (14 species), Linyphiidae (13), Thomisidae (8), Araneidae (7) and Salticidae (7). By contrast, 11 out of 21 families were represented by a single species.

Long-term changes

The composition of the spider assemblage varied over the 8 years of study, as shown by the changes in relative abundance of the 7 most common species ($\rho = 0.55$, $P = 0.01$; Fig. 4.1). *A. vittatus* had a relatively moderate abundance in 2002-2004, which decreased in 2006 and remained low until 2009. *P. cespitum* was also more common at the beginning (2002-2003) than at the end of the study (2008-2009). In contrast, abundances of *C. leucaspis* and *I. hamatus* were low in 2002-2003 and increased slightly until 2008-2009. Abundances of *Cheiracanthium mildei*, *N. subfusca* and *Theridion* spp. changed little over time.

Effect of ant exclusion in the canopies

At species level, the spider assemblage was significantly affected by ant exclusion in the years 2005 to 2009 (pseudo-$F_{1,14} > 2.99$, $P < 0.0016$; Tables 4.1, s4.2). After adjusting the level of significance for each year, permutational ANOVAs showed that *A. vittatus* (Theridiidae, $P = 0.0026$; Fig. 4.2, Table s4.3), *C. mildei* (Miturgidae, $P = 0.0022$), *C. leucaspis* (Clubionidae, $P = 0.014$), *Kochiura aulica* (Theridiidae, $P < 0.012$), *Macaroeris nidicolens* (Salticidae, $P = 0.0082$), *N. subfusca* (Araneidae, $P = 0.018$), *Oxyopes lineatus* (Oxyopidae, $P = 0.012$), *Platnickina tincta* (Theridiidae, $P < 0.018$), *Theridion* spp. (Theridiidae, $P < 0.011$), and *Xysticus* sp. (Thomisidae, $P < 0.0006$) were more abundant in ant-free trees in at least one of the years. The negative effect of ants was especially strong on *K. aulica*, *P. tincta*, *Theridion* spp. (Theridiidae), and on *Xysticus* sp. (Thomisidae), as their abundances were affected in 3 or 4 years, while the other species were affected in only 1 year. On the contrary, *I. hamatus* (Salticidae) was more abundant in control trees in 2008 ($P = 0.0074$).

Ant exclusion increased spider richness in 2006, 2007 and 2009 ($P < 0.032$; Table 4.2). Spider richness was positively correlated with abundance ($R^2 = 0.77$, $P = 0.0069$) but also with the year of the experiment, although to a lesser degree ($R^2 = 0.59$, $P = 0.032$). There was a correlation between the spider and the ant assemblages (ρ = 0.55, *P* = 0.004), but the relationship vanished when the ant *L. grandis* was removed from the analysis (ρ = 0.21, *P* = 0.075).

Monthly variations in species abundance

The negative effect of ants on most of the analysed spider species was reflected by their changes in abundance between control and ant-free trees over the months. Spider abundances were similar in both treatments in winter and early spring. In May-June, coinciding with the start of intense ant activity in the canopies, abundances became higher in the banded trees than in the controls (see Fig. s4.1). In contrast, abundances of most species reached a minimum in May-June, increased abruptly in July and peaked in late summer. Notable exceptions to this seasonal trend were *O. lineatus* and *Xysticus* sp.: these species appeared in the citrus canopies in late spring, peaked in June-July and almost vanished thereafter.

Influence of taxonomic resolution on the detection of effects

The relative abundance of the spider families also changed gradually over the years (ρ = 0.40, *P* = 0.01). At family level, the spider assemblage was significantly affected by ant exclusion in the years 2005 to 2009 (pseudo-$F_{1,14}$ > 2.82, *P* < 0.0097; Table 4.1, Table s4.4). After adjusting the level of significance for each year, univariate permutational ANOVAs showed that Araneidae (*P* = 0.0092; Fig. 4.3, Table s4.5), Clubionidae (*P* = 0.015), Miturgidae (*P* = 0.0023), Oxyopidae (*P* = 0.011), Theridiidae (*P* < 0.0046), and Thomisidae (*P* < 0.0033) were more abundant in trees without ants in at least one of the years. Gnaphosidae (*P* = 0.014) and Salticidae (*P* = 0.0033) were more numerous in control trees in 2008. The spider assemblage analysed at family level was related to the ant assemblage (ρ = 0.62, *P* = 0.02), but when *L. grandis* was removed from the analysis the relationship became weaker (ρ = 0.31, *P* = 0.033).

Discussion

Our 8-year exclusion experiment revealed that ants had a widespread influence on the spider assemblage, although the effect was only evident in the last 5 years of the study (2005-2009). Analyses at the family level were effective in detecting assemblage differences between treatments but they concealed contrasting responses to ant exclusion in related species.

Effect of ants on the spider assemblage

From 2005 to 2009 we detected a severe negative effect of tree-foraging ants on spiders: in the trees with ants, 10 of the 17 species analysed had lower abundances and species richness was lower than in ant-free trees. While other studies have also found that ants decrease the abundances of canopy spiders (Philpott et al. 2004; Vanek & Potter 2010; Piñol et al. 2012a), to our knowledge no removal experiments in other systems have ever previously analysed the effect of predators or competitors on the individual spider species constituting an assemblage. In three studies conducted in the canopies of North American pine stands, Halaj et al. (1997) and Mooney (2006, 2007) classified spiders into two functional groups (hunters, web-weavers) and reported a substantial negative impact of ants on hunters, and a slight effect on web-weavers (Mooney 2007). In the studied Mediterranean citrus grove we found that ants foraging on canopies strongly reduced the abundances of both hunting (*C. mildei*, *C. leucaspis*, *M. nidicolens*, *O. lineatus*, *Xysticus* sp.) and web-building species (*A. vittatus*, *K. aulica*, *N. subfusca*, *P. tincta*, *Theridion* spp.). The diversity of lifestyles within these two broad categories (Uetz et al. 1999; Cardoso et al. 2011) indicates that the attack of ants is indiscriminate and that these species do not share any trait that makes them especially vulnerable to the activity of ant workers. Nevertheless, the spiders most affected (*K. aulica*, *P. tincta*, *Theridion* spp., *Xysticus* sp.) were all sit-and-wait predators (Foelix 2010), which suggests that sedentary habits may make individuals more susceptible to ant foraging.

By contrast, the species *I. hamatus*, *Dipoena melanogaster* and *Aphantaulax trifasciata* were more common in ant-frequented trees in almost all the years, although the trends were only significant for *I. hamatus*. One plausible explanation is that these species feed preferably on ants, as described for *Dipoena* and *Icius* spiders (Umeda et al. 1996; Pekár et al. 2012). Similarly, previous experiments have reported a decrease in the abundance of Zodariidae (Gibb 2003) and *Gnaphosa* (Moya-Laraño & Wise 2007) following ant exclusion, because these spiders prey on ants.

Long-term exclusion experiment

During the first 3 years of the study ants had no noticeable effect on the spider assemblage. Yet ants had a marked influence from 2005 onwards, coinciding with an increase in their abundance in the canopies —mostly due to *L. grandis*— that continued until the end of the experiment (Piñol et al. 2012a). Indeed, there was a highly significant relationship between the spider and the ant assemblages when *L. grandis* was included in the analysis, indicating that this species is the main driver of the influence of ants on the spider assemblage. The grove itself underwent several changes between 2002 and 2009: due to its conversion to organic agriculture, agrochemicals stopped being used in 2004, and the irrigation system was improved in 2006 to boost the effect of organic fertilizer. Moreover, the trees were planted in 1999 and at that time they were small and the vegetal ground cover was scarce. However, it is difficult to ascertain a clear link between any of these agricultural modifications and the prominent changes suffered by the ant community. In contrast, the long-term changes observed in the abundance of the most common spider species were rather modest, and total spider abundance did not steadily increase with time like ant abundance but rather remained relatively high over the course of the study, apart from the 2 middle years (2005-2006).

The shift in ant abundance in the canopies over the experimental period allows us to divide the study into two distinct parts: a first part (2002-2004) in which the numbers of ants were too low to produce any detectable effect on spiders, and a second (2005-2009) in which ant numbers increased considerably, leading to a pervasive influence on the spider assemblage. These contrasting outcomes within the same study highlight the significance of long-term ecological experiments. Had we run our experiment for less than 4 years, we would have missed the importance of ants on spiders in this system. Indeed, the results of the second part of the study resemble those of two independent short-term experiments conducted between 2006 and 2009 in the same setting, which also showed a negative influence of ants on certain canopy spiders: theridiids and thomisids in Piñol et al. (2010), and araneids and theridiids in Mestre et al. (2012). Since multiple-year ant-exclusion experiments are largely lacking (Schmitz et al. 2000; Piñol et al. 2012a), our findings are difficult to compare with previous studies. In a 2-year experiment, ants had a constant negative effect (James et al. 1999), whereas in a 4-year experiment by Lenoir et al. (2003) ground ants had variable, albeit slight effects on spiders.

Taxonomic resolution and detection of effects

Family-level identifications were as successful as species-level identifications in detecting shifts in assemblage composition between ant-excluded and control trees. Therefore, multivariate analyses of the canopy spider assemblage identified to family were sufficient to detect the general effect of ants. Overall, univariate analyses of families showed the same differences in abundance between treatments as analyses of the most abundant species within these families (Araneidae: *N. subfusca*; Clubionidae: *C. leucaspis*; Dictynidae: *Nigma walckenaeri*; Gnaphosidae: *A. trifasciata*; Linyphiidae: *Styloctetor romanus*; Miturgidae: *C. mildei*; Oxyopidae: *O. lineatus*; Thomisidae: *Xysticus* sp.). These equivalent results with two taxonomic resolutions probably arose because these families were clearly dominated by a single species, so the detected effects on it persisted to family level (Bertasi et al. 2009). Nevertheless, both the positive effect of ants on salticids and the negative effect on theridiids are misleading because they failed to reflect opposite responses of related species to ant exclusion: while most analysed theridiid species increased numerically in ant-free trees, *D. melanogaster* was less frequent in these trees, and the reduction in salticid abundance in ant-free trees was caused by the low numbers of *I. hamatus*, although the less common *M. nidicolens* was in fact more abundant in ant-excluded trees. Studies of taxonomic sufficiency in other assemblages of terrestrial arthropods also show the limitations of identification to family level (Grimbacher et al. 2008; Bang & Faeth 2011), although it can sometimes be an appropriate taxonomic surrogate for species-level determinations (Schnell et al. 2003; Caruso & Migliorini 2006).

Conclusion

This study showed that the far-reaching impact of ants on the canopy spider assemblage only surfaced after the third year of ant exclusion. The influence of ants on spiders was negative for species with very varied lifestyles but it was more prominent in sedentary spiders. Although analyses at family level satisfactorily detected assemblage differences between treatments, critical information about species-specific responses to ant exclusion was lost with this approach. Our findings reveal that the effects of experimental manipulations on ecological research can vary greatly over time, emphasizing the need for long-term studies to document species interactions.

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Tables

Table 4.1. Summary of the PERMANOVA table of the effect of ant exclusion on the spider assemblage from 2002 to 2009, at the species and family level.

	Species		Family	
Year	Pseudo-F	*P* (perm)	Pseudo-F	*P* (perm)
2002	1.70	0.076	1.67	0.13
2003	1.31	0.23	1.76	0.11
2004	1.29	0.20	1.13	0.36
2005	3.28	0.0007	3.13	0.0046
2006	4.16	0.0006	5.62	0.0002
2007	2.99	0.0016	2.82	0.0097
2008	4.02	0.0003	6.01	0.0008
2009	5.17	0.0002	9.86	0.0002

Table 4.2. Summary of the ANOVA table of the effect of ant exclusion on spider richness (S) from 2002 to 2009.

Treatment	Ants		No ants		ANOVA	
Year	Mean	SE	Mean	SE	Pseudo-F	*P* (perm)
2002	3.80	0.34	2.91	0.53	1.10	0.35
2003	4.06	0.13	3.97	0.22	0.21	0.64
2004	4.58	0.34	4.99	0.29	0.99	0.33
2005	3.70	0.25	3.32	0.22	1.26	0.27
2006	3.83	0.34	5.82	0.29	14.94	0.0007
2007	5.52	0.22	6.49	0.33	5.86	0.032
2008	6.58	0.38	7.21	0.37	1.32	0.26
2009	5.58	0.19	6.95	0.27	16.92	0.0009

Figures

Fig. 4.1. Variations over time in the relative abundance of the 7 most common spider species in the grove over the 8 years of study, considering only control trees. Codes: Avitt (*Anelosimus vittatus*), Cmil (*Cheiracanthium mildei*), Cleu (*Clubiona leucaspis*), Iham (*Icius hamatus*), Nsub (*Neoscona subfusca*), Pces (*Philodromus cespitum*), Ther (*Theridion* spp.), Other (the sum of the remaining species).

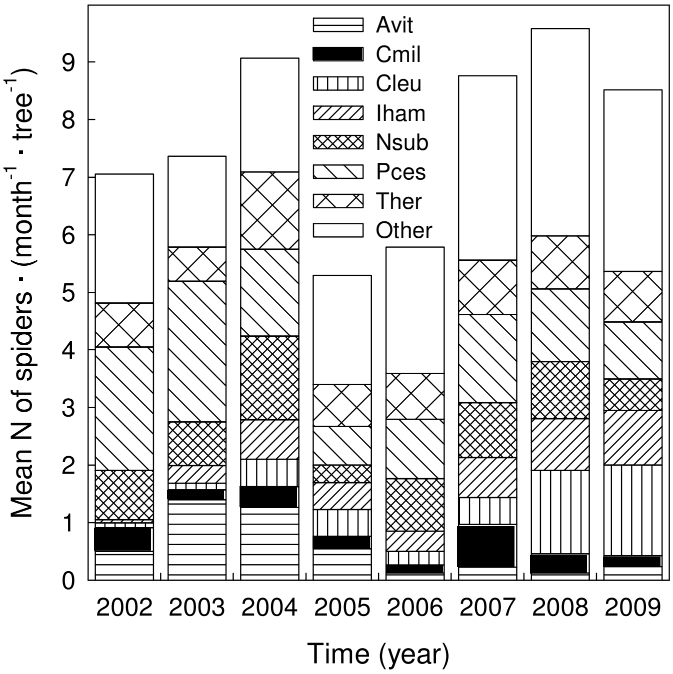


Fig. 4.2. Abundance of the most common spider species in the grove over the 8 years of study, in control (Ants) and banded (No ants) trees. Species are ordered by decreasing abundance. Means ± SE are shown (▪: *P* < 0.05; *: significant after FDR correction).

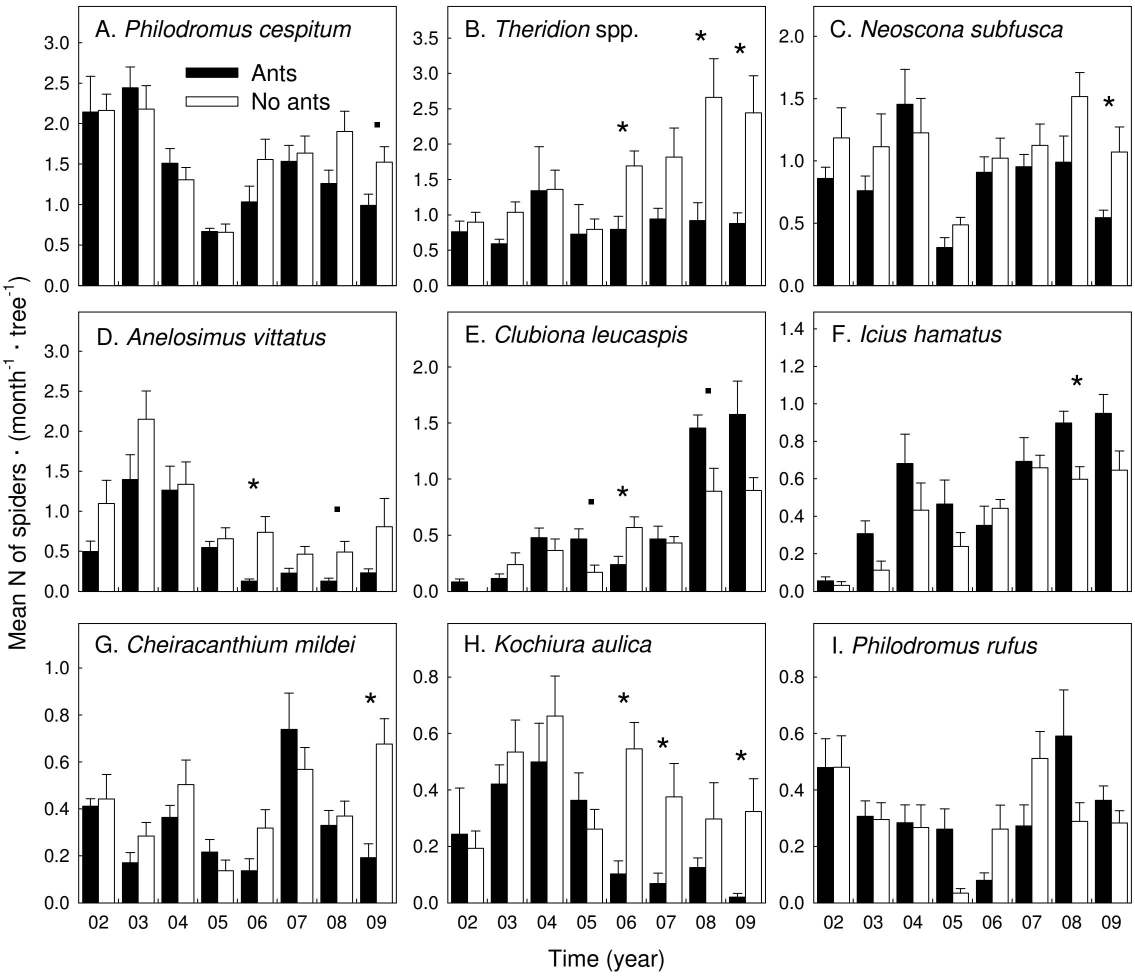


Fig. 4.2 (continued). Abundance of the most common spider species in the grove over the 8 years of study, in control (Ants) and banded (No ants) trees. Species are ordered by decreasing abundance. Means ± SE are shown (▪: $P < 0.05$; *: significant after FDR correction).

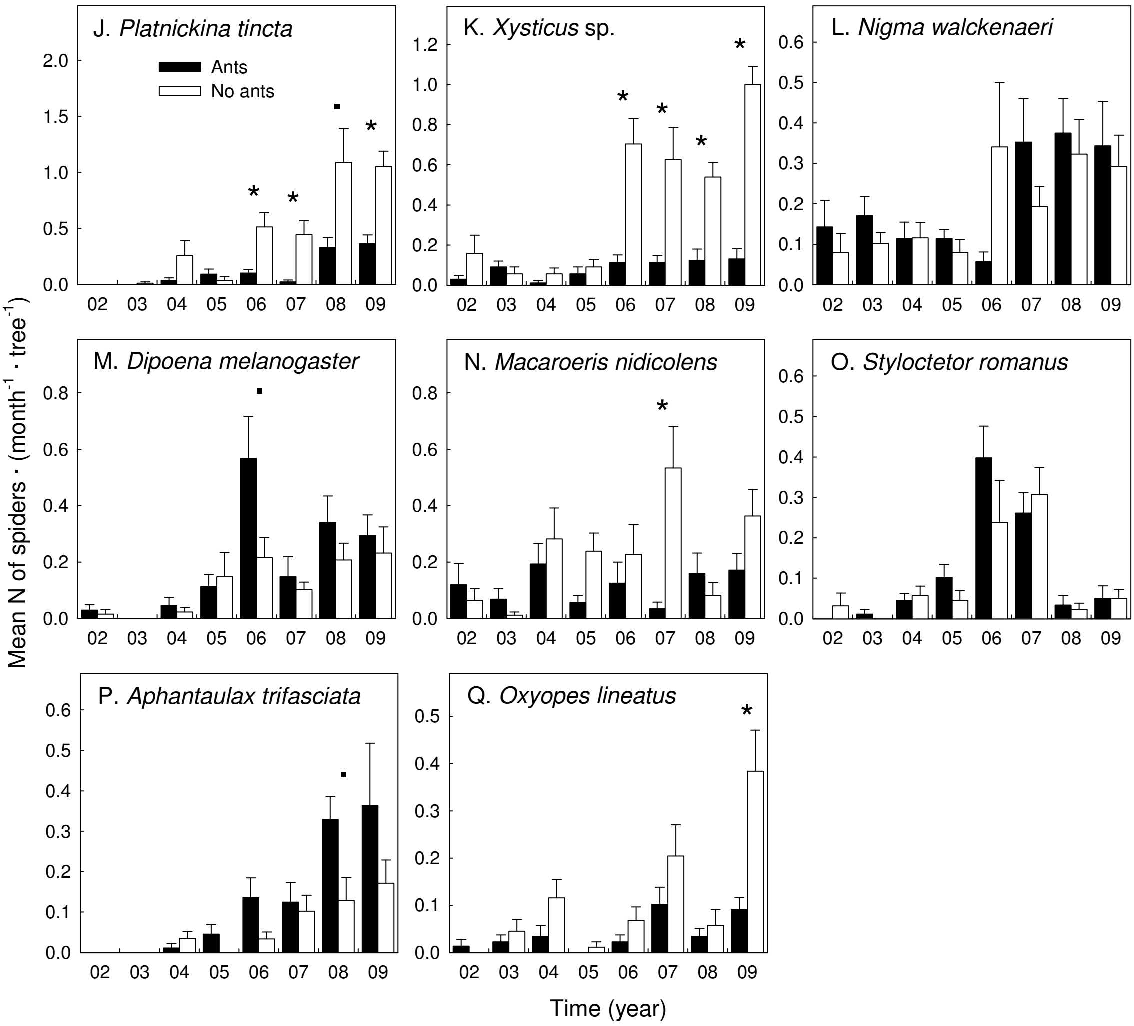
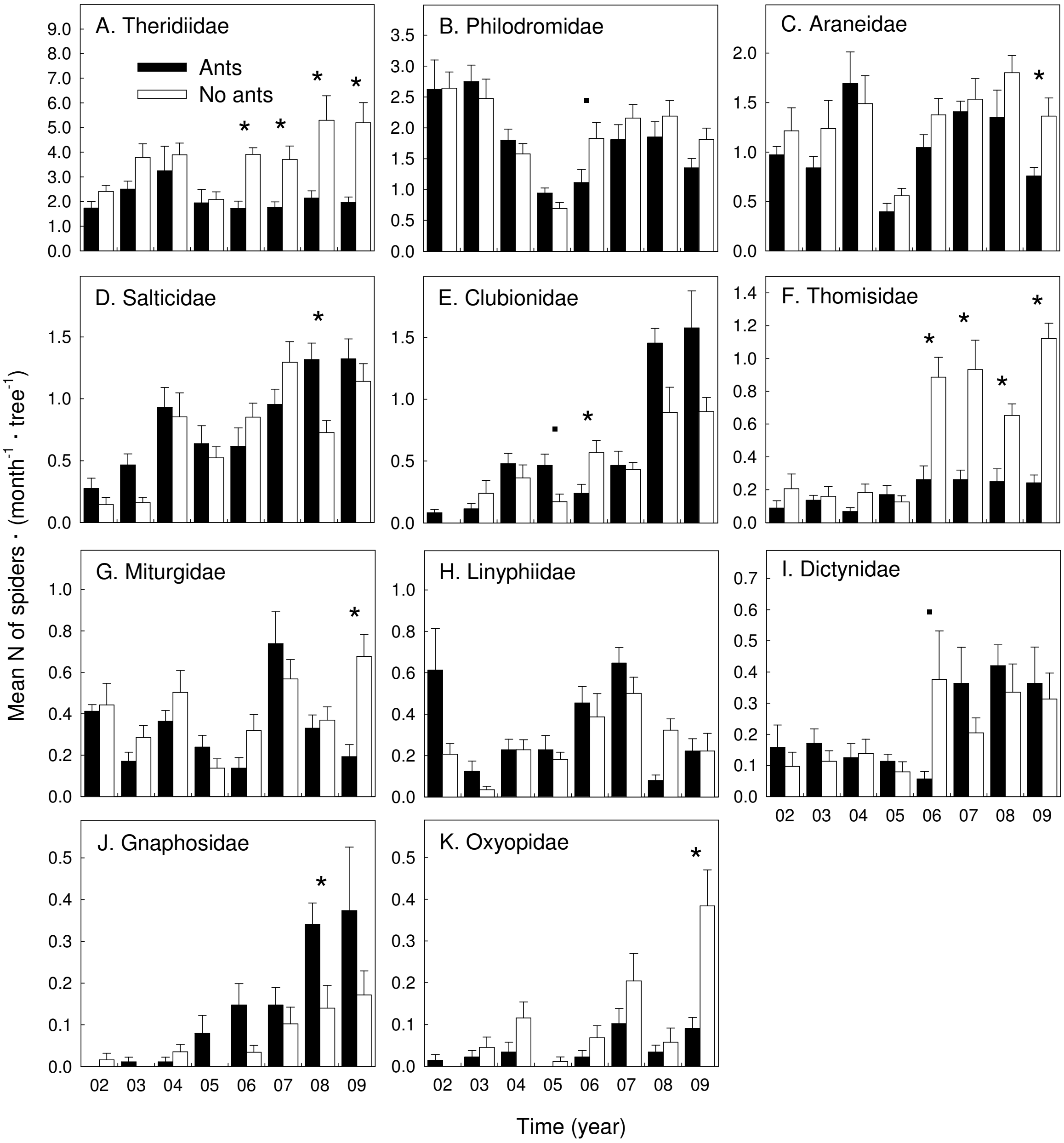


Fig. 4.3. Abundance of the most common spider families in the grove over the 8 years of study, in control (Ants) and banded (No ants) trees. Families are ordered by decreasing abundance. Means ± SE are shown (▪: *P* < 0.05; *: significant after FDR correction).



Supplementary material

Table s4.1. Complete list of spider species collected in the canopies of citrus trees by beating trays over the 8 years of study. Nomenclature follows Platnick (2011).

Family	Species	# individuals
Anyphaenidae	*Anyphaena alboirrorata* Simon, 1878	1
	Anyphaena sabina L. Koch, 1866	14
Araneidae	*Araniella cucurbitina* (Clerck, 1757)	69
	Cyclosa oculata (Walckenaer, 1802)	2
	Cyrtarachne ixoides (Simon, 1870)	1
	Cyrtophora citricola (Forsskål, 1775)	184
	Mangora acalypha (Walckenaer, 1802)	35
	Neoscona subfusca (C. L. Koch, 1837)	1465
	Undetermined Araneidae	29
	Zygiella x-notata (Clerck, 1757)	29
Clubionidae	*Clubiona leucaspis* Simon, 1932	829
Corinnidae	*Trachelas minor* O. P.-Cambridge, 1872	1
Dictynidae	*Lathys humilis* (Blackwall, 1855)	15
	Marilynia bicolor (Simon, 1870)	6
	Nigma walckenaeri (Roewer, 1951)	315
Gnaphosidae	*Aphantaulax trifasciata* (O. P.-Cambridge, 1872)	139
	Gnaphosa sp. Latreille, 1804	1
	Leptodrassus sp. Simon, 1878	1
	Micaria sp. Westring, 1851	3
	Poecilochroa senilis Westring, 1874	1
	Zelotes spp. Gistel, 1848	2
	Undetermined Gnaphosidae	4
Linyphiidae	*Centromerus albidus* Simon, 1929	1
	Erigone dentipalpis (Wider, 1834)	1
	Frontinellina frutetorum (C. L. Koch, 1834)	1
	Gongylidiellum murcidum Simon, 1884	1
	Meioneta rurestris (C. L. Koch, 1836)	55
	Ostearius melanopygius (O. P.-Cambridge, 1879)	2
	Pelecopsis mengei (Simon, 1884)	71
	Parapelecopsis nemoralis (Blackwall, 1841)	6
	Silometopus ambiguus (O. P.-Cambridge, 1905)	18
	Styloctector romanus (O. P.-Cambridge, 1872)	146
	Tenuiphantes tenuis (Blackwall, 1852)	21
	Typhocrestus bogarti Bosmans, 1990	14
	Walckenaeria monoceros (Wider, 1834)	7
	Undetermined Linyphiidae	74
Mimetidae	*Ero aphana* (Walckenaer, 1802)	25
Miturgidae	*Cheiracanthium mildei* L. Koch, 1864	512
	Cheiracanthium montanum L. Koch, 1877	2
Oonopidae	*Oonopinus* sp. Simon, 1893	1

Table s4.1 (continued). Complete list of spider species collected in the canopies of citrus trees by beating trays over the 8 years of study. Nomenclature follows Platnick (2011).

Family	Species	# individuals
Oxyopidae	*Oxyopes lineatus* Latreille, 1806	112
Philodromidae	*Philodromus cespitum* (Walckenaer, 1802)	2435
	Philodromus rufus Walckenaer, 1826	484
	Thanatus vulgaris Walckenaer, 1826	2
	Tibellus sp. Simon, 1875	1
Pholcidae	*Pholcus* sp. Walckenaer, 1805	1
Pisauridae	*Pisaura mirabilis* (Clerck, 1757)	2
Salticidae	*Ballus chalybeius* (Walckenaer, 1802)	118
	Chalcoscirtus infimus (Simon, 1868)	15
	Evarcha jucunda (Lucas, 1846)	2
	Heliophanus apiatus Simon, 1868	11
	Icius hamatus (C. L. Koch, 1846)	701
	Macaroeris nidicolens Wunderlich, 1992	243
	Salticus scenicus (Clerck, 1757)	16
	Undetermined Salticidae	21
Segestridae	*Segestria senoculata* Latreille, 1804	3
Sparassidae	*Olios argelasius* (Walckenaer, 1805)	135
Theridiidae	*Anelosimus vittatus* (C. L. Koch, 1836)	1201
	Dipoena melanogaster (C. L. Koch, 1837)	245
	Euryopis episinoides (Walckenaer, 1847)	30
	Kochiura aulica (C. L. Koch, 1838)	488
	Neottiura uncinata (Lucas, 1846)	4
	Paidiscura pallens (Blackwall, 1834)	21
	Phylloneta impressa Archer, 1950	7
	Platnickina tincta (Walckenaer, 1802)	415
	Rhomphaea rostrata (Simon, 1873)	2
	Steatoda nobilis (Thorell, 1875)	103
	Theridion mystaceum L. Koch, 1870	19
	Theridion pinastri L. Koch, 1872	26
	Theridion varians Hahn, 1833	3
	Theridion spp. Walckenaer, 1805	1926
	Undetermined Theridiidae	121
Thomisidae	*Heriaeus hirtus* (Latreille, 1819)	1
	Monaeses paradoxus (Lucas, 1846)	1
	Ozyptila sp. Simon, 1864	5
	Runcinia grammica (C. L. Koch, 1837)	78
	Synema globosum (Fabricius, 1775)	70
	Thomisus onustus Walckenaer, 1805	6
	Tmarus staintoni (O. P.-Cambridge, 1873)	18
	Xysticus sp. C. L. Koch, 1835	353
Titanoecidae	*Nurscia albomaculata* (Lucas, 1846)	1
Uloboridae	*Uloborus walckenaerius* Latreille, 1806	10
TOTALS		13560

Table s4.2. Complete PERMANOVA table of the effect of ant exclusion on the spider assemblage from 2002 to 2009 (a-h) at the species level.

Source	df	SS	MS	Pseudo-F	*P* (perm)
(a) year 2002					
Treatment	1	1102.10	1102.10	1.70	0.076
Res	13	8440.10	649.24		
Total	14	9542.20			
(b) year 2003					
Treatment	1	540.07	540.07	1.31	0.23
Res	14	5758.80	411.34		
Total	15	6298.90			
(c) year 2004					
Treatment	1	759.99	759.99	1.29	0.20
Res	14	8247.50	589.11		
Total	15	9007.50			
(d) year 2005					
Treatment	1	2188.20	2188.20	3.28	0.0007
Res	14	9349.90	667.85		
Total	15	11538.00			
(e) year 2006					
Treatment	1	2760.50	2760.50	4.16	0.0006
Res	14	9299.10	664.22		
Total	15	12060.00			
(f) year 2007					
Treatment	1	1496.20	1496.20	2.99	0.0016
Res	14	7004.90	500.35		
Total	15	8501.10			
(g) year 2008					
Treatment	1	1937.40	1937.40	4.02	0.0003
Res	14	6743.10	481.65		
Total	15	8680.60			
(h) year 2009					
Treatment	1	2601.80	2601.80	5.17	0.0002
Res	16	8053.90	503.37		
Total	17	10656.00			

Table s4.3. Summary of the ANOVA table of the effect of ant exclusion on the most abundant spider species from 2005 to 2009 (▪: $P < 0.05$; *: significant after FDR correction; nt: not tested).

Year	2005		2006		2007		2008		2009	
Species	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*
Anelosimus vittatus	0.17	0.69	13.60	0.0026*	3.70	0.07	7.81	0.02▪	3.48	0.08
Aphantaulax trifasciata	nt	nt	nt	nt	nt	nt	7.49	0.02▪	0.37	0.54
Cheiracanthium mildei	nt	nt	4.91	0.054	0.45	0.51	0.43	0.57	14.47	0.0022*
Clubiona leucaspis	8.71	0.01▪	7.51	0.014*	0.00	0.96	6.33	0.03▪	4.25	0.06
Dipoena melanogaster	nt	nt	5.11	0.04▪	nt	nt	1.00	0.34	nt	nt
Icius hamatus	1.49	0.23	1.42	0.26	0.00	0.99	10.19	0.0074*	4.05	0.06
Kochiura aulica	0.96	0.35	19.67	0.0018*	11.66	0.0053*	nt	nt	9.81	0.012*
Macaroeris nidicolens	nt	nt	nt	nt	11.24	0.0082*	nt	nt	1.69	0.21
Neoscona subfusca	4.42	0.06	0.18	0.67	0.45	0.50	3.82	0.07	6.45	0.018*
Nigma walckenaeri	nt	nt	3.75	0.08	0.96	0.35	0.27	0.63	0.05	0.84
Oxyopes lineatus	nt	nt	nt	nt	nt	nt	nt	nt	8.73	0.012*
Philodromus cespitum	0.10	0.75	2.90	0.12	0.13	0.73	4.49	0.06	5.49	0.03▪
Philodromus rufus	nt	nt	nt	nt	4.61	0.06	1.62	0.23	1.50	0.24
Platnickina tincta	nt	nt	7.60	0.018*	25.42	0.0008*	5.55	0.03▪	15.66	0.0014*
Styloctetor romanus	nt	nt	2.97	0.11	0.18	0.68	nt	nt	nt	nt
Theridion spp.	0.59	0.49	7.88	0.0082*	4.04	0.06	9.65	0.011*	11.45	0.0033*
Xysticus sp.	nt	nt	26.73	0.0004*	16.12	0.0006*	20.07	0.0006*	59.00	0.0001*

Table s4.4. Complete PERMANOVA table of the effect of ant exclusion on the spider assemblage from 2002 to 2009 (a-h) at the family level.

Source	df	SS	MS	Pseudo-F	*P* (perm)
(a) year 2002					
Treatment	1	416.44	416.44	1.67	0.13
Res	13	3243.50	249.50		
Total	14	3660.00			
(b) year 2003					
Treatment	1	471.78	471.78	1.76	0.11
Res	14	3749.30	267.81		
Total	15	4221.10			
(c) year 2004					
Treatment	1	292.54	292.54	1.13	0.36
Res	14	3620.10	258.58		
Total	15	3912.60			
(d) year 2005					
Treatment	1	810.60	810.60	3.13	0.0046
Res	14	3624.20	258.87		
Total	15	4434.80			
(e) year 2006					
Treatment	1	1497.20	1497.20	5.62	0.0002
Res	14	3730.30	266.45		
Total	15	5227.50			
(f) year 2007					
Treatment	1	482.73	482.73	2.82	0.0097
Res	14	2396.40	171.17		
Total	15	2879.10			
(g) year 2008					
Treatment	1	1016.90	1016.90	6.01	0.0008
Res	14	2369.20	169.23		
Total	15	3386.10			
(h) year 2009					
Treatment	1	1746.20	1746.20	9.86	0.0002
Res	16	2833.00	177.06		
Total	17	4579.20			

Table s4.5. Summary of the ANOVA table of the effect of ant exclusion on the most abundant spider families from 2005 to 2009 (▪: $P < 0.05$; *: significant after FDR correction; nt: not tested).

Year	2005		2006		2007		2008		2009	
Family	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*	Pseudo-F	*P*
Araneidae	2.29	0.15	1.89	0.18	0.14	0.71	2.29	0.15	8.41	0.0092*
Clubionidae	8.71	0.01▪	7.51	0.015*	0.00	0.96	6.33	0.03▪	4.25	0.06
Dictynidae	nt	nt	4.72	0.04▪	0.80	0.38	1.31	0.30	0.03	0.87
Gnaphosidae	nt	nt	nt	nt	nt	nt	8.14	0.014*	0.49	0.50
Linyphiidae	nt	nt	0.54	0.47	2.00	0.18	nt	nt	nt	nt
Miturgidae	nt	nt	4.91	0.06	0.45	0.50	0.43	0.57	14.47	0.0023*
Oxyopidae	nt	nt	nt	nt	nt	nt	nt	nt	8.73	0.011*
Philodromidae	4.19	0.06	4.99	0.04▪	1.33	0.27	0.91	0.35	3.68	0.07
Salticidae	0.33	0.57	2.16	0.17	2.55	0.13	12.66	0.0033*	0.74	0.41
Theridiidae	0.19	0.69	25.08	0.0005*	12.72	0.0025*	11.10	0.0046*	25.22	0.0002*
Thomisidae	nt	nt	16.31	0.0018*	14.97	0.0017*	11.23	0.0033*	54.09	0.0001*

Fig. s4.1. Monthly abundance of the most common spider species in the grove, in control (Ants) and banded (No ants) trees, adding together the data from the 8 years of study. Species are ordered by decreasing abundance. Means ± SE are shown.

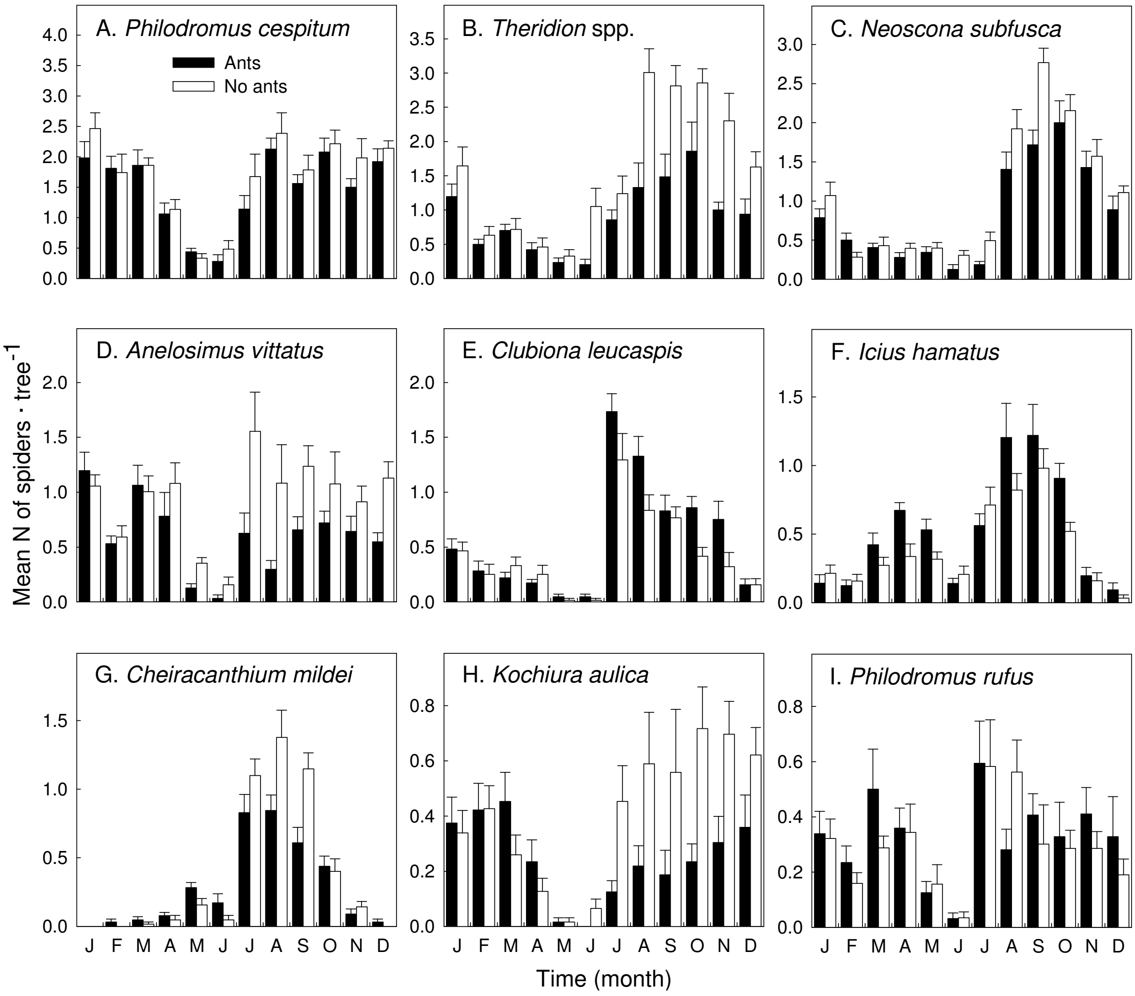
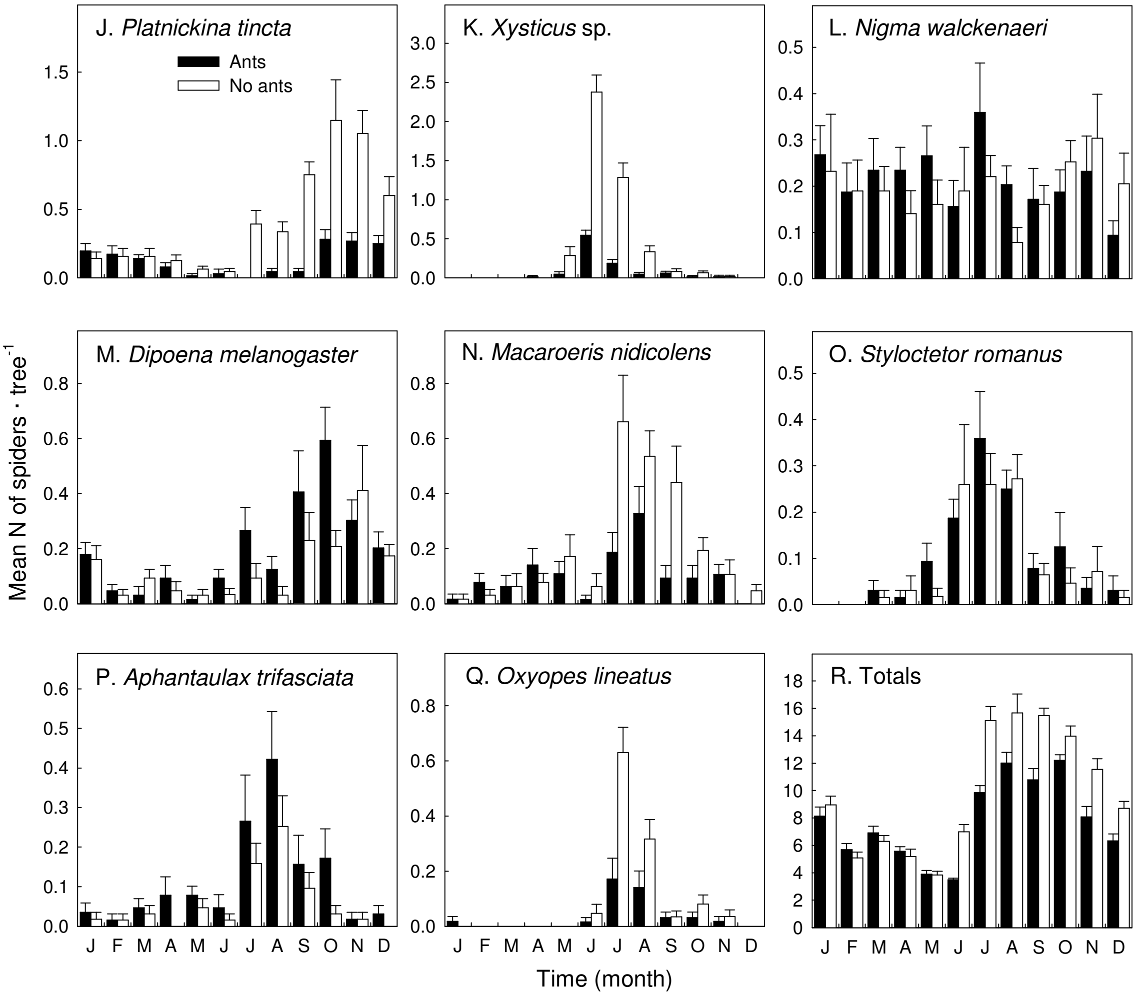


Fig. s4.1 (continued). Monthly abundance of the most common spider species in the grove, in control (Ants) and banded (No ants) trees, adding together the data from the 8 years of study. Species are ordered by decreasing abundance. Means ± SE are shown.



5

Trophic ecology of canopy- and ground-living spiders in a Mediterranean agroecosystem: a stable isotope analysis


L. Mestre

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ABSTRACT

Spiders are dominant predators that consume a great variety of prey and reduce herbivore numbers in terrestrial habitats. Although the feeding habits of certain species are well known, the trophic structure of spider assemblages still needs to be investigated. The analysis of stable isotopes is suitable for characterizing trophic relationships between organisms because it tracks the energy flow in food webs and indicates the average number of trophic transfers between a given species and the base of the web. Using this technique, we studied the trophic groups of spiders and their links within the arthropod food web of a Mediterranean organic citrus grove. We assessed the trophic positions of the 25 most common spider species relative to other arthropod predators and potential prey in the 4 seasons of the year, both in the canopy and on the ground. The analyses showed great seasonal variation in the isotopic signatures of some arthropod species, as well as the existence of various trophic groups and a wide range of trophic levels in spider species, even in those belonging to the same family. Differences in $\delta^{15}N$ between spiders and the most abundant prey in the grove usually spanned two trophic levels or more. Our findings indicate a widespread occurrence of trophic-level omnivory and intraguild predation in the food web and caution against using spider families or guilds as surrogates for testing ecological hypotheses.

Keywords: agroecosystem; ants; food web; intraguild predation; trophic niche; $\delta^{15}N$; $\delta^{13}C$.

Introduction

In terrestrial habitats, spiders are dominant generalist predators that consume a great variety of prey and reduce herbivore numbers (Riechert & Lawrence 1997; Hooks et al. 2006). In recent years, manipulative experiments have revealed the complexity of the interactions that take place in terrestrial arthropod communities and the impact of intraguild predation and competition on the strength of trophic cascades (Cardinale et al. 2003; Finke & Denno 2005). Ecologists have also begun to disentangle the trophic links that structure food webs but data obtained with direct observations or captive feeding studies are limited in scope (Greenstone 1999; Tiunov 2007).

The analysis of stable nitrogen and carbon isotopes (expressed as $\delta^{15}N$ and $\delta^{13}C$, respectively) of individuals is a useful tool for characterizing trophic relationships between organisms (Vander Zanden & Rasmussen 2001; Boecklen et al. 2011). Stable isotopes undergo a fractionation process by which $\delta^{15}N$ and $\delta^{13}C$ are enriched in the heavy isotope with increasing trophic levels (trophic enrichment). The carbon isotope fractionation with each trophic transfer is very small and largely retrieves the isotopic signal of the food source, so it is used to track the energy flow in food webs. By contrast, the enrichment of $\delta^{15}N$ is considerable and is useful for estimating the trophic levels of individuals (Gannes et al. 1997; Post 2002). Therefore, the isotopic signature of a species can be interpreted as the average number of trophic transfers between the species and the base of the food web (Ponsard & Arditi 2000). This approach has been successfully applied to the study of the trophic ecology of vertebrates for a long time (Hobson et al. 1994; Jennings et al. 2002), and it is increasingly being used in arthropod communities both in natural (Collier et al. 2002; Kupfer et al. 2006) and in agricultural settings, where the biocontrol potential of spiders has been assessed (McNabb et al. 2001; Wise et al. 2006). However, comprehensive studies on the trophic structure of spider communities are largely lacking (but see Sanders & Platner 2007).

We performed a stable isotope analysis to determine the trophic positions of the most common spider species of a Mediterranean organic citrus grove. Specifically, we wanted (1) to assess the trophic positions of the 25 most common spider species in the food web relative to other predators and potential prey. (2) As the strong seasonality intrinsic to the Mediterranean climate should influence the diverse spider community and the structure of the whole food web, we analysed the trophic levels of important spider species and other arthropods at different times of the year. (3) Since ants play a key role in the community and particularly affect insect and spider abundances in the trees in the studied grove (Piñol et al. 2009, 2012a), we also tested whether their presence changed the diet of spiders. This work is an exploration of the trophic groups of spiders and their links within the arthropod food web.

Material and methods

Study site

The grove is located at La Selva del Camp (Catalonia, NE Spain; 41º 13' 07″N, 1º 8' 35″E), an area with a Mediterranean climate. There are ca. 300 Clementine trees (*Citrus clementina* var. *clemenules*) grafted on the hybrid rootstock Carrizo citrange (*Poncirus trifoliata* (L.) Raf. x *Citrus sinensis* (L.) Osb.); these are watered during dry periods. Grasses and other weeds form a permanent ground cover, which is mowed a few times every year.

Sampling methodology

From February to November 2009 arthropods were collected once a month from the canopies of 3 rows of 23 trees each, using beating trays. Canopy-foraging ants (mainly *Lasius grandis* and *Formica rufibarbis*) were excluded from 9 of these trees by a sticky band that prevented them climbing up to the canopies. The band consisted of a polybutene-based sticky ring wrapped around a plastic film attached to a padding material that encircled the trunk (Samways & Tate 1985). Ground arthropods were sampled 3 times (February, June, September) with pairs of pitfall traps (7 cm depth and 5.5 cm diameter) on opposite sides of all the trees. The traps were opened, filled with water mixed with detergent and left open for 48 hours. Some ground spider species were collected with corrugated cardboard bands wrapped around the base of the tree trunks. The bands were left in place for a few days in September to let spiders use them as shelters. All the arthropods were preserved in 70% ethanol right after collection.

In the laboratory, arthropods were identified to species, and the most abundant ones were selected for stable isotope analysis: spiders (15 species from the canopies and 10 from the ground; Table 5.1), ants from the ground (4 species: *Messor structor*, *Pheidole pallidula*, *L. grandis*, *F. rufibarbis*) and from the canopies (*L. grandis*, *F. rufibarbis*), other predators from the canopies (the earwig *Forficula pubescens* and the heteropterans *Cardiastethus fasciiventris* [Anthocoridae] and *Pilophorus perplexus* [Miridae]), primary consumers from the canopies (the aphid *Aphis spiraecola*, the coccid *Ceroplastes sinensis*, and the psocopterans *Ectopsocus briggsi* and *Trichopsocus clarus*) and detritivores from the ground (the isopod *Armadillidium vulgare* and one sample of ~100 individuals of unidentified epidaphic collembolans from several pitfall traps; see Table s5.1 for a detailed account).

When possible, individuals of a given species were taken from different months to test for temporal changes in isotope ratios (Table 5.2). Of the spiders, only *Philodromus cespitum* (Philodromidae) was abundant during several months, whereas the other species were abundant only on 1 or 2 sampling dates. Due to phenology, individuals of the spiders *Clubiona leucaspis* (Clubionidae), *Icius hamatus* (Salticidae), *Philodromus rufus* (Philodromidae), and *Platnickina tincta* (Theridiidae) from different months belonged to different life stages (Table 5.1). All the individuals from the other arthropod species belonged to either immature or adult stages, apart from the aphids *A. spiraecola* and *C. sinensis*.

Previous research in the grove has shown that abundances of the spiders *Aphantaulax trifasciata* (Gnaphosidae) and *I. hamatus* (Salticidae) increase in ant-frequented trees, whereas those of *P. tincta*, *Theridion* spp. (Theridiidae) and *Xysticus* sp. (Thomisidae) decrease (Mestre et al. unpublished). We thus chose individuals from ant-excluded and control trees to search for potential ant-driven changes in the trophic levels or foraging strategies, and thereby the isotope ratios, of these spiders. Individuals of the other arthropod species were retrieved from either control or ant-excluded trees (except *A. spiraecola*).

Stable isotope analyses

About 0.2 mg of dry sample material was loaded into tin capsules, combusted under O_2 excess in an elemental analyser (EuroVector EA, Hekatech, Wegberg, Germany) and converted to CO_2, N_2 and H_2O. After removing H_2O with a water trap, the combustion products were flushed in a helium stream through the dilutor box into the Isotope Ratio Mass Spectrometer (ISOPRIME, Elementar, Hanau, Germany), which was coupled via a variable open-split interface to the elemental analyser. Samples were standardized to IAEA-N2 and IAEA-CH-6 (International Atomic Energy Agency, Vienna, Austria) and an IVA protein standard with two distinct isotopic signatures (33802155). Repeated measurement precision was 0.15‰ and 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. Carbon and nitrogen isotope ratios are reported relative to VPDBee and atmospheric air, respectively, and expressed as δ-notation in [‰]:

$$\delta^{A}X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \cdot 1000$$

where R_{sample} and $R_{standard}$ are the ratios of the heavier isotope to the lighter isotope from the sample and the standard, respectively, and X is the element (C or N) considered.

For most species, we had to combine individuals into 1 sample, but for large spiders (*Olios argelasius, Dysdera crocata*), *F. pubescens* and *A. vulgare* we only used the anterior part of the body.

Statistical analyses

We analysed the bivariate ($\delta^{15}N$ and $\delta^{13}C$) isotopic signature of individuals with permutational multivariate ANOVAs (PERMANOVAs), using the Euclidean distance. Sample sizes were at least N=5, usually N=6 or higher. We run a one-way analysis to test for differences between months for the above-mentioned species. Because some species were collected from more than 2 months, if the main analysis was significant we run *a posteriori* pairwise comparisons to test which months had different isotope ratios. We then ran a two-way PERMANOVA to compare the isotope ratios of spider species that occurred in the canopies of both ant-excluded trees and control trees between treatments, with the factors "species" and "ant exclusion" (exclusion, control), and the interaction.

Our main aim was to compare the isotope ratios of spiders to classify them into trophic groups. Because the spiders and insects were collected in different months, we considered 4 different time periods (February-April, May-June, August-September, October-November) and we tested for differences between the spiders' isotope ratios from each period. If these analyses were significant, we conducted *a posteriori* pairwise comparisons as described above to find the differences between species. We did not conduct statistical analyses of the isotope ratios of the other arthropods because we used them solely as a framework for assessing the relative trophic positions of spiders within the food web.

We adjusted the level of significance of the *a posteriori* tests by setting a conservative threshold of $P < 0.01$. Analyses were run with the software PERMANOVA+ for PRIMER v.6 (Anderson et al. 2008). Results are shown as the mean ± SE

Results

Ant exclusion did not affect the isotope ratios of spiders (Table 5.3), so we pooled individuals from both treatments for the between-species comparisons (see Table s5.2 for the monthly abundances of all species).

Isotope ratios changed over time for some predators (*P. cespitum*, *C. fasciiventris*) and herbivores (*E. briggsi*; Fig. 5.1, Table 5.2), thus endorsing the decision to compare only the isotope ratios in spiders from the same time period. The isotope ratios of *E. briggsi* varied between months with no apparent pattern (see pairwise comparisons in Table s5.3), but the ratios of *T. clarus*, *F. pubescens*, *P. perplexus*, *A. vulgare* and ants did not vary over time ($P >$ 0.14). The spiders *C. leucaspis* and *I. hamatus* had different isotope ratios depending on their life stage, although these differences were confounded with month.

In the February-April period, the isotope ratios of the 3 most abundant spiders (*C. leucaspis*, *P. cespitum* and *P. rufus*) were not significantly different (pseudo-$F_{2,32}$ = 0.81, P = 0.88; Fig. 5.2A). The analyses of May-June showed distinct trophic groups of spiders differing considerably in δ^{15}N values (pseudo-$F_{7,42}$ = 18.69, P = 0.0001; Fig. 5.2B). Canopy spiders had very similar isotopic signatures, except for *I. hamatus*, which was isotopically close to ground spiders. Differences in δ^{15}N were also high in ground spiders, even when they belonged to overlapping trophic groups. For instance, *Pardosa* spiders were separated by at least 4‰ δ^{15}N from *Pelecopsis* spiders, which were the ones with the highest δ^{15}N values.

There were great differences in the isotope ratios of the spiders from August-September (pseudo-$F_{13,109}$ = 18.69, P = 0.0001; Fig. 5.2C). All the ground spiders had similar isotopic signatures, except for *Marilynia bicolor*, which had lower δ^{15}N values. There was a high degree of overlapping between the trophic groups of canopy spiders, although *A. trifasciata*, *P. cespitum* and *P. tincta* tended to have lower δ^{15}N ratios. In general, canopy spiders had lower δ^{13}C ratios than ground spiders, but the ratios of *Dipoena melanogaster* were indistinguishable from those of ground spiders. In October-November three trophic groups of canopy spiders could be identified, their main difference being the δ^{15}N ratios (pseudo-$F_{6,48}$ = 6.17, P = 0.0001; Fig. 5.2D; see Tables s5.4-6 for pairwise comparisons). *P. cespitum* and *Neoscona subfusca* had a lower trophic level than *Theridion* spp. and *O. argelasius*, with *Nigma walckenaeri* and *P. tincta* falling between.

Whereas in February-March the primary consumers (psocopterans) had different isotope ratios, in May-June all the primary consumers in the canopy (*A. spiraecola*, *C. sinensis* and *E. briggsi*) were similar in this respect (Fig. 5.3, Table s5.1). The ants *L. grandis* and *F. rufibarbis* were collected from the canopy and the ground and had similar isotopic values in all the seasons. In May-June and in August-September, the earwig *P. pubescens* and the heteropteran *P. perplexus* had similar δ^{15}N values to these ants but usually had lower δ^{13}C values. The ground ant *M. structor* was the ant with the lowest δ^{15}N values.

Discussion

We found great temporal variation in the stable isotope ratios in both the predators and the primary consumers. The presence of canopy-foraging ants did not affect the isotope ratios of spiders. In 3 of the 4 time periods considered, analyses assigned spider species to different trophic groups, but there was considerable overlapping between them. Our results show that different spider species belong to different trophic levels within the food web, even in cases of species from the same family. These results from stable isotope analysis confirm observations that trophic-level omnivory and intraguild predation are widespread.

The temporal shifts in the isotope ratios of the philodromid spider *P. cespitum* and the anthocorid bug *C. fasciiventris*) probably followed fluctuations in prey availability, leading to changes in their diet. For *C. leucaspis* and *I. hamatus*, however, life stage could also play a role in these changes (Oelbermann & Scheu 2002). The isotope ratios of the psocopteran *E. briggsi* changed notably between months, although the $\delta^{15}N$ always remained one of the lowest values recorded, consistent with the diet of vegetal material (algae, fungus, etc. scraped from surfaces) of plant-dwelling psocopterans (Resh & Cardé 2009). In contrast, the isotope ratios of spiders were not significantly different in ant-excluded and ant-frequented trees. Thus, although ants foraging in the canopies affect the abundance of some spiders and insects (Mestre et al. unpublished), their activity did not modify the feeding habits of spiders or, at least, this was not reflected in their isotopic signatures.

In February-April there were only 3 spider species in the canopies common enough to be analysed; they belonged to a single trophic group and had a trophic level between psocopterans and ants. In May-June there were also only 3 abundant spiders in the canopies: whereas *Xysticus* sp. and *B. chalybeius* had $\delta^{15}N$ values just above those of the primary consumers, *I. hamatus* was more than 4‰ higher in $\delta^{15}N$ than the former spiders and had a similar isotopic signature to that of canopy-foraging ants, which are its preferred prey (Pekár et al. 2012). We found a similar result for the polyphagous ground spider *D. crocata*, which is able to overcome the defensive cuticle of isopods (Pollard et al. 1995) and was 4.5‰ enriched in $\delta^{15}N$ above the isopod *A. vulgare*. Lycosids (*P. proxima* and *P. hortensis*) were isotopically indistinguishable from each other, and so were linyphiids (*P. parallela* and *P. bucephala*). These spiders usually feed on collembolans (McNabb et al. 2001; Agustí et al. 2003) and the isotopic position of these spiders denotes that collembolans represent a large proportion of their diet in this grove. *Pelecopsis* spiders, however, had much higher $\delta^{15}N$ ratios than *Pardosa* spiders, suggesting that linyphiids may be preying on each other, or on species we did not analyse.

August-September was the period with the greatest diversity of arthropods. In the canopies, all the spiders and predatory insects were at least 7.5‰ more enriched in δ^{15}N than psocopterans, which were the most abundant primary consumers in that period (Table s5.2). *I. hamatus* had lower δ^{13}C than in spring, indicating that it may consume prey other than ants. In contrast, the ant-specialist *D. melanogaster* (Umeda et al. 1996) was enriched in δ^{13}C compared to other canopy spiders and had similar isotope ratios to *F. rufibarbis*. The ant-specialist ground spiders *E. episinoides* and *Z. styliferum* (Porter & Eastmond 1982; Pekár et al. in press) had the same isotopic signatures as *D. melanogaster* and were about 4‰ higher in δ^{15}N than *M. structor*. Other ground spiders had also similar δ^{13}C values and higher δ^{15}N values with respect to ants, so they were possibly preying on them or on their predators. The higher δ^{13}C values of arthropods depending on a ground energy source, may be caused by drought-induced plant stress, which is known to increase the δ^{13}C content in their tissues (Farquhar et al. 2007). In October-November some spiders seemed to be disconnected from the flux of energy coming from psocopterans, and thus carbon could have been coming from a source we had not considered.

Acknowledging that seasonality could be the cause of some of the reported patterns, stable isotope analysis identified several trophic groups in the spider assemblage. This classification based on isotopic signatures was independent of taxonomy most of the time, because species from the same family sometimes belonged to different trophic groups. Among salticids, *I. hamatus* had a higher trophic level than *B. chalybeius*. *P. tincta*, *Theridion* spp., *E. episinoides* and *D. melanogaster* (all theridiids) also had contrasting signatures, like the gnaphosids *A. trifasciata* and *Nomisia exornata*. As expected, ground spiders were isotopically distinct from canopy spiders, but some exceptions to this general result were canopy species (*I. hamatus*, *D. melanogaster*) feeding on a ground-based source (ants). Even within a given time period, there was a wide range of trophic levels in spiders: in May-June the δ^{15}N values between species with the highest level (*P. parallela*) and those with lowest level (*B. chalybeius*) spanned more than 8‰ difference, and about 4 ‰ in August-September (*N. exornata* vs. *M. bicolor*). These findings reflect the existence of a high trophic diversity in spiders, probably due to the great variety of lifestyles and foraging strategies within this group.

Stable isotope data must always be interpreted with great caution because fractionation factors —on which estimates of trophic positions rely— are unknown for most species. Since fractionation depends on both consumer species and the organisms they eat (Vander Zanden & Rasmussen 2001; Vanderklift & Ponsard 2003), some field studies dealing with few species include laboratory tests to determine fractionation factors. In spiders, however, only the values of *Pardosa* feeding on collembolans and aphids have been calculated (Oelbermann & Scheu 2002; Wise et al. 2006). Because this procedure becomes impractical when dealing with more species (Schneider et al. 2004; Ikeda et al. 2010), researchers rely on reviews of published studies that calculate average fractionation (Post 2002; Vanderklift & Ponsard 2003). McCutchan et al. (2003) reported isotope shifts for predators of invertebrates: 1.4‰ for $\delta^{15}N$ and 0.5‰ for $\delta^{13}C$. Taking these estimates, the separation between the trophic groups of spiders in the grove ranged over 2-3 levels. Some species with known feeding habits (linyphiids, *D. crocata*, *E. episinoides*, *Z. styliferum*) were more than two trophic levels above their usual prey. These patterns suggest that intraguild predation and trophic-level omnivory play a key role in the structuring of the food web. However, it is increasingly recognised that fractionation varies greatly, depending on many factors, such as feeding rate, nutritional status, life-history level and trophic position (Tiunov 2007; Boecken et al. 2011). Another limitation is that stable isotopes can only discriminate between sources with contrasting isotopic signatures, which can lead to incorrect assignations of a source to a consumer. Furthermore, the delays between consumption and the incorporation of the isotopic signature of the diet are poorly understood (McCutchan et al. 2003), and they could explain the seeming disconnection between spiders and primary consumers in October-November.

In summary, stable isotope analysis revealed the existence of different trophic levels in the spider community and provided insights into the structure of the food web. The recurrent large differences between the $\delta^{15}N$ contents of some spider species and those of their prey and primary consumers indicated the prevalence of intraguild predation and trophic-level omnivory in spiders. $\delta^{13}C$ values showed that the canopy and the ground food webs were basically disconnected, except in the case of a few ant-eating canopy spiders. Significantly, we found great trophic differences between spider species belonging to the same family, providing evidence against the use of families or guilds as surrogates for testing ecological hypotheses.

ACKNOWLEDGMENTS

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Tables

Table 5.1. Complete list of spider species selected for stable isotope analysis. $\delta^{15}N$ and $\delta^{13}C$ values are given.

Family	Species	Location	Month	Stage	Treatment	N	$\delta^{15}N$		$\delta^{13}C$	
							mean	SE	mean	SE
Araneidae	*Neoscona subfusca* (C. L. Koch, 1837)	canopy	October	young	control	6	9.1	0.6	-23.5	0.4
Clubionidae	*Clubiona leucaspis* Simon, 1932	canopy	March	adult	control	6	9.4	0.5	-23.7	0.4
			September	young	control	10	11.7	0.3	-25.6	0.3
					exclusion	6	12.4	0.3	-24.9	0.3
Dictynidae	*Marilynia bicolor* (Simon, 1870)	ground	September	young	---	6	9.6	0.4	-22.3	0.7
	Nigma walckenaeri (Roewer, 1951)	canopy	November	adult	control	5	10.2	0.4	-24.1	0.2
Dysderidae	*Dysdera crocata* C. L. Koch, 1838	ground	June	adult	---	6	14.5	0.3	-22.6	0.8
Gnaphosidae	*Aphantaulax trifasciata* (O. P.-Cambridge, 1872)	canopy	August	young	control	6	10.1	0.4	-24.2	0.1
					exclusion	5	11.3	0.5	-24.2	0.2
	Nomisia exornata (C. L. Koch, 1839)	ground	September	young	---	6	13.9	0.3	-21.9	0.6
Linyphiidae	*Pelecopsis bucephala* (O. P.-Cambridge, 1875)	ground	June	adult	---	5	16.8	1.6	-24.4	0.4
	Pelecopsis parallela (Wider, 1834)	ground	June	adult	---	6	15.8	1.0	-24.2	0.1
Lycosidae	*Pardosa hortensis* (Thorell, 1872)	ground	June	adult	---	6	11.8	0.5	-24.4	0.3
	Pardosa proxima (C. L. Koch, 1847)	ground	June	adult	---	6	11.4	0.3	-24.6	0.1
Miturgidae	*Cheiracanthium mildei* L. Koch, 1864	canopy	September	young	exclusion	6	12.5	0.3	-24.5	0.2
Oxyopidae	*Oxyopes lineatus* Latreille, 1806	canopy	August	young	control	6	12.1	0.6	-23.8	0.7
Philodromidae	*Philodromus cespitum* (Walckenaer, 1802)	canopy	February	young	control	6	9.2	0.4	-23.9	0.3
			March			6	6.7	0.7	-24.2	0.3
			April			6	8.7	0.6	-23.5	0.2
			August			5	10.5	0.7	-23.6	0.2
			September			10	10.2	0.4	-24.0	0.3
			October			6	9.4	0.7	-22.5	0.2
			November			6	9.1	0.2	-23.7	0.4
	Philodromus rufus Walckenaer, 1826	canopy	March	young	control	6	8.5	0.8	-23.8	0.2
			April	adult		5	8.9	0.8	-24.0	0.1

Table 5.1 (continued). Complete list of spider species selected for stable isotope analysis. $\delta^{15}N$ and $\delta^{13}C$ values are given.

Family	Species	Location	Month	Stage	Treatment	N	$\delta^{15}N$		$\delta^{13}C$	
							mean	SE	mean	SE
Salticidae	*Ballus chalybeius* (Walckenaer, 1802)	canopy	June	adult	control	5	8.4	0.4	-24.0	0.3
	Icius hamatus (C. L. Koch, 1846)	canopy	May	adult	control	6	12.5	0.9	-23.0	0.1
			September	young	control	10	11.8	0.3	-24.4	0.2
					exclusion	5	11.1	1.0	-23.7	0.2
Sparassidae	*Olios argelasius* (Walckenaer, 1805)	canopy	October	adult	control	5	12.0	0.5	-24.4	0.4
Theridiidae	*Dipoena melanogaster* (C. L. Koch, 1837)	canopy	September	young	control	10	12.4	0.3	-22.7	0.4
			October			5	13.2	0.3	-22.7	0.6
	Euryopis episinoides (Walckenaer, 1847)	ground	September	young	---	6	11.8	0.5	-22.3	0.3
	Platnickina tincta (Walckenaer, 1802)	canopy	September	adult	exclusion	6	9.7	0.5	-24.0	0.2
			October	young	control	5	10.6	0.7	-24.7	0.6
					exclusion	5	8.0	1.4	-24.5	0.6
	Theridion spp. Walckenaer, 1805	canopy	September	young	control	10	11.9	0.3	-24.6	0.2
			October		control	5	12.0	0.5	-24.4	0.5
					exclusion	6	11.6	0.4	-24.6	0.3
Thomisidae	*Xysticus* sp. C. L. Koch, 1835	canopy	June	young	control	5	8.9	0.3	-23.9	0.3
					exclusion	6	8.5	0.6	-24.1	0.1
Titanoecidae	*Nurscia albomaculata* (Lucas, 1846)	ground	September	young	---	6	13.4	0.8	-20.7	0.9
Zodariidae	*Zodarion styliferum* (Simon, 1870)	ground	September	young	---	5	12.0	0.2	-22.0	0.3

Table 5.2. ANOVA table of the effect of month on isotope ratios (*: $P < 0.01$).

Species	df	Pseudo-F	*P* (perm)
Spiders			
Clubiona leucaspis	1,14	18.51	0.0002*
Dipoena melanogaster	1,13	0.64	0.55
Icius hamatus	1,14	6.37	0.0036*
Philodromus cespitum	6,44	5.00	0.0002*
Philodromus rufus	1,9	0.17	0.65
Platnickina tincta	1,9	1.44	0.29
Theridion spp.	1,13	0.19	0.80
Ants			
Formica rufibarbis	2,16	0.51	0.66
Lasius grandis	2,15	0.95	0.42
Messor structor	1,10	1.74	0.22
Pheidole pallidula	1,10	1.61	0.25
Other arthropods			
Ectopsocus briggsi (psocopteran)	4,17	5.15	0.0029*
Trichopsocus clarus (psocopteran)	1,6	0.07	0.88
Cardiastethus fasciiventris (heteropteran)	2,14	16.40	0.0001*
Pilophorus perplexus (heteropteran)	1,9	2.12	0.14
Forficula pubescens (earwig)	1,10	2.28	0.15
Armadillidium vulgare (isopod)	1,10	1.61	0.24

Table 5.3. ANOVA table of the effect ant exclusion on isotope ratios of spiders.

Factor	df	SS	MS	Pseudo-F	*P* (perm)
Species	5	133.88	26.78	6.93	0.0001
Ant exclusion	1	1.91	1.91	0.50	0.60
Species x Ant exclusion	5	15.58	3.12	0.81	0.59
Residual	90	347.51	3.86		

Figures

Fig. 5.1. Monthly variation of isotope ratios of *Philodromus cespitum* (A) and the insect species *Ectopsocus briggsi* and *Cardiastethus fasciiventris* (B) found in the tree canopies. Means ± SE are shown. Numbers indicate months.

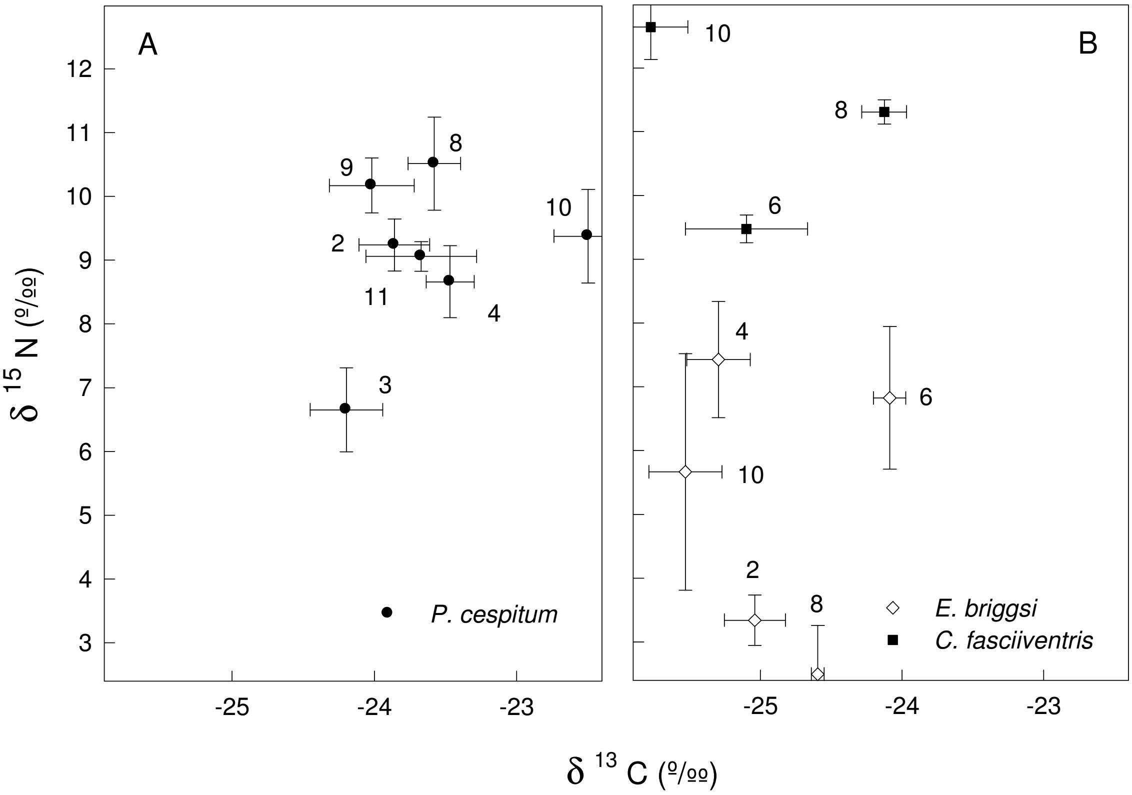


Fig. 5.2. Isotope ratios of spiders sampled at 4 different periods of the year 2009 (A-D). Means ± SE are shown. Different superscript letters indicate statistically significant differences between species from each time period, delimiting trophic groups. For clarity, most groups are encircled. Codes: Atri (*Aphantaulax trifasciata*), Bch (*Ballus chalybeius*), Cle (*Clubiona leucaspis*), Cmi (*Cheiracanthium mildei*), Dcr (*Dysdera crocata*), Dme (*Dipoena melanogaster*), Eep (*Euryopis episinoides*), Iha (*Icius hamatus*), Mbi (*Marilynia bicolor*), Nal (*Nurscia albomaculata*), Nex (*Nomisia exornata*), Nsu (*Neoscona subfusca*), Nwa (*Nigma walckenaeri*), Oar (*Olios argelasius*), Oli (*Oxyopes lineatus*), Pbu (*Pelecopsis bucephala*), Pce (*Philodromus cespitum*), Pho (*Pardosa hortensis*), Ppa (*Pelecopsis parallela*), Ppr (*Pardosa proxima*), Pru (*Philodromus rufus*), Pti (*Platnickina tincta*), The (*Theridion* spp.), Xys (*Xysticus* sp.), Zst (*Zodarion styliferum*).

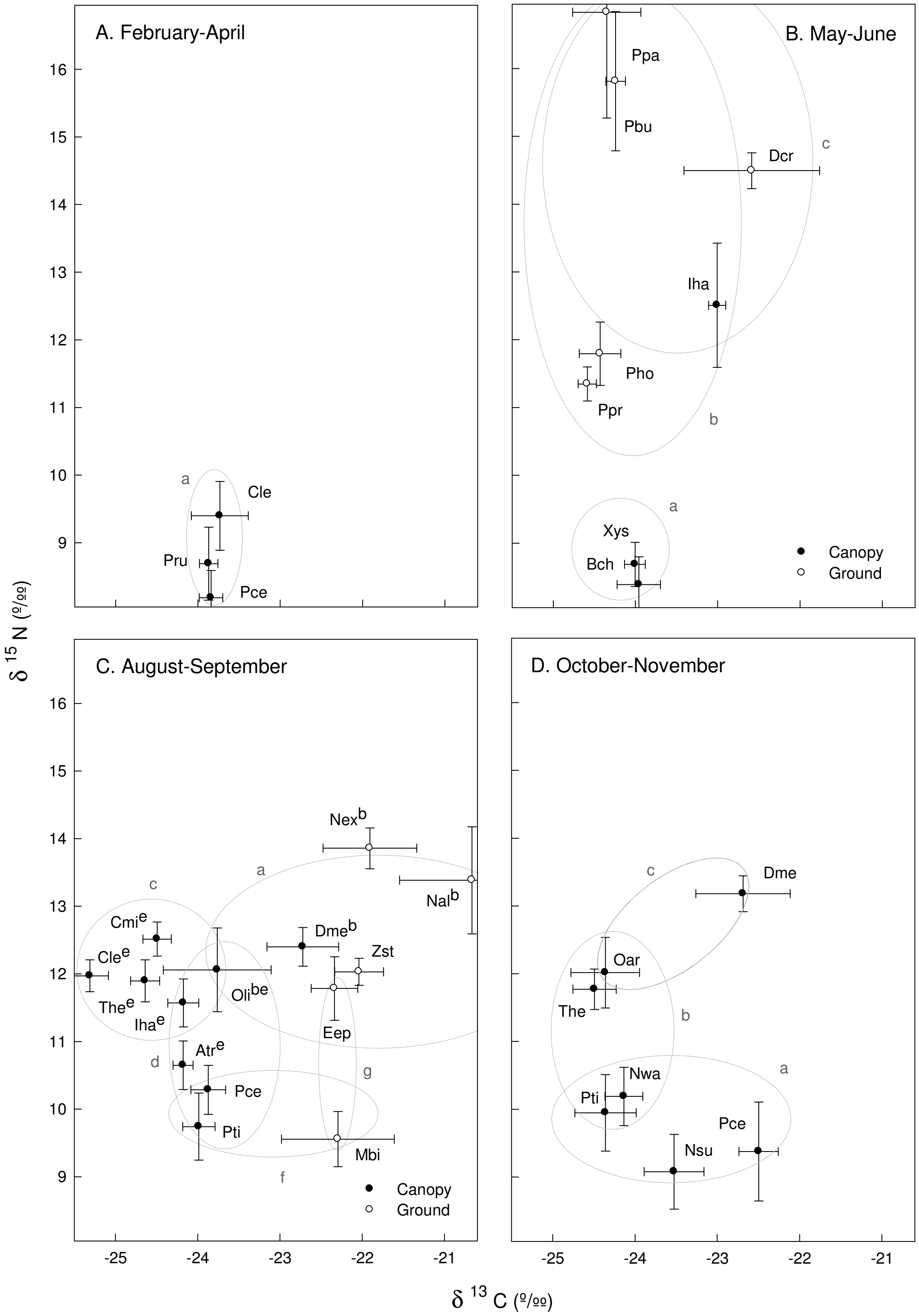
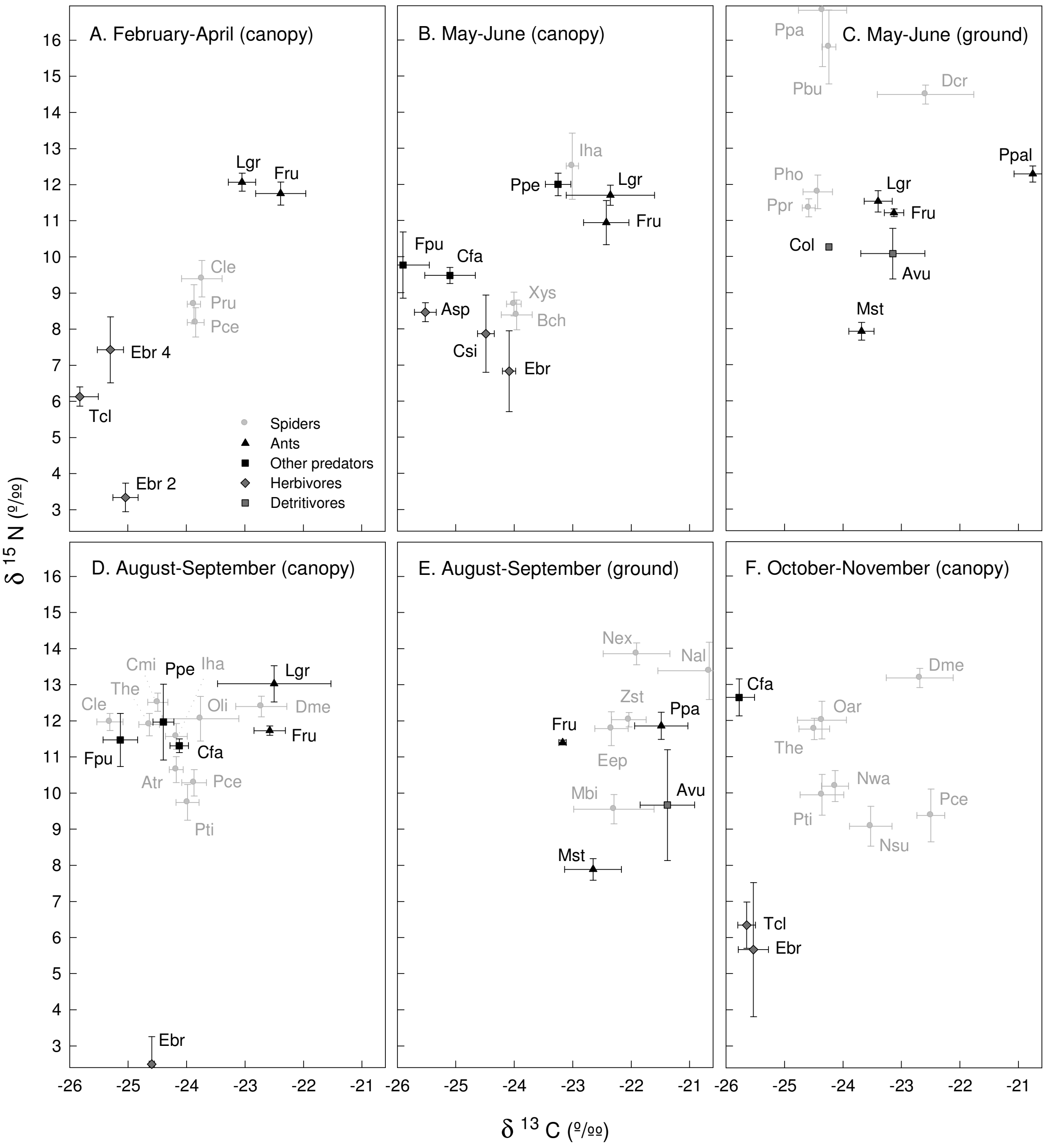

A. February-April
B. May-June
C. August-September
D. October-November
$\delta^{15}N$ (‰)
$\delta^{13}C$ (‰)
16
15
14
13
12
11
10
9
-25
-24
-23
-22
-21
a
Cle
Pru
Pce
Ppa
Pbu
Dcr
c
Iha
Pho
Ppr
b
a
Xys
Bch
Canopy
Ground
Nex^b
a
Nal^b
c
Cmi^e
Dme^b
Zst
Cle^e
The^e
Oli^be
Iha^e
Eep
Atr^e
d
g
Pce
Pti
Mbi
f
Canopy
Ground
c
Dme
Oar
The
b
a
Nwa
Pti
Pce
Nsu

Fig. 5.3. Isotope ratios of arthropods found in the tree canopies and on the ground at 4 different periods of the year 2009 (A-F). Means ± SE are shown. Codes: Asp (*Aphis spiraecola*), Avu (*Armadillidium vulgare*), Cfa (*Cardiastethus fasciiventris*), Col (Collembola), Csi (*Ceroplastes sinensis*), Ebr (*Ectopsocus briggsi*; numbers after codes indicate month), Fpu (*Forficula pubescens*), Fru (*Formica rufa*), Lgr (*Lasius grandis*), Mst (*Messor structor*), Ppal (*Pheidole pallidula*), Ppe (*Pilophorus perplexus*), Tcl (*Trichopsocus clarus*). The isotopic values of the spider species in Fig. 5.2. are shown here again to place the spiders in the context of the food web.


A. February-April (canopy)
B. May-June (canopy)
C. May-June (ground)
D. August-September (canopy)
E. August-September (ground)
F. October-November (canopy)
δ 15 N (º/ºº)
δ 13 C (º/ºº)
16
15
14
13
12
11
10
9
8
7
6
5
4
3
-26
-25
-24
-23
-22
-21
Spiders
Ants
Other predators
Herbivores
Detritivores
Lgr
Fru
Cle
Pru
Pce
Ebr 4
Tcl
Ebr 2
Iha
Ppe
Fpu
Cfa
Xys
Bch
Asp
Csi
Ebr
Ppa
Pbu
Dcr
Ppal
Pho
Ppr
Col
Avu
Mst
Cmi
The
Oli
Dme
Atr
Pti
Nex
Nal
Zst
Eep
Mbi
Oar
Nwa
Nsu

Supplementary material

Table s5.1. List of all arthropod species (except spiders) selected for stable isotope analysis. $\delta^{15}N$ and $\delta^{13}C$ values are given.

Group	Family	Species	Month	Stage	Ant exclusion	Location	N	$\delta^{15}N$		$\delta^{13}C$	
								mean	SE	mean	SE
Collembola			June	mix	---	ground	1	10.3	---	-24.2	---
Dermaptera	Forficulidae	*Forficula* (=*Guanchia*) *pubescens* (Gene, 1837)	June	young	control	canopy	6	11.5	0.7	-25.1	0.3
			September	adult			6	9.8	0.9	-25.9	0.5
Hemiptera	Anthocoridae	*Cardiastethus fasciiventris* (Garbiglietti, 1869)	June	adult	exclusion	canopy	5	9.5	0.2	-25.1	0.4
			August				5	11.3	0.2	-24.1	0.2
			October				5	12.6	0.5	-25.8	0.3
	Aphididae	*Aphis spiraecola* Patch, 1914	June	mix	mix	canopy	8	8.5	0.3	-25.5	0.2
	Coccidae	*Ceroplastes sinensis* Del Guercio, 1900	June	mix	control	canopy	6	7.9	1.1	-24.5	0.1
	Miridae	*Pilophorus perplexus* (Doublas & Scott, 1875)	June	adult	control	canopy	6	12.0	0.3	-23.3	0.2
			August				5	12.0	1.1	-24.4	0.2
Hymenoptera	Formicidae	*Lasius grandis* Forel, 1909	April	adult	control	canopy	7	12.1	0.3	-23.1	0.2
			June				7	11.7	0.3	-22.4	0.8
			September				2	13.0	0.5	-22.5	1.0
			June		---	ground	6	11.5	0.3	-23.4	0.2
		Formica rufibarbis Fabricius, 1793	April	adult	control	canopy	5	11.8	0.3	-22.4	0.4
			June				7	10.9	0.6	-22.4	0.4
			September				5	11.7	0.1	-22.6	0.3
			June		---	ground	6	11.2	0.1	-23.1	0.2
			September				6	11.4	0.1	-23.2	0.1

Table s5.1 (continued). List of all arthropod species (except spiders) selected for stable isotope analysis. δ^{15}N and δ^{13}C values are given.

Group	Family	Species	Month	Stage	Ant exclusion	Location	N	δ^{15}N		δ^{13}C	
								mean	SE	mean	SE
Hymenoptera	Formicidae	*Messor structor* (Latreille, 1798)	June	adult	---	ground	6	7.9	0.3	-23.7	0.2
			September				6	7.9	0.3	-22.7	0.5
		Pheidole pallidula (Nylander, 1849)	June	adult	---	ground	6	12.3	0.2	-20.8	0.3
			September				6	11.9	0.4	-21.5	0.5
Isopoda	Armadillidiidae	*Armadillidium vulgare* (Latreille, 1804)	June	young	---	ground	6	10.1	0.7	-23.2	0.6
			September				6	9.7	1.5	-21.4	0.5
Psocoptera	Ectopsocidae	*Ectopsocus briggsi* McLachlan, 1899	February	adult	control	canopy	5	3.3	0.4	-25.0	0.2
			April				5	7.4	0.9	-25.3	0.2
			June				4	6.8	1.1	-24.1	0.1
			August				4	2.5	0.8	-24.6	0.1
			October				4	5.7	1.9	-25.5	0.3
	Trichopsocidae	*Trichopsocus clarus* (Banks, 1908)	April	adult	control	canopy	4	6.1	0.4	-25.8	0.3
			October				4	6.3	0.6	-25.7	0.2

Table s5.2. Monthly abundances of the analysed arthropod species between February and November 2009. Numbers in bold indicate the months from which individuals were selected for stable isotope analysis.

Method	Group	Species	02-09	03-09	04-09	05-09	06-09	07-09	08-09	09-09	10-09	11-09	Total
Beating trays	Spiders	*Aphantaulax trifasciata*	1	1	3	3	1	13	**16**	7	5	2	52
		Ballus chalybeius	3	0	0	4	**6**	1	5	3	4	4	30
		Cheiracanthium mildei	0	0	2	9	3	19	21	**21**	11	0	86
		Clubiona leucaspis	7	**12**	7	1	30	78	46	**21**	21	15	238
		Dipoena melanogaster	1	4	5	2	2	7	2	**8**	**14**	5	50
		Icius hamatus	7	15	14	**16**	9	18	15	**21**	34	7	156
		Neoscona subfusca	10	5	6	10	1	5	16	42	**23**	27	145
		Nigma walckenaeri	6	5	3	6	5	15	2	5	6	**9**	62
		Olios argelasius	3	3	1	1	0	0	3	2	**5**	2	20
		Oxyopes lineatus	0	0	0	0	3	26	**13**	1	3	1	47
		Philodromus cespitum	**33**	**32**	**12**	2	1	7	**21**	**18**	**48**	**30**	204
		Philodromus rufus	2	**10**	**9**	1	1	11	0	3	5	11	53
		Platnickina tincta	15	7	8	3	2	13	2	**22**	**29**	27	128
		Theridion spp.	21	19	16	11	6	40	43	**45**	**65**	44	310
		Xysticus sp.	0	0	0	0	**69**	31	4	4	2	2	112
	Hemiptera	*Aphis spiraecola*	0	0	0	8	**46**	10	0	0	10	0	74
		Cardiastethus fasciiventris	4	9	9	6	**25**	31	**40**	36	**30**	30	220
		Ceroplastes sinensis	262	88	80	60	**101**	27	44	105	826	541	2134
		Pilophorus perplexus	0	0	0	31	**51**	57	**17**	15	2	0	173
	Ants	*Lasius grandis*	3	58	213	420	433	182	63	101	60	42	1575
		Formica rufibarbis	0	3	24	25	60	30	31	41	55	25	294
	Psocoptera	*Ectopsocus briggsi*	**243**	242	**316**	230	**366**	145	**55**	15	**129**	69	1810
		Trichopsocus clarus	17	49	**89**	35	42	90	24	103	**273**	427	1149

Table s5.2 (continued). Monthly abundances of the analysed arthropod species between February and November 2009. Numbers in bold indicate the months from which individuals were selected for stable isotope analysis.

Method	Group	Species	02-09	03-09	04-09	05-09	06-09	07-09	08-09	09-09	10-09	11-09	Total
Pitfall traps	Spiders	*Dysdera crocata*	0	---	---	---	**12**	---	---	17	---	---	29
		Pardosa hortensis	10	---	---	---	**21**	---	---	0	---	---	31
		Pardosa proxima	8	---	---	---	**121**	---	---	19	---	---	148
		Pelecopsis bucephala	0	---	---	---	**12**	---	---	1	---	---	13
		Pelecopsis parallela	1	---	---	---	**26**	---	---	3	---	---	30
		Zodarion styliferum	2	---	---	---	6	---	---	**8**	---	---	16
	Ants	*Lasius grandis*	1	---	---	---	**523**	---	---	8	---	---	531
		Formica rufibarbis	0	---	---	---	**421**	---	---	**143**	---	---	564
		Messor structor	2	---	---	---	**97**	---	---	**123**	---	---	220
		Pheidole pallidula	3	---	---	---	**872**	---	---	**1467**	---	---	2339
	Isopoda		3	---	---	---	**210**	---	---	**71**	---	---	284
Cardboard bands	Spiders	*Euryopis episinoides*	---	---	---	---	---	---	---	**89**	---	---	89
		Marilynia bicolor	---	---	---	---	---	---	---	**19**	---	---	19
		Nomisia exornata	---	---	---	---	---	---	---	**106**	---	---	106
		Nurscia albomaculata	---	---	---	---	---	---	---	**31**	---	---	31

Table s5.3. ANOVA table of the pairwise comparisons of isotope ratios between months in different spider and insect species (*: $P < 0.01$).

Months	df	Pseudo-F	*P* (perm)
(a) *Philodromus cespitum*			
February vs March	1,38	9.35	0.015
February vs April	1,38	0.84	0.40
February vs August	1,38	2.30	0.15
February vs September	1,38	1.48	0.24
February vs October	1,38	2.29	0.14
February vs November	1,38	0.16	0.87
March vs April	1,38	5.38	0.029
March vs August	1,38	14.30	0.0043*
March vs September	1,38	16.39	0.0009*
March vs October	1,38	9.45	0.009*
March vs November	1,38	8.61	0.0038*
April vs August	1,38	3.88	0.07
April vs September	1,38	3.84	0.052
April vs October	1,38	1.54	0.23
April vs November	1,38	0.36	0.72
August vs September	1,38	0.37	0.68
August vs October	1,38	2.08	0.17
August vs November	1,38	2.99	0.046
September vs October	1,38	3.64	0.048
September vs November	1,38	2.31	0.12
October vs November	1,38	1.86	0.19
(b) *Cardiastethus fasciiventris*			
June vs August	1,12	15.83	0.0071*
June vs October	1,12	17.89	0.0073*
August vs October	1,12	14.65	0.0076*
(c) *Ectopsocus briggsi*			
February vs April	1,17	13.75	0.0059*
February vs June	1,17	13.02	0.0092*
February vs August	1,17	1.52	0.25
February vs October	1,17	1.90	0.26
April vs June	1,17	2.23	0.18
April vs August	1,17	16.32	0.0065*
April vs October	1,17	0.92	0.42
June vs August	1,17	11.62	0.028
June vs October	1,17	2.18	0.20
August vs October	1,17	3.42	0.18

Table s5.4. ANOVA table of the pairwise comparisons of isotope ratios among spider species between May and June 2009 (*: $P < 0.01$).

Species	df	MS	Pseudo-F	*P* (perm)
Icius hamatus vs *Xysticus* sp.	1,42	60.58	23.35	0.0005*
Icius hamatus vs *Ballus chalybeius*	1,42	48.78	14.52	0.0031*
Icius hamatus vs *Dysdera crocata*	1,42	12.37	2.57	0.08
Icius hamatus vs *Pardosa hortensis*	1,42	7.60	2.24	0.14
Icius hamatus vs *Pardosa proxima*	1,42	11.50	4.14	0.045
Icius hamatus vs *Pelecopsis parallela*	1,42	37.34	6.49	0.035
Icius hamatus vs *Pelecopsis bucephala*	1,42	48.97	6.74	0.037
Xysticus sp. vs *Ballus chalybeius*	1,42	0.32	0.24	0.75
Xysticus sp. vs *Dysdera crocata*	1,42	138.78	57.87	0.0002*
Xysticus sp. vs *Pardosa hortensis*	1,42	38.22	26.20	0.0001*
Xysticus sp. vs *Pardosa proxima*	1,42	28.82	27.57	0.0001*
Xysticus sp. vs *Pelecopsis parallela*	1,42	197.38	65.11	0.0003*
Xysticus sp. vs *Pelecopsis bucephala*	1,42	194.87	55.03	0.0013*
Ballus chalybeius vs *Dysdera crocata*	1,42	106.84	35.23	0.0021*
Ballus chalybeius vs *Pardosa hortensis*	1,42	32.28	22.01	0.0039*
Ballus chalybeius vs *Pardosa proxima*	1,42	24.99	32.12	0.0019*
Ballus chalybeius vs *Pelecopsis parallela*	1,42	150.59	36.83	0.0043*
Ballus chalybeius vs *Pelecopsis bucephala*	1,42	158.72	29.74	0.0076*
Dysdera crocata vs *Pardosa hortensis*	1,42	32.06	10.34	0.0016*
Dysdera crocata vs *Pardosa proxima*	1,42	41.66	16.79	0.0022*
Dysdera crocata vs *Pelecopsis parallela*	1,42	13.43	2.46	0.083
Dysdera crocata vs *Pelecopsis bucephala*	1,42	20.30	2.94	0.076
Pardosa hortensis vs *Pardosa proxima*	1,42	0.67	0.62	0.45
Pardosa hortensis vs *Pelecopsis parallela*	1,42	48.53	11.98	0.012
Pardosa hortensis vs *Pelecopsis bucephala*	1,42	60.90	11.86	0.02
Pardosa proxima vs *Pelecopsis parallela*	1,42	60.14	17.53	0.012
Pardosa proxima vs *Pelecopsis bucephala*	1,42	72.31	16.59	0.0085*
Pelecopsis parallela vs *Pelecopsis bucephala*	1,42	2.50	0.31	0.60

Table s5.5. ANOVA table of the pairwise comparisons of isotope ratios among spider species between August and September 2009 (*: $P < 0.01$).

Species	df	MS	Pseudo-F	*P* (perm)
Philodromus cespitum vs *Clubiona leucaspis*	1,109	38.06	17.66	0.0001*
Philodromus cespitum vs *Icius hamatus*	1,109	13.09	5.17	0.017
Philodromus cespitum vs *Dipoena melanogaster*	1,109	34.76	12.99	0.0002*
Philodromus cespitum vs *Theridion* spp.	1,109	19.14	9.06	0.0018*
Philodromus cespitum vs *Cheiracanthium mildei*	1,109	22.96	10.94	0.0017*
Philodromus cespitum vs *Platnickina tincta*	1,109	1.32	0.55	0.55
Philodromus cespitum vs *Aphantaulax trifasciata*	1,109	1.44	0.65	0.49
Philodromus cespitum vs *Oxyopes lineatus*	1,109	11.84	4.00	0.037
Philodromus cespitum vs *Marilynia bicolor*	1,109	12.93	4.37	0.019
Philodromus cespitum vs *Euryopis episinoides*	1,109	19.71	8.12	0.0016*
Philodromus cespitum vs *Nomisia exornata*	1,109	71.24	27.30	0.0002*
Philodromus cespitum vs *Nurscia albomaculata*	1,109	85.23	20.47	0.0001*
Philodromus cespitum vs *Zodarion styliferum*	1,109	33.11	15.64	0.0002*
Clubiona leucaspis vs *Icius hamatus*	1,109	11.24	5.51	0.0026*
Clubiona leucaspis vs *Dipoena melanogaster*	1,109	42.40	20.41	0.0001*
Clubiona leucaspis vs *Theridion* spp.	1,109	2.82	1.84	0.17
Clubiona leucaspis vs *Cheiracanthium mildei*	1,109	4.21	2.99	0.055
Clubiona leucaspis vs *Platnickina tincta*	1,109	29.36	17.32	0.0001*
Clubiona leucaspis vs *Aphantaulax trifasciata*	1,109	19.75	11.99	0.0002*
Clubiona leucaspis vs *Oxyopes lineatus*	1,109	9.18	4.19	0.019
Clubiona leucaspis vs *Marilynia bicolor*	1,109	65.16	29.31	0.0001*
Clubiona leucaspis vs *Euryopis episinoides*	1,109	38.75	22.53	0.0001*
Clubiona leucaspis vs *Nomisia exornata*	1,109	66.11	34.90	0.0001*
Clubiona leucaspis vs *Nurscia albomaculata*	1,109	102.90	30.53	0.0001*
Clubiona leucaspis vs *Zodarion styliferum*	1,109	56.30	40.50	0.0002*
Icius hamatus vs *Dipoena melanogaster*	1,109	16.79	6.63	0.0023*
Icius hamatus vs *Theridion* spp.	1,109	1.93	0.98	0.39
Icius hamatus vs *Cheiracanthium mildei*	1,109	4.25	2.21	0.13
Icius hamatus vs *Platnickina tincta*	1,109	14.50	6.52	0.011
Icius hamatus vs *Aphantaulax trifasciata*	1,109	5.39	2.61	0.10
Icius hamatus vs *Oxyopes lineatus*	1,109	1.53	0.55	0.57
Icius hamatus vs *Marilynia bicolor*	1,109	32.56	11.71	0.0005*
Icius hamatus vs *Euryopis episinoides*	1,109	14.66	6.51	0.0014*
Icius hamatus vs *Nomisia exornata*	1,109	44.45	18.26	0.0001*
Icius hamatus vs *Nurscia albomaculata*	1,109	66.87	16.77	0.0001*
Icius hamatus vs *Zodarion styliferum*	1,109	28.28	14.63	0.0001*
Dipoena melanogaster vs *Theridion* spp.	1,109	19.62	9.83	0.0003*
Dipoena melanogaster vs *Cheiracanthium mildei*	1,109	11.82	6.07	0.0082*
Dipoena melanogaster vs *Platnickina tincta*	1,109	32.49	13.80	0.0003*
Dipoena melanogaster vs *Aphantaulax trifasciata*	1,109	27.16	12.83	0.0004*
Dipoena melanogaster vs *Oxyopes lineatus*	1,109	3.99	1.28	0.3094*
Dipoena melanogaster vs *Marilynia bicolor*	1,109	31.03	9.98	0.0001*
Dipoena melanogaster vs *Euryopis episinoides*	1,109	1.98	0.83	0.47
Dipoena melanogaster vs *Nomisia exornata*	1,109	10.46	3.96	0.043
Dipoena melanogaster vs *Nurscia albomaculata*	1,109	19.49	4.11	0.022
Dipoena melanogaster vs *Zodarion styliferum*	1,109	5.70	2.91	0.08
Theridion spp. vs *Cheiracanthium mildei*	1,109	1.50	1.48	0.24
Theridion spp. vs *Platnickina tincta*	1,109	19.04	13.34	0.0024*

Table s5.5 (continued). ANOVA table of the pairwise comparisons of isotope ratios among spider species between August and September 2009 (*: *P* < 0.01).

Species	df	MS	Pseudo-F	*P* (perm)
Theridion spp. vs *Aphantaulax trifasciata*	1,109	9.27	6.47	0.013
Theridion spp. vs *Oxyopes lineatus*	1,109	2.65	1.24	0.32
Theridion spp. vs *Marilynia bicolor*	1,109	41.17	18.87	0.0004*
Theridion spp. vs *Euryopis episinoides*	1,109	19.90	13.60	0.0002*
Theridion spp. vs *Nomisia exornata*	1,109	42.38	24.76	0.0001*
Theridion spp. vs *Nurscia albomaculata*	1,109	67.47	17.66	0.0002*
Theridion spp. vs *Zodarion styliferum*	1,109	33.57	34.95	0.0003*
Cheiracanthium mildei vs *Platnickina tincta*	1,109	23.85	21.12	0.0022*
Cheiracanthium mildei vs *Aphantaulax trifasciata*	1,109	13.89	11.23	0.0029*
Cheiracanthium mildei vs *Oxyopes lineatus*	1,109	2.03	0.96	0.43
Cheiracanthium mildei vs *Marilynia bicolor*	1,109	40.77	18.65	0.0026*
Cheiracanthium mildei vs *Euryopis episinoides*	1,109	15.55	13.18	0.0014*
Cheiracanthium mildei vs *Nomisia exornata*	1,109	25.48	16.68	0.0017*
Cheiracanthium mildei vs *Nurscia albomaculata*	1,109	46.22	10.32	0.0024*
Cheiracanthium mildei vs *Zodarion styliferum*	1,109	25.60	60.58	0.002*
Platnickina tincta vs *Aphantaulax trifasciata*	1,109	3.35	2.07	0.16
Platnickina tincta vs *Oxyopes lineatus*	1,109	14.78	5.38	0.020
Platnickina tincta vs *Marilynia bicolor*	1,109	8.68	3.15	0.07
Platnickina tincta vs *Euryopis episinoides*	1,109	20.66	11.80	0.0049*
Platnickina tincta vs *Nomisia exornata*	1,109	63.79	30.39	0.0025*
Platnickina tincta vs *Nurscia albomaculata*	1,109	72.89	14.43	0.0026*
Platnickina tincta vs *Zodarion styliferum*	1,109	31.60	29.87	0.0024*
Aphantaulax trifasciata vs *Oxyopes lineatus*	1,109	7.42	3.25	0.06
Aphantaulax trifasciata vs *Marilynia bicolor*	1,109	18.42	7.93	0.0017*
Aphantaulax trifasciata vs *Euryopis episinoides*	1,109	18.15	10.99	0.0004*
Aphantaulax trifasciata vs *Nomisia exornata*	1,109	59.98	31.84	0.0002*
Aphantaulax trifasciata vs *Nurscia albomaculata*	1,109	76.95	19.98	0.0005*
Aphantaulax trifasciata vs *Zodarion styliferum*	1,109	31.82	26.55	0.0004*
Oxyopes lineatus vs *Marilynia bicolor*	1,109	22.96	5.85	0.027
Oxyopes lineatus vs *Euryopis episinoides*	1,109	5.74	2.05	0.15
Oxyopes lineatus vs *Nomisia exornata*	1,109	18.21	5.71	0.019
Oxyopes lineatus vs *Nurscia albomaculata*	1,109	30.94	4.78	0.025
Oxyopes lineatus vs *Zodarion styliferum*	1,109	13.16	6.10	0.009*
Marilynia bicolor vs *Euryopis episinoides*	1,109	14.90	5.31	0.01
Marilynia bicolor vs *Nomisia exornata*	1,109	55.99	17.74	0.0024*
Marilynia bicolor vs *Nurscia albomaculata*	1,109	51.97	8.51	0.0084*
Marilynia bicolor vs *Zodarion styliferum*	1,109	18.59	8.33	0.0022*
Euryopis episinoides vs *Nomisia exornata*	1,109	13.46	6.26	0.001*
Euryopis episinoides vs *Nurscia albomaculata*	1,109	16.08	3.15	0.05
Euryopis episinoides vs *Zodarion styliferum*	1,109	2.23	2.00	0.18
Nomisia exornata vs *Nurscia albomaculata*	1,109	5.29	0.97	0.42
Nomisia exornata vs *Zodarion styliferum*	1,109	9.62	6.41	0.0051*
Nurscia albomaculata vs *Zodarion styliferum*	1,109	6.75	1.41	0.29

Table s5.6. ANOVA table of the pairwise comparisons of isotope ratios among spider species between October and November 2009 (*: *P* < 0.01).

Species	df	MS	Pseudo-F	*P* (perm)
Philodromus cespitum vs *Dipoena melanogaster*	1,48	55.98	23.14	0.0002*
Philodromus cespitum vs *Theridion* spp.	1,48	48.78	22.46	0.0001*
Philodromus cespitum vs *Platnickina tincta*	1,48	11.10	3.44	0.04
Philodromus cespitum vs *Nigma walckenaeri*	1,48	7.23	3.28	0.049
Philodromus cespitum vs *Neoscona subfusca*	1,48	0.86	0.33	0.71
Philodromus cespitum vs *Olios argelasius*	1,48	37.83	14.53	0.0001*
Dipoena melanogaster vs *Theridion* spp.	1,48	18.03	10.01	0.001*
Dipoena melanogaster vs *Platnickina tincta*	1,48	42.57	12.49	0.0017*
Dipoena melanogaster vs *Nigma walckenaeri*	1,48	27.61	17.40	0.0072*
Dipoena melanogaster vs *Neoscona subfusca*	1,48	47.81	20.51	0.0024*
Dipoena melanogaster vs *Olios argelasius*	1,48	11.34	4.80	0.027
Theridion spp. vs *Platnickina tincta*	1,48	16.53	5.92	0.01
Theridion spp. vs *Nigma walckenaeri*	1,48	9.03	5.75	0.013
Theridion spp. vs *Neoscona subfusca*	1,48	31.77	15.73	0.0002*
Theridion spp. vs *Olios argelasius*	1,48	0.30	0.15	0.87
Platnickina tincta vs *Nigma walckenaeri*	1,48	0.35	0.11	0.88
Platnickina tincta vs *Neoscona subfusca*	1,48	5.22	1.48	0.24
Platnickina tincta vs *Olios argelasius*	1,48	15.39	4.32	0.040
Nigma walckenaeri vs *Neoscona subfusca*	1,48	4.38	2.22	0.13
Nigma walckenaeri vs *Olios argelasius*	1,48	9.23	4.60	0.037
Neoscona subfusca vs *Olios argelasius*	1,48	27.97	10.62	0.0045*

6

Settling where the food is: prey abundance promotes colony formation and increases group size in a web-building spider

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ABSTRACT

The parasocial-route hypothesis postulates that coloniality in spiders is driven by the occurrence of high prey densities. This hypothesis is partially supported by comparative studies of colonial species. However, experimental evidence is lacking to confirm that prey availability directly promotes colony formation. We used the web-building spider *Cyrtophora citricola* (Araneidae) as a model species to investigate the effect of prey availability on coloniality. We conducted field surveys on colonies located on acacia trees in the Arava valley (Israel) to compare colony group size between sites differing markedly in insect abundance. We then performed experiments in net houses to test (1) the effect of prey remains in the female's webs on juvenile establishment decisions and (2) the effect of food supply on web-site fidelity of juveniles. Colony group size and reproductive investment were greater in prey-rich sites than in poor sites. In the experiments, juveniles released on adult females webs that contained remains of prey settled with higher probability than those released on empty webs. Once established, food deprivation slightly increased the number of juveniles leaving the female web, suggesting that they are reluctant to disperse after settlement. Relocation in *C. citricola* is costly, as their webs demand high energy investment. Hence, cues of prey availability are crucial, enabling spiders to acquire information about habitat quality before investing in web construction. Together, our findings provide evidence that prey availability facilitates coloniality and thus supports the parasocial route in the evolution of spider group living.

Keywords: coloniality; *Cyrtophora citricola*; group living; indirect cues; optimal foraging; site fidelity; site selection; spider.

Introduction

Habitat selection is a trait with strong implications for individual fitness, and a wide variety of strategies used by animals to select a suitable environment have been described (Morris 2003). Among the factors that play a role in site selection are predation risk (Díaz et al. 2006; Thomson et al. 2006), micro-climate conditions (Wilson 1998; Kolbe & Janzen 2002) and abundance of food resources (Stapp 1997; Walther & Gosler 2001). Cues available to an organism in the environment can give information about habitat suitability and quality. In addition, animals that live in groups either permanently or during part of their life cycle can cue in on features of their conspecifics that provide information about the habitat (Aragon et al. 2006; Salomon 2009). For example, group members may provide cues regarding food availability or quality (Boulinier et al. 2008).

Among more than 41,000 described species of spiders (Platnick 2010), approximately 60 are known to live in groups. Group-living spiders are classified into three categories: social, sub-social and colonial. Most sub-social and social spiders are web-building species that live in communal webs, and individuals cooperate in prey capture and care of the young to different degrees. Colonial spiders, by contrast, occur in aggregations of individual webs in which spiders catch their own prey and breed independently (see reviews by Whitehouse & Lubin 2005; Lubin 2010). In some colonial species, spiders can decide either to build a solitary web or to build a web within the framework of a colony. Coloniality —spiders living in colonies— is thus facultative and much effort has been invested in discovering the local factors that promote it (Uetz & Hieber 1997). Among the advantages of coloniality vs. living solitarily are increased prey capture, greater web-building efficiency by reducing silk costs and protection against predators and parasites (Uetz 1989; Lloyd & Elgar, 1997; Uetz et al. 2002). However, living in colonies bears costs, namely risk of cannibalism, competition for prey, disease or parasite transmission and even increased visibility to predators (Elgar 1989; Hieber & Uetz 1990; Leborgne et al. 1998).

According to optimal foraging models (Charnov 1976; Krebs & Davies 1997), animals adjust their foraging behaviour to maximize their energy intake, thereby selecting the habitats with highest expected returns. At the same time, individuals have to balance the potential costs of searching for foraging sites, such as predation risk and competition (Nonacs 2001). Assessing prey availability in a site before settling is critical to web-building spiders because construction of a web requires investment of energy and relocation is both expensive and risky (Tanaka 1989; Zschokke & Vollrath 2000). Solitary web-builders have two ways of retrieving information about this key feature of habitat quality. The first one plays a role in site selection and concerns habitat assessment before settling using indirect cues of prey presence (Pasquet et al. 1994; Herberstein et al. 2000). The second, influencing web-site fidelity, takes place after settling and involves assessment of prey capture and habitat stability (McNett & Rypstra 1997; Nakata & Ushimaru 1999).

Studies on colonial spiders show that prey availability is positively correlated with colony group size (Uetz et al. 1982; Smith 1985) and with increased tolerance among individuals (Hodge & Uetz 1995). Even solitary web-building spiders sometimes occur in temporary aggregations at sites with high insect density (Rypstra 1985). If living in colonies located in prey-rich areas results in a higher fitness to individuals, the behaviours leading to settling and remaining in such colonies should be favourably selected, potentially leading to the evolution and maintenance of coloniality (Uetz et al. 1982). Therefore, it is thought that coloniality in spiders is driven by the occurrence of high prey densities at certain sites, an evolutionary pathway to group living that is referred to as the "parasocial route" (Michener 1969; Shear 1970; Whitehouse & Lubin 2005). Nevertheless, there is no experimental evidence that food availability directly promotes colony formation and the mechanisms connecting food availability at a site to group size and individual fitness remain largely unexplored.

In this study we used the colonial web-building spider, *Cyrtophora citricola* (Araneidae) to investigate the relationships between prey availability, colony group size and female reproductive success, and the role of prey cues and availability in determining juvenile web-site selection. *C. citricola* occurs in the Mediterranean basin, subtropical and tropical areas of Asia and Africa (Blanke 1972), and has recently colonized the American continent (Álvares & De Maria 2004). It adapts to a wide range of habitats, from mesic areas to deserts and anthropogenic ecosystems such as gardens and citrus groves (Leborgne et al. 1998; Piñol et al. 2010). The web of *C. citricola* is a three-dimensional structure composed of a non-sticky horizontal orb-web with an open hub and a tangle of threads above and below the orb-web. Within a colony, the individual web is a territory and the owner responds aggressively towards invaders, although spiders tolerate meeting one another in the communal network (Lubin 1974). Females produce up to 10 cocoons arranged in a string where every new cocoon is placed below the previous one. They do not show maternal care but tolerate spiderlings in their web. Juveniles may remain in the parent colony and construct small webs within the tangle of threads of the adult webs, or disperse to join another colony or to establish a new one (Blanke 1972; YL personal observations). Individuals of *C. citricola* are facultatively colonial and have flexible behaviour with regard to decisions of joining or leaving a colony (Whitehouse & Lubin 2005). Thus, *C. citricola* appears to be an excellent model species to investigate the relationship between web-site selection and prey availability.

We adopted the parasocial route hypothesis as a conceptual framework to predict that local prey enhancement enables *C. citricola* colonies to increase in group size, and propose higher reproductive success and immigration of juveniles as possible mechanisms by which prey availability could favour coloniality. To test our predictions we addressed three main questions: (1) Do colonies in sites with high insect abundance host more spiders and is the reproductive output of females higher? (2) Do indirect cues of food availability influence juvenile decisions to settle in a colony? And (3) does food supply itself affect site tenacity of established juveniles?

Methods

Field surveys

Colonies of *C. citricola* are found on scattered acacia trees (mainly *Acacia raddiana* and *A. tortilis*) in dry washes and oases near springs (Rao & Lubin 2010) in the Arava valley, a hyper-arid region along the Afro-Syrian rift valley, southern Israel. Nineteen acacia trees with colonies were surveyed in spring (15-29 March) and early summer (27 May-1 June) of 2009. A group of trees (N = 8) was selected from two sites near an organic fertilizer depot (hereafter referred to as "compost sites") that attracted large numbers of flies. The other group of acacia trees (N = 11) was surveyed at "non-compost sites" along a gravel road at increasing distances from the two fertilizer depot sites. Among the trees occupied by *C. citricola* colonies in every site, we chose ones that allowed easy access and inspection of the spider webs. To ensure spatial independence, all selected trees within a site were separated by a minimum distance of 50 m, and the trees from non-compost sites were at least 2 km from the compost sites. Since in the surroundings of the focal trees and over the whole study area there were many other acacia trees, we considered it highly unlikely that spiders moved from one focal tree to another during the observation period.

In the first survey (March), tree canopy height and 2 perpendicular canopy diameters were measured to calculate tree canopy volume. All spiders from a single tree were considered to belong to the same colony although webs tended to cluster together in groups of different sizes connected by frame threads. To estimate colony volume, three dimensions of all the groups in the tree were measured and the resulting volumes were summed. For each group, the number of juveniles, males, subadult and adult females, cocoon strings and cocoons were recorded by visual counts. When a group was too large or not easily accessible in all its volume, a 50 x 50 cm frame was randomly placed in front of the webbing and all spiders, strings and cocoons within a prism defined by the frame and the depth of the webbing were counted. The prism population estimates were multiplied by the estimated number of prisms in the total web volume. All measurements were taken to the nearest centimeter with a retractable tape measure except canopy height, which was taken with the aid of a telescopic measuring stick. Females sitting below a cocoon strings and females of similar size to these were considered to be adults. The number of males and juveniles was pooled in the analyses because of the difficulty of reliably distinguishing them in the field: the size and colour of an adult *C. citricola* male is the same as those of a juvenile and its swollen pedipalps are only visible in frontal view.

In the second survey (May) there were few spiders in the colonies and the empty webs looked old, and most were partially destroyed. Following the same methodology as in the first survey, the number of strings and cocoons in each colony was recorded.

Flying insects were sampled on the periphery of each of the acacia trees used in the surveys. Two sticky traps (23 x 14 cm) were hung in each of the trees for a 24-hour period at the end of the first and second surveys. The traps were placed in the tree canopies at a height of 2 m next to the colonies, on the south and east side of the tree. After removal, the trapped insects on both sides of the traps were counted and classified to order and size class with the aid of a hand lens. Two body-length classes were established: "small insects" (< 4 mm) and "medium insects" (4-6 mm). Although sticky traps also captured a few arachnids (13 individuals), we use the term "insects" throughout the paper for clarity.

Net-house experiments

In May 2009, two experiments were conducted in semi-natural conditions inside three net houses located on the Sede Boqer Campus of Ben-Gurion University of the Negev, Israel, to determine the effect of prey availability on juvenile web-site selection. Inside the net houses there were 36 *Acacia gerrardii* trees planted in large pots (12 per net house). The trees were watered and pruned regularly and at the time of the experiments they had an approximate height of 140 cm. Grasses were uprooted regularly to keep the ground free of vegetation.

On 2 April 2009, cocoons from a single colony from a non-surveyed site in the Arava valley were collected and brought to the laboratory (room temperature ca. 25 ºC and 16:8 Light:Dark photoperiod). After 5-15 days juveniles hatched and were separated into groups of three from the same brood and maintained in glass vials with twigs that served as web attachment points. The juveniles were fed *Drosophila* fruit flies *ad libitum* 3 times per week until they were 1 month old. These flies were reared on a protein-enriched medium (created by adding crushed commercial dry dog food to the standard fruit fly medium) that has been shown to decrease mortality in a wolf spider (Mayntz & Toft 2001). In the end mortality was about 20% of the ca. 2,000 individuals hatched in the laboratory and one case of cannibalism was observed. Before the experiments, juveniles were starved for 4 days.

On 23 April 2009, adult *C. citricola* females were collected from another site in the Arava valley and were placed each in a different tree in the net houses. The trees were covered with a mesh that was removed in a few days, after the females had built webs. The females were then fed every day with 2 grasshopper nymphs (*Locusta migratoria*), 2 mealworms (*Tenebrio molitor* larvae) and 10 fruit flies. After a week on this feeding regime, prey carcasses and any cocoons produced by the females were removed and the first experiment started. There was another 1-week lapse between the first and the second experiments in order to feed the females and to let them rebuild their webs and again, any new cocoons and prey carcasses were removed. The amount of prey given to females before the experiments was intentionally 5-6 times higher than the prey captured in natural conditions [based on data from Blanke (1972)]. This way we ensured that all females were satiated and would not react to small juveniles as prey during the experiment. Before each experiment, the females were assigned to treatments and the web volume was estimated by measuring with a retractable tape the radius of the horizontal orb-web and the height of the threads above and below the orb-web. The volume was calculated as the sum of the volumes of two cones sharing a common base (the horizontal orb-web).

As environmental gradients were expected both within and among net houses, treatments were randomized within each net house and dispersed among the net houses, with equal numbers of trees for each treatment in the three net houses. Juveniles of different broods were distributed equally between treatments to control for possible family effects. All counts were done by the same observer (LM).

Prey remains experiment

To assess the effect of prey remains on the establishment decisions of dispersing juveniles released on a female web, females were assigned to two feeding treatments for 4 days (N = 16 each). In the first treatment (+remains), females were fed daily with 2 grasshopper nymphs, 1 small-sized mealworm and 5 fruit flies. Females of the second treatment (-remains) were fed 5 fruit flies per day. After the 4 days we stopped feeding all the females and the fly remains were gently removed from webs of the females in the -remains treatment, while all prey remains were left in webs of the +remains group. Females of the -remains treatment were not given larger-sized insects because of the difficulty in removing them without tearing the web. Nevertheless, we considered that 20 flies in 4 days were enough to satiate a female spider that had been fed in excess during the previous week.

The following day we released 15 juveniles of around 3 mm in size in each female web and for the following 3 days we counted the number of juveniles in each web at dawn and recorded whether they had built webs.

Prey supplementation experiment

To assess the effect of extra prey on web-site tenacity of juveniles established in a female web, the prey remains from all the female webs were removed and then 12 juveniles were released on each web. The day after release, groups of juveniles in different trees were assigned to two feeding treatments: +flies and -flies (N = 17 each). Juveniles in the -flies trees received no prey, whereas juveniles in the +flies trees received 1 fruit fly each a day, provided after the counts. Each fly was placed with forceps onto the juvenile web mesh and captured by the spider. Flies were previously anaesthetized with cold inside a portable ice chest.

For 8 days we counted the number of juveniles in each female web at dawn, as well as the number of them that had built their own web. Likewise, we recorded the number of juveniles that died and recorded any new cocoons, which could not be removed without disturbing the spiders.

Statistical analyses

We employed generalized linear models (GLM) to analyse the data from the field surveys. We used a Poisson distribution (log link) accounted for overdispersion for the colony and insect counts and a Gamma distribution (inverse link) for the canopy and colony volumes, which were continuous variables. We modelled "site" (compost, non-compost) as a fixed factor and discarded tree canopy volume because it did not differ significantly between the two types of sites (GLM: t_{17} = 0.57, P = 0.58). We compared the most abundant insect orders (mean number of individuals captured per tree and per date > 35 in at least one of the two groups of sites) and we pooled the remaining orders. We tested for non-linear relationships between insect abundance and colony measures with generalized additive models (GAM) using cubic regression splines.

We analysed the net-house experiments with GLM using a Poisson distribution for juvenile counts (log link) and a Binomial distribution for the proportion of juveniles building webs (logit link), both checked for overdispersion. We included "feeding treatment" as a fixed factor (+remains, -remains in the prey remains experiment; +flies, -flies, in the food supplementation experiment). To study juvenile settlement behaviour in the prey remains experiment, we also included "day" (day 1, day 2, day 3) as a fixed factor allowing for interactions with the feeding treatment. We implemented a first-order autoregressive correlation structure to accommodate for temporal autocorrelation between days (Zuur et al. 2009). In the prey supplementation trial we performed two analyses to test the number of juveniles remaining in the trees in the first and last day respectively. Since the volume of the adult females' webs did not significantly differ between treatments in either the prey remains experiment (GLM with Gamma distribution: t_{30} =

0.75, $P = 0.46$) or the prey supplementation experiment ($t_{32} = 0.35$, $P = 0.73$) it was not included as a covariate.

All analyses were conducted with R version 2.12.0 (R Development Core Team 2010). We used the package "geepack" to analyse the temporally autocorrelated data of the prey remains experiment (Halekoh et al. 2006) and "mgcv" to run GAM. The package "mgcv" estimates the effective degree of smoothness (e.d.f.) of the model terms as part of the fitting process (Wood 2008). A significant value of e.d.f. above 1 indicates a non-linear relationship.

Results

Field surveys

Colony measures

Colonies in the compost sites in March had more juveniles and males ($t_{17} = 2.40$, $P = 0.028$), subadult ($t_{17} = 2.66$, $P = 0.017$) and adult females ($t_{17} = 2.92$, $P = 0.0096$), cocoon strings ($t_{17} = 2.76$, $P = 0.013$) and cocoons ($t_{17} = 2.61$, $P = 0.018$) than colonies in non-compost sites (Fig. 6.1A). In contrast, these colonies were not significantly larger in volume than in non-compost sites (GLM: $t_{17} = 1.09$, $P = 0.29$; Fig. 6.1B).

At the end of May, there were few individuals remaining in the colonies and the vast majority of webs were deserted and partly destroyed. At this stage, cocoon strings were seen in 7 of the 8 compost-site colonies, and 5 of the 11 non-compost sites. There were no significant differences in either the number of cocoon strings (GLM: $t_{17} = 1.01$, $P = 0.33$) or the number of cocoons ($t_{17} = 1.28$, $P = 0.22$) between compost and non-compost sites.

Insect abundance

In the March survey 13,309 insects were captured. More insects were captured in compost-site trees (mean ± SE = 1232 ± 306) than in non-compost-site trees (mean ± SE = 314 ± 66; GLM: $t_{17} = 3.74$, $P = 0.0016$) and this difference was due to the orders Diptera (flies) and Thysanoptera (thrips; Table 6.1). Diptera were non-linearly correlated to all colony measures (all GAM: e.d.f. > 2.35, $P < 0.047$) except for the number of subadult females, for which the result was only marginally significant (e.d.f. = 2.31, F = 3.03, $P = 0.063$). The relationship between the abundance of dipterans and colony traits measures was bell-shaped: positively related up to 130-170 individuals and negatively related beyond that threshold. No relationships were found between the number of insects of the remaining groups or the total number of insects and the colony measures (all $P > 0.063$).

More small and medium insects were captured in the compost-site trees than in the non-compost-site trees (small insects: GLM: t_{17} = 3.51, P = 0.0027; medium insects: t_{17} = 2.27, P = 0.036; Fig. 6.2). There were non-linear relationships between the abundance of medium insects and the numbers of females (GAM: e.d.f. = 2.43, F = 4.26, P = 0.022), cocoon strings (e.d.f. = 2.35, F = 4.82, P = 0.015) and cocoons (e.d.f. = 2.49, F = 3.77, P = 0.032). The shape of these relationships was bell-shaped, with peak numbers between 80 and 90 medium insects. No other relationships were found between the number of insects of either size class and the colony measures (all $P > 0.088$).

In the second survey in May 11,974 insects were captured. The total number of insects captured by the sticky traps in the trees did not differ significantly between compost (627 ± 112) and non-compost sites (632 ± 96; GLM: t_{17} = 0.035, P = 0.97). There were no differences in the abundance of any insect group between trees from the two groups of sites (Table 6.2) or in the number of small insects and medium insects (small insects: t_{17} = -0.65, P = 0.53; medium insects: t_{17} = 0.83, P = 0.42).

Net-house experiments

Prey remains experiment

More juveniles in the +remains treatment stayed in the trees than in the -remains treatment (GLM: treatment effect: Wald $\chi^2_{1,90}$ = 11.08, P = 0.00087). The number of juveniles slightly declined with time (Wald $\chi^2_{2,90}$ = 4.47, P = 0.035), but the interaction between time and treatment was not significant (Wald $\chi^2_{2,90}$ = 2.71, P = 0.10; Fig. 6.3). The proportion of juveniles that had built their own web was higher in the +remains than in the -remains treatment already from the first day (+remains: 82.3%, -remains: 68.8%; Wald $\chi^2_{1,90}$ = 8.44, P = 0.0037), although in both treatment groups this proportion increased with time (Wald $\chi^2_{2,90}$ = 14.91, P = 0.00011). The interaction was not significant (Wald $\chi^2_{2,90}$ = 1.13, P = 0.29).

Prey supplementation experiment

Five juveniles died during the experiment, 2 in the +flies and 3 in the -flies treatment. On the first day after release, there were no differences in the number of juveniles remaining in the trees (GLM: t_{32} = 0.78, P = 0.44). However, more juveniles in the +flies treatment than in the –flies treatment remained in the trees on the last day of the experiment (t_{32} = 2.67, P = 0.012; Fig. 6.4). There was no difference in the proportion of juveniles that built their own web on either of the days ($t_{32} < 0.088$, $P > 0.93$).

Discussion

Our field surveys confirmed that the compost sites had more potential prey, and showed that colony group size was greater in prey-rich than in prey-poor sites. However, we did not find a positive correlation between group size and insect abundance in the trees. In the net-house experiments, juvenile settling decisions were strongly and positively influenced by the presence of dead prey remains in a conspecific web and there was a small but positive effect of prey supply on juvenile web-site tenacity.

In early spring (March), *C. citricola* colonies at compost sites hosted more than 10 times as many juveniles and males, subadult and adult females as colonies in non-compost sites. Colony volume nevertheless did not differ between the sites; therefore, in compost-sites the density of webs was greater and individual webs were closer to each other than those in non-compost sites. There was a 4-fold difference in insect abundance between the two types of sites and especially there were more small insects (< 4 mm) at the compost sites. The most abundant prey were small Thysanoptera and Diptera. This coincides with the preferred prey of the spider, as *C. citricola* eats mainly small insects (YL personal observations) and Diptera are a major component of the spiders' diet (Blanke 1972). In early summer (May), the colonies underwent a seasonal decline: at this stage there were few adults and the webs of the young were difficult to discern among the old colony webbing. Insect abundance did not differ between the compost and non-compost sites in this season.

Our results agree with previous studies of group size in other colonial spiders. In *Philoponella oweni* (Uloboridae), colonies became smaller when insect availability decreased (Smith 1985). In *Metepeira spinipes* (Araneidae), colony group size decreased when colonies were transplanted from sites with high insect abundance to sites with low abundance (Uetz et al. 1982). Our observations of increased web density in colonies from prey-rich sites also support previous studies showing that prey abundance increased tolerance among individuals in a colonial species (Hodge & Uetz 1995) and in a solitary species (Gillespie 1987). Surprisingly, none of the colony measures was correlated to insect abundance. However, we found unimodal relationships between colony measures and numbers of Diptera and of medium-sized insects. It is possible that above a certain threshold of prey availability, other factors influence colony group size.

Colonies situated in prey-rich sites had more cocoons strings and more cocoons than those in prey-poor sites, indicating that the reproductive investment of prey-rich-site females was higher. Cocoons were not collected in the first census (March) so as not to disturb the colonies. In the second census (May), the number of cocoons remaining in the colonies was too small to allow us to accurately assess fecundity or hatching success, and thus we lack data on reproductive success. In another study, prey-supplemented solitary females of *C. citricola* produced more cocoons, with more eggs per cocoon than non-supplemented females, but no data were provided about the number of hatched juveniles (Blanke 1974). It remains to be tested therefore whether differences in reproductive investment are responsible for the larger colony group sizes in prey-rich sites than in prey-poor sites.

A recurrent question regarding the causes of coloniality is whether there is any advantage in colonial over solitary life (Caraco et al. 1995; Rao et al. 2009). In a study in Sicily, solitary and colonial *C. citricola* individuals found in the same habitat did not differ in body size, prey capture or egg production (Leborgne et al. 1998). The authors suggested that the coexistence of both strategies in this species allow it to cope with environmental variability. Similar results were found in *P. oweni* (Smith 1982). When we compared spider colonies from sites differing in prey abundance, we found colonies in prey-rich sites to be much more populated than in prey-poor sites. Hence, coloniality may be favoured over solitary life, not because of an increase in prey capture success by colonial spiders, but rather because this strategy is enabled by locally high prey availability, as predicted by the parasocial route hypothesis.

We performed two experiments in semi-natural conditions to gain insight into the underlying mechanisms by which group size in colonies is favoured by local prey abundance. In the prey remains experiment, juveniles released on webs with prey carcasses settled with higher probability and built a web faster than juveniles arriving in empty female webs. The prey remains were empty exoskeletons of insects fed upon by the adults that were dropped into the lower barrier web threads or left on the orb-web. These remains could be investigated by the young, but they would have little, if any, nutritional value for them. Furthermore, we did not observe juveniles feeding away from their own webs. The results support our hypothesis that prey remains in conspecific webs serve as indirect cues of local food availability that are quickly assessed by juveniles in order to make establishment decisions. Previous studies report that web-site selection in solitary spiders is based on factors such as micro-climate conditions (Tolbert 1979), vegetation characteristics (McNett & Rypstra 2000) and predator avoidance (Hodge & Uetz 1992; Blamires et al. 2007). In addition, solitary spiders arriving in a new site build a web with greater probability in presence of visual and vibratory cues of prey availability (Pasquet et al. 1994; Herberstein et al. 2000; Thévenard et al. 2004). In our work we demonstrate for the first time that an indirect cue such as prey remains induce dispersing juveniles to settle in a foreign colony. Unlike webs of typical orb-weaving araneids, *C. citricola* webs require great investment of energy and silk, and are not renewed daily but maintained over a long period of time (Lubin 1974; Opell 1998). As a consequence, web relocation in this species is constrained due to energetic and material (silk) costs. Cues of prey availability are therefore of crucial importance, because they enable spiders to acquire information about habitat quality before web-construction and may eliminate the need for costly habitat sampling (i.e. feeding experience).

Two related factors may account for why some juveniles settled in the vicinity of females whose webs where empty. First, there is evidence in solitary spiders that the presence of a conspecific increases the probability of web-building in a new site (Enders 1977; Leborgne & Pasquet 1987). Because long-term site tenacity is determined by a stable food supply (Turnbull 1964; Hodge 1987), conspecific presence is a reasonable indicator of habitat quality in many animal species (Stamps 1987, 1991; Smith & Peacock 1990). Second, web-builders are more inclined to settle in vacant spider webs or close to silk fragments than in sites lacking any silk, a behaviour that may arise either from a silk-saving strategy or because, as a sign of previous residence, silk too denotes habitat quality (Hoffmaster 1986; Schuck-Paim & Alonso 2001). In fact, a recent study showed that juvenile *C. citricola* prefer establishing in trees with occupied or empty conspecific webs over trees with no webs (Rao & Lubin 2010), indicating that dispersing juveniles are more inclined to build a web within the framework of a colony than solitarily. We conclude that settling in colonies is favoured in *C. citricola*, as the colony provides to incoming spiders immediate information of habitat quality by means of different factors related to prey availability, namely presence of silk, conspecifics and prey remains, that are unavailable to spiders arriving in an unoccupied site.

In the prey supplementation experiment, food supply following settlement in a female web slightly improved site fidelity, as the trees with starved juveniles had on average 1 spider less at the end of the trial. Juvenile mortality was negligible and there were no cases of cannibalism, as all dead spiders were found on their webs. It could be argued that the difference between the +flies and –flies treatments was small because individuals from the –flies treatment were not completely food deprived. Inside the net houses there were small insects such as homopterans and psocopterans that, if preyed upon, could be enough to satiate a juvenile spider. Nevertheless, over the experiment period, only a few spiders where found with such prey carcasses in their webs, which suggests that this potentially confounding effect can be dismissed. Some web-building spiders respond promptly to low prey supply by relocating their webs (Olive 1982; Nakata & Ushimaru 1999). In *C. citricola*, resistance to relocation is consistent with optimal foraging models when we consider the high costs of web construction in this species (see above in this section). We inferred from the prey remains experiment that these spiders make a high settling investment based on immediate, indirect cues of habitat quality. Subsequent feeding experience at a site may take a long time to counteract the initial investment. Spiders that build energetically expensive webs relocate less frequently than orb-weavers that build low-energy webs (Tanaka 1989; Blackledge & Wenzel 2001). As risks of dispersal make relocation even more expensive (Vollrath 1985; Lubin et al. 1993), the costs of staying in a poor-quality site may be outweighed by costs that spiders must incur to disperse. Furthermore, the extremely patchy distribution of resources in deserts (Huenneke & Noble 1996) reduces the chances of dispersers reaching a suitable site, and therefore spiders from populations in arid environments can be expected to be particularly resistant to relocation. A similar argument was presented to explain why pit-building antlions do not relocate their trapping pits when faced with food shortage (Scharf & Ovadia 2006). For species with high costs of trap construction and relocation, such as *C. citricola*, predicting habitat quality before establishment in a new site may be of greater survival value than assessing current feeding state after costly establishment.

Our results highlight the importance of prey supply in colony formation and maintenance in *C. citricola*, providing unique experimental support for the parasocial route hypothesis of coloniality. Strikingly, individuals of *C. citricola* were able to predict local prey abundance when arriving in a colony and make settling decisions accordingly. An analogous strategy of assessing habitat quality has been documented in some colonially breeding bird species. This strategy, so-called prospecting, is performed by birds recently arrived in a colony and consists of observing the activity of conspecifics in order to gather information about the quality of the potential breeding site (Boulinier & Danchin 1997; Doligez et al. 2002). In fact, colonial spiders have been already compared to bird flocks due to the flexible composition of their aggregations (Rypstra 1979). That there is a parallel between between strategies of two phylogenetically distant animal groups (spiders and birds) suggests a unified framework for studying habitat selection using different sources of information (Dall et al. 2005).

In conclusion, our findings show compelling evidence that prey abundance increases group size in *C. citricola* colonies by favouring juvenile web-site selection. Availability of food resources thus promotes group formation in this facultatively colonial spider, which constitutes a strong argument in support of the existence of a parasocial pathway driving the evolution of spider coloniality.

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Tables

Table 6.1. The number of insects per tree sampled over a 24-hour period in March 2009 in compost and non-compost sites.

Order	Compost		Non-compost		
	Mean	SE	Mean	SE	GLM
Thysanoptera	771	317	93	26	t_{17} = 2.87, P = 0.011
Diptera	233	45	52	18	t_{17} = 3.82, P = 0.0014
Hymenoptera	188	45	112	26	t_{17} = 1.56, P = 0.14
Homoptera	15	6	41	21	t_{17} = 1.08, P = 0.29
Others	13	3	6	1	t_{17} = 2.88, P = 0.010

Table 6.2. The number of insects per tree sampled over a 24-hour period in May 2009 in compost and non-compost sites.

Order	Compost		Non-compost		
	Mean	SE	Mean	SE	GLM
Thysanoptera	248	45	237	38	t_{17} = 0.19, P = 0.85
Hymenoptera	132	35	97	9	t_{17} = 1.17, P = 0.26
Diptera	38	6	130	57	t_{17} = 1.51, P = 0.15
Homoptera	19	5	38	7	t_{17} = 2.03, P = 0.059
Coleoptera	91	36	73	16	t_{17} = 0.50, P = 0.62
Others	92	40	51	7	t_{17} = 1.32, P = 0.20

Figures

Fig. 6.1. Numbers of individuals, cocoon strings and cocoons per tree (A) and colony volume (B) in compost and non-compost sites in March 2009. Means ± SE are shown. Asterisks indicate a significant difference (*: $P < 0.05$; **: $P < 0.01$). Juv = juveniles. Subad = subadults.

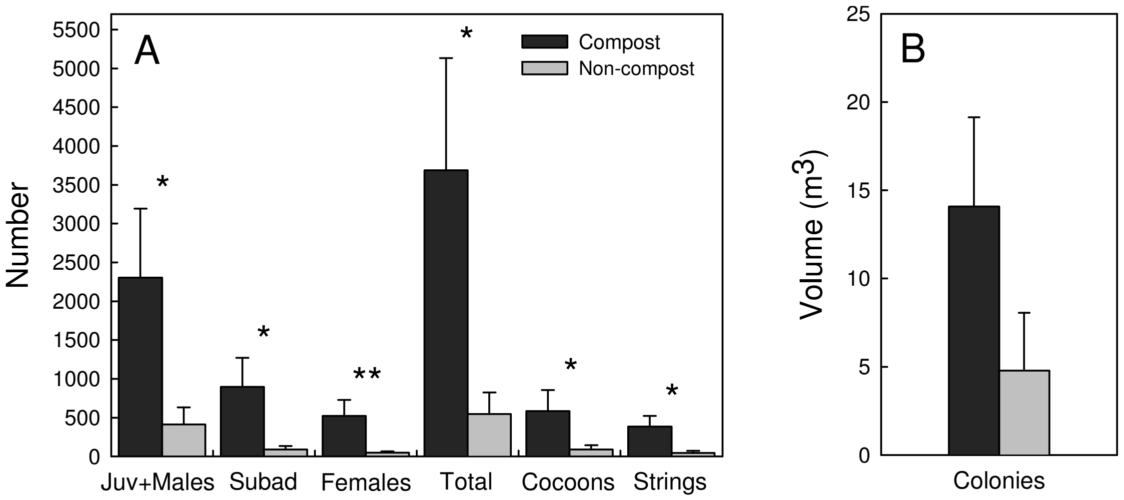


Fig. 6.2. The number of small and medium insects captured with sticky traps in the trees in compost and non-compost sites in March 2009. Means ± SE are shown. Asterisks indicate a significant difference (*: $P < 0.05$; **: $P < 0.01$).

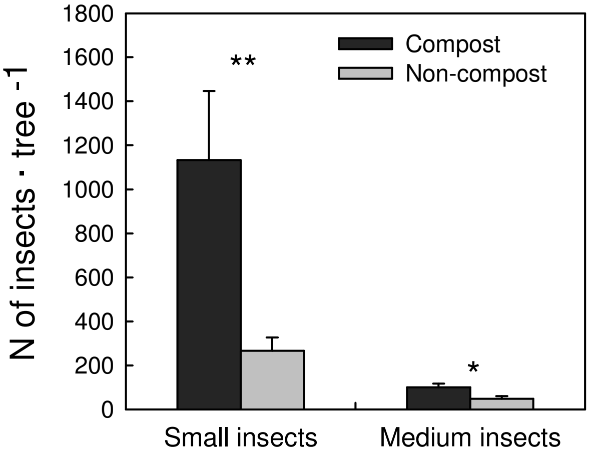


Fig. 6.3. The number of juveniles remaining in the trees over time (days) in the +remains and -remains treatments in the prey remains experiment. Means ± SE are shown.

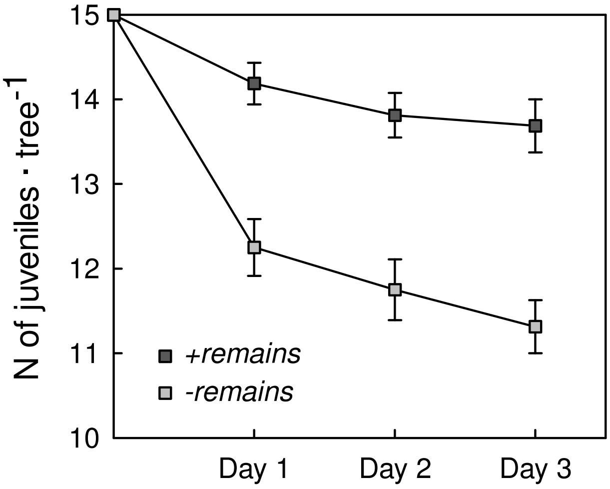
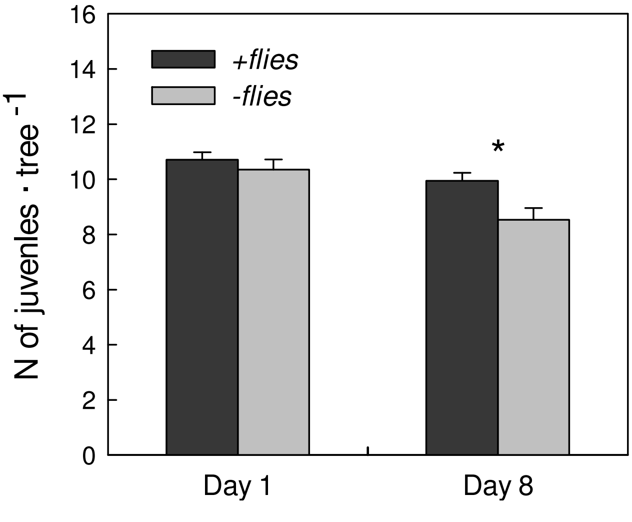


Fig. 6.4. The number of juveniles remaining in the trees on the first and last days in the +flies and -flies treatments in the prey supplementation experiment. Means ± SE are shown. An asterisk indicates a significant difference (*: $P < 0.05$).



7

Food stress during juvenile and maternal development shapes natal and breeding dispersal in a spider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ABSTRACT

Dispersal is affected by a broad array of environmental conditions, including those experienced by parents. This enables offspring to combine parental habitat cues with information on the current environmental conditions in determining dispersal strategies. Despite the potential importance of such parental effects on both the timing of dispersal and dispersal distance, empirical evidence for either remains scarce. We tested the strength of maternal effects on dispersal in the dwarf spider *Erigone dentipalpis*, establishing specifically, the influence of food supply across two generations on dispersal propensity in juveniles and adults. The latter perform either short-distance (rappelling) or long-distance (ballooning) dispersal. Direct, but not maternal, starvation negatively affected fitness-related, life-history traits in offspring, and only starved juveniles emigrated towards new habitat. Adult rappelling decreased in food-deprived males, indicating an asymmetry in sex-related costs of short-distance dispersal. In contrast, the propensity of ballooning was determined by the interplay between maternal and direct feeding regimes: sustained high levels of food availability across generations decreased ballooning, while starvation of the mother or during the juvenile stage induced intermediate ballooning responses relative to conditions in which both mothers and offspring were starved. Our findings thus demonstrate the presence of different evolutionary mechanisms behind long-and short-distance dispersal strategies, and importantly highlight the role of maternal effects in the dynamics of spatially structured populations.

Keywords: emigration; habitat quality; information; movement ecology; transgenerational plasticity; spider.

Introduction

Dispersal is a key trait for organisms inhabiting dynamic environments with major consequences for gene flow and population dynamics (Ronce 2007). It is a compound behavior consisting of three phases, namely departure, transience, and settlement, each of them influenced by a wide array of costs and selection pressures (Bonte et al. 2012). Because of these costs, informed dispersal strategies in response to specific habitat cues such as density or local disturbance have evolved (Ronce et al. 2001; Clobert et al. 2009; Bocedi et al. 2012).

Information on the environmental conditions experienced by past generations can be transmitted to progeny via parental effects. Such transgenerational phenotypic plasticity is likely to exert a strong influence on offspring fitness and behavior (Mousseau & Fox 1998; Massot & Clobert 2000; Ims & Hjermann 2001). Parental effects arise when parental phenotypes influence offspring phenotypes over and above directly transmitted genetic effects (Plaistow & Benton 2009). Maternal effects in particular have recently received much attention given their broad impact on individuals' life histories (Donohue 2009; Harris & Uller 2009), population dynamics (Inchausti & Ginzburg 2009; Plaistow & Benton 2009) and spatial processes (Duckworth 2009). Maternal effects are favored by between-generation heterogeneity in habitat quality (Jablonka et al. 1995; Marshall & Uller 2007) and are expected to be a prominent driver of dispersal, depending on the environmental context. They are likely to provide juveniles with information that, due to their lack of experience or exploration abilities, they would otherwise not be available, enabling them to combine current and maternal cues to reach an optimal dispersal strategy (Massot et al. 2002).

Some plants and insects possess polymorphic dispersal mechanisms. The selection pressures impacting dispersal distance are different for long- and short-distance dispersal and arise from specific cost-benefit ratios (Higgins et al. 2003; Bowler & Benton 2005; Bonte et al. 2009). In general, dispersal distance is directly related to the spatial extent of the driving factors, for instance the spatial scale of food shortage or other disturbances (Levin et al. 2003). Organisms may also show variation in the timing of the dispersal event, i.e. the relative frequency of natal vs. breeding dispersal. The timing depends primarily on the age-structure of the population with higher expected natal dispersal if inbreeding avoidance is high or if competition among offspring is higher than for adults (Johst & Brandl 1999). These factors in turn depend on pre-breeding survival rates (Schjørring 2002), the strength of competition, and environmental fluctuations (Johst & Brandl 1999). Interestingly, and as demonstrated in the common lizard (Léna et al. 1998; Meylan et al. 2007), maternal effects can provide this information when the environmental conditions experienced by the mother are a reliable indicator of conditions in the subsequent generation (Dufty et al. 2002). Despite the importance of both timing and distance of dispersal for population dynamics, empirical studies are largely lacking (Clobert et al. 2008; Bonte et al. 2009).

Experimental studies on maternal effects and dispersal impose highly standardized breeding conditions over successive generations. Consequently, we selected the dwarf spider *Erigone dentipalpis* (Linyphiidae) as a model organism for our study. *Erigone* spiders are common residents of disturbed habitats and have multiple generations a year depending on the prevailing climatological conditions (Weyman 1995; Downie et al. 2000). They provide an ideal study system for experimental research on dispersal because they have a short development time and a specific and unique dispersal behavior that is expressed under laboratory settings (Weyman et al. 1994; Bonte et al. 2003a,b, 2008a,b). In general, environmental conditions and population densities are highly correlated among generations within the same season, causing maternal effects to be a reliable source of information for offspring (De Meester & Bonte 2010). *Erigone* juveniles are mostly sedentary but may disperse out of the natal (social) environment through ambulatory movements. Adults, in contrast, have two major dispersal strategies that depend on the use of silk (Bell et al. 2005; Bonte et al. 2008b), further referred to as breeding dispersal. The first adult dispersal strategy, ballooning, is long-distance aerial dispersal based on wind currents that carry the spider attached to a small silk thread. The second one, referred to as rappelling, involves short-distance displacement of a few meters that are bridged by the individual using a silk thread. For the initiation of both rappelling and ballooning dispersal, the spider climbs to an elevated point and performs a stereotypical display called tiptoe behavior, which consists in stretching the legs while raising the tip of the abdomen to produce the silk thread. *Erigone* spiders decide to disperse by either rappelling or ballooning based on personal information resulting from temperature conditions during development (Bonte et al. 2008b), local densities, and also using the presence of silk threads as a source of public information (De Meester & Bonte 2010).

In spiders, natal dispersal occurs during the juvenile stage, as opposed to breeding dispersal, which occurs when adult, both prior and after mating (Bonte et al. 2009). Natal dispersal acts as a strategy to avoid local food competition during the first growth stages. In contrast to larger spider species (Bonte et al. 2007a,b), juvenile *Erigone* spiders do not rappel or balloon (though subadults may also engage in such aerial dispersal), and natal dispersal only involves walking short distances (Bell et al. 2005). Because moving large distances is at the cost of energetic expenditures and predation risks, long-distance displacements by ambulatory movements are likely disfavored (Bonte et al. 2012). Ballooning, being the long-distance dispersal strategy in adults, is likely to be devoted to the avoidance of disturbance and to the colonization of temporally suitable habitats at large spatial scales (Bonte et al. 2008b).

Rappelling strategies, on the other hand, enable females to spread offspring (egg sacs) acrosss fairly short distances (some meters) within a habitat as a bet-hedging strategy to secure reproduction in a spatially heterogeneous environment. For males, rappelling is anticipated to be an efficient mate location strategy (Bonte et al. 2008b). Ballooning is considered to impose high mortality risks because of the high uncertainty of landing in a suitable habitat (Bonte et al. 2006, 2007a). In contrast, as a short-distance dispersal strategy, rappelling ensures displacements within the same habitat at lower risk but at likely higher energetic costs due to the need of several long silk threads (Bonte et al. 2008b).

In this study, we tested the hypothesis that food limitation during maternal and juvenile development affects both the timing and the mode of dispersal in *E. dentipalpis*. More specifically, we predicted (1) that acute food deprivation would induce natal dispersal in young spiders due to increased resource-competition among kin and (2) that breeding dispersal would increase under both immediate and maternal food limitation, with food restriction experienced by mothers and by developing juveniles favoring high-risk, long-distance dispersal events in order to escape long-term deteriorating habitat conditions. In contrast, (3) we expected short-distance breeding dispersal to only be affected by acute (local) food shortage through its negative impact on body condition.

Materials and Methods

Breeding of spiders and experimental design

At the beginning of October 2009, we collected adult females in a permanent, managed dune slack in De Westhoek dune nature reserve (De Panne, Belgium). Because we collected over a large area and never collected from clusters, we assume that (1) females were not related and (2) they had not performed inbred matings. In the laboratory, these wild-caught females were reared individually on moist plaster of Paris in small breeding containers (diameter: 4 cm), in standardized conditions (25 ºC, Light:Dark = 16:8, relative humidity ~ 100%) and fed *ad libitum* with springtails *Sinella curviseta* (Collembola). We used a single egg sac from 17 different females to produce the F1 generation. All F1 spiders were reared individually as outlined above for the wild-caught population. We randomly assigned F1 juveniles of each clutch to one of two feeding treatments ("well fed" or "poorly fed"). The treatments "well fed" or "poorly fed" constituted the provisioning of either 50 or 3 springtails once a week. On maturation, we mated F1 adults within the same feeding treatment group (42 well-fed and 56 poorly-fed adults) to produce the F2 generation and kept the females with their assigned feeding regime until death. We avoided inbreeding in the F2 generation by mating spiders born to different mothers (non-sib matings). The spiders of the F2 generation came from 14 F1 mothers, 7 from each feeding treatment. The F2 offspring of the two groups were split in the same two feeding regimes and they were raised until maturity. This two-factorial design allowed us to test the effects of both current feeding regime (F2) and maternal feeding regime (F1) on dispersal motivation in the resulting four groups of F2 offspring. We reared all spiders individually to avoid density effects on dispersal (De Meester and Bonte 2010).

Quantification of life-history traits

The eventual dispersal strategy is affected by body condition. This may be a proximate mechanism when individuals in bad physical condition are unable to convert the necessary energy toward dispersal structures such as wings or silk threads (Bonte et al. 2012) or an ultimate strategy as a response to kin-competition or environmental stochasticity (Bonte & De la Peña 2009). Previous studies have shown that life-history traits are affected by inbreeding (Bonte 2009), developmental stress (Bonte et al. 2008b), and changes in body condition. Therefore, we assessed the following traits after testing F2 adults for breeding dispersal (see further): longevity after maturation, latency to the first egg sac, and female fecundity, measured as number of eggs in the first egg sac. Unmated adult *Erigone* females lay unfertilized egg batches and we used these batches as a proxy of fecundity (Bonte et al. 2008b). We also recorded maturation latency of F2 juveniles. We checked all spiders on alternate days.

Natal dispersal tests

To test the effect of food stress on F2 natal dispersal, we used pairs of breeding containers connected at the sides with a plastic tube (length: 8 cm; diameter: 3 mm) that would allow a juvenile placed in one container to walk into the other one. Next, we used a subset of offspring from F1 well-fed mothers and put each juvenile into one container of a pair. We assigned these juveniles at random to one of the feeding treatments (70 well fed and 70 poorly fed) and we examined them on alternate days to record natal dispersal. Once a juvenile dispersed, we relocated it to a single container until adulthood. We did not use all offspring from F1 well-fed mothers but instead used a subset because differences in the breeding protocol between the juveniles tested for natal dispersal (paired containers) and those not tested (single container) could influence breeding dispersal behavior. Unfortunately, we could not use a subset of offspring from F1 poorly-fed mothers due to the relatively low fecundity of these females and we kept all of those offspring for the breeding dispersal tests (see results). Because of this, F2 natal dispersal could only be tested as a response to current but not by maternal food supply, because all F1 mothers came from the well-fed treatment.

Breeding dispersal tests

We tested F2 adults for their dispersal propensity 1-2 days after reaching adulthood. From F1 poorly-fed mothers, we tested 44 well-fed and 55 poorly-fed adult offspring. From F1 well-fed mothers, we tested 129 well-fed and 82 poorly-fed adult offspring. To conduct dispersal tests, we transferred the spiders to a climatic chamber at a temperature of 28 ± 2 °C and relative humidity = 30%. The testing platform had four upright wooden sticks and was placed in a water bath to prevent spiders from escaping by walking. Two fans produced an upward air current with an average velocity of 1 $m \cdot s^{-1}$ ideal for eliciting dispersal. We tested the spiders in pairs chosen at random. For a period of 10 minutes, we registered the dispersal mode (rappelling or ballooning) of each individual [for more information, see Bonte et al. (2008a)].

Data analysis

We employed generalized linear mixed models to analyse the effect of feeding treatment on life history and dispersal. For natal dispersal, we used sex, current feeding treatment, and the interactions between them as fixed factors, and mother-ID as a random factor to correct for similarity due to common natal origin. There was no variation due to grand-maternal origin (see also Bonte 2009) because only 2 pairs among the 14 F1 mothers were sibs, so the remaining 10 F1 mothers were not related to each other. We used models assuming a Binomial distribution (logit-link function) to test the presence/absence of dispersal and a Poisson distribution (log-link function) for dispersal latency (i.e., day of emigration). We corrected in all cases for over/underdispersion due to possible higher variances compared with theoretical expectations.

For both breeding dispersal and life-history traits, the fixed factors were sex, current feeding treatment, maternal feeding treatment and their interactions, and we modeled mother-ID as a random effect. We applied a Binomial distribution (logit-link function) to test the prevalence of rappelling or ballooning, and a Poisson distribution (log-link function, again, all corrected for over/underdispersion) for count data on life-history traits. Likewise, we tested the potential influence of juvenile dispersal on adult ballooning or rappelling, adding the former as a covariate when necessary. We used manual stepwise backward selection to discard non-significant interactions ($\alpha > 0.10$) and the Satterthwaite procedure to approximate denominator degrees of freedom. The applied mixed models successfully incorporate unbalanced designs and uneven sample sizes. In our case, the breeding design was not balanced in respect of the maternal origin of the F2 generation. In addition, sample sizes were large but uneven: 44 well-fed and 55 poorly-fed offspring of F1 poorly-fed mothers, and 129 well-fed and 82 poorly-fed offspring of F1 well-fed mothers. Finally, we used multiple egg sacs of all F1 mothers and different numbers of siblings randomly collected from the first series of produced egg sacs. The analyses were conducted with proc Glimmix (SAS 9.1.3 2003).

Results

Life-history traits

Maturation latency was twice as long in poorly-fed than in well-fed juveniles ($F_{1,438} = 657.07$, $P < 0.0001$; Fig. 7.1A) but there was no effect of sex ($F_{1,438} = 0.84$, $P = 0.36$), nor of maternal (F1) feeding treatment ($F_{1,14.38} = 0.95$, $P = 0.35$). Longevity was shorter in poorly-fed spiders ($F_{1,327} = 151.57$, $P < 0.0001$), although females lived longer than males irrespective of the feeding treatment ($F_{1,327} = 49.19$, $P < 0.0001$). Furthermore, there was an interaction between sex and current feeding treatment, as differences in adult longevity between sexes were more pronounced in well-fed spiders ($F_{1,327} = 8.47$, $P = 0.0039$; Fig. 7.1B). Longevity was reduced by 21% in males, and by 34% in females. Again, there was no effect of maternal feeding treatment ($F_{1,5.34} = 0.09$, $P = 0.78$). Mother-ID explained part of the variation in life-history traits (maturation latency: $\sigma = 0.017 \pm 0.0076$ SE; longevity: $\sigma = 0.051 \pm 0.036$ SE).

F1 females continued receiving food after maturation and were allowed to mate in order to produce the F2 generation. Poorly-fed F1 mothers had fewer eggs in their first egg sac (poorly-fed, mean ± SE: 3.14 ± 0.67; well-fed: 23.57 ± 1.84; $F_{1,12} = 78.81$, $P < 0.0001$) and a longer first egg sac latency (10.71 ± 1.24) than well-fed mothers (2.86 ± 0.64; $F_{1,12} = 27.58$, $P = 0.0002$). After interrupting food supply to all F2 offspring tested for breeding dispersal, no poorly-fed F2 females laid egg sacs, whereas well-fed females laid their first unfertilized egg sac after 7.84 ± 0.60 days, with 23.84 ± 0.97 eggs. There was no significant influence of maternal (F1) feeding regime on either first egg sac latency ($F_{1,15.75} = 2.92$, $P = 0.11$) or fecundity ($F_{1,9.04} = 0.26$, $P = 0.63$) of F2 females. However, mother-ID was a source of variation in these traits (first egg sac latency: $\sigma = 0.13 \pm 0.071$ SE; fecundity: $\sigma = 0.090 \pm 0.053$ SE).

Natal dispersal

Although no F2 juveniles fed *ad libitum* dispersed, 39.6% of food-deprived juveniles did, with an emigration latency of 21.13 ± 2.32 days. Sex had no effect on either propensity ($F_{1,56} = 1.22$, $P = 0.27$) or latency to emigrate ($F_{1,17.39} = 1.11$, $P = 0.31$). Variation because of mother-ID was minor ($\sigma \sim 0$). As stated in the methods section, we could not test effects of maternal (F1) feeding treatment for this kind of dispersal, because starved mothers had too few offspring to be split among different treatments.

Breeding dispersal

Neither rappelling ($F_{1,115}$ = 0.27, *P* = 0.60) nor ballooning ($F_{1,116}$ = 0.43, *P* = 0.51) were affected by natal dispersal decisions. Similarly, neither dispersal behavior was influenced by breeding protocol in spiders born to well-fed mothers (rappelling: $F_{1,345}$ = 0.11, *P* = 0.74; ballooning: $F_{1,345}$ = 0.37, *P* = 0.55) There was an interaction between sex and current feeding treatment in rappelling propensity ($F_{1,436.7}$ = 6.17, *P* = 0.013), because poorly-fed males displayed lower rappelling probabilities than well-fed males (least significant difference [LSD], *t* = 2.91, *P* = 0.02; Fig. 7.2A). Food stress increased ballooning probability ($F_{1,28.04}$ = 17.14, *P* = 0.0003), because food-deprived individuals were more prone to balloon (0.19 ± 0.035) than well-fed ones (0.043 ± 0.015). A significant interaction between current and maternal feeding treatment ($F_{1,27.06}$ = 5.63, *P* = 0.025) revealed that well-fed spiders with well-fed mothers hardly ballooned (~1%), whereas the ballooning probability in the other groups of spiders was 13-23% (LSD, $t \leq -3.28$, $P \leq 0.014$; Fig. 7.2B). No variation caused by mother-ID was detected ($\sigma \sim 0$).

Discussion

We found that food supply had a pervasive influence on all aspects of *E. dentipalpis* dispersal behavior. Food stress induced ambulatory emigration during the juvenile stage. Male rappelling decreased under current food shortage, whereas an interaction between maternal and current food deprivation caused a marked increase in long-distance ballooning. Our results hereby provide evidence of within- and transgenerational evolutionary mechanisms underlying breeding dispersal strategies.

Current (F2) food deprivation negatively affected all life-history traits, delaying maturity, reducing longevity and decreasing fecundity. Both male and female longevity decreased substantially, but the relative decrease in females was higher relative to males. Food deprivation during development consequently had a large effect on longevity in the two sexes. We found no evidence of maternal (F1) effects on body condition-related life-history traits.

Although no well-fed juveniles dispersed, nearly 40% of their starved counterparts did, but natal dispersal took place towards the end of the juvenile stage. This finding suggests huge costs of dispersing, such as energetic demands and predation risk (Lubin et al. 1993; Nonacs 2001). As expected, neither current nor maternal food deprivation led to an increase in short-distance rappelling. In species living in fragmented landscapes, leaving a poor quality habitat requires long dispersal distances (Bonte et al. 2010) that would entail excessive energetic investments in silk production if these distances were to be covered by consecutive within-habitat rappelling events (Janetos 1982; Craig 1997), especially for individuals deficient in body condition. Even more, male rappelling propensity dropped sharply under current food deprivation, whereas in females it remained unaffected. Sex differences in dispersal behaviors emerging from particular selection pressures have been reported in other arthropods (Albrectsen & Nachman 2001; Caudill 2003), but mechanisms underlying our patterns are not clear. The sex-bias here is not due to changes in population sex ratio because individuals were reared under the same conditions (De Meester & Bonte 2010), but rather the results of sex-specific changes in body condition and subsequent costs of dispersal (Bonte et al. 2012). Because females experienced a larger reduction in important fitness-related life-history traits (longevity) relative to males, the decrease in male rappelling may be a consequence of the greater costs they incur to produce silk (Bonte et al. 2008b), but this needs to be explored in the future. Consistent with the predictions that movements over short spatial scales should rely mostly on immediate habitat conditions, effects of maternal feeding regime were absent for rappelling.

Our results show that ballooning probability increased under either maternal or current starvation. Very few studies have addressed the interactions between current and maternal information on dispersal. For instance, emigration probability in the common lizard is influenced by fluctuating humidity levels between maternal and offspring environments (Massot et al. 2002). In the bean aphid, mothers raised under crowded conditions produce higher proportions of winged progeny, but the offspring level of crowding is the sole determinant of the proportion of actual migrants (Shaw 1970). *E. dentipalpis* appears to be highly sensitive to food shortage: ballooning propensity was much lower in spiders that experienced high levels of resource availability over two generations than in spiders that were themselves starved and/or had starved mothers. Interestingly, the ballooning probability is very similar in cases where either mothers or juveniles experienced food deprivation (Fig. 7.2B), indicating the presence of cumulative effects on dispersal independent of the sequence of starvation. This is rather surprising because we might expect that the current feeding regime would be most informative of the prevailing environmental conditions. This expectation is tendentious and implies that not body condition as such, but rather the continuity of resource depletion among generations determines long-distance dispersal strategies. Such a response is expected to be adaptive when information on the absence of resources is consistent among generations (Dufty et al. 2002).

Dispersal is favored in habitats that undergo temporal changes in quality (McPeek & Holt 1992; Travis & Dytham 1999; Travis 2001). Under these environmental conditions, it is adaptive as it allows individuals to track and exploit patches with transient resource availability and/or it enables parents to have their offspring scattered throughout the landscape, thus hedging the bets of locating a suitable patch (Ronce 2007). Likewise, spiders living in unstable habitats have higher ballooning propensities than spiders from more permanent habitats (Thomas & Jepson 1999; Entling et al. 2011), and food shortage and overcrowding are proximate cues of habitat deterioration (Weyman et al. 2002; Bonte et al. 2003a). Long-distance dispersal by ballooning is an "aerial lottery" that entails high mortality because spiders lack efficient control mechanisms to guide their flight (Suter 1999). Therefore, individuals are expected to maximize the amount of habitat information before initiating aerial dispersal. By manipulating feeding regimes across two generations we have demonstrated that *E. dentipalpis* do integrate maternal and direct cues of food availability in decision-making for long-distance dispersal. Given the short maturation times and infrequent displacements of juveniles, maternal effects represent an efficient source of information about the recent past environment and allow offspring to put current information into a broader temporal context, confirming our expectations on information use for long-distance dispersal events. Moreover, this factorial experiment serves to highlight that reactions of spiders to food supply are more complex than previously assumed and corroborates previous suggestions (e.g. Ronce et al. 2001) that the influence of an ecological factor on dispersal is not confined to a single point in time but acts through its temporal variation across generations.

Maternal effects are increasingly being recognized as key determinants of population dynamics, because they not only affect offspring life-history traits, such as survival and reproduction (Rossiter 1996; Benton et al. 2001, 2008), but also dispersal behavior and gene flow. Therefore, maternal effects have the potential to change the dynamics of spatially structured populations (Donohue 1999; Ronce 2007; Bonte & De la Peña 2009). Our results demonstrate that maternal and current food supplies differentially affect *E. dentipalpis* dispersal strategies, and confirm that these are driven by different evolutionary mechanisms. Although within-habitat rappelling was exclusively influenced by acute starvation, the interaction between maternal and current environments shaped long-distance ballooning. As such, both immediate and past environmental conditions are expected to have important consequences for metapopulation cohesiveness and persistence by inducing lag responses in population dynamics (Plaistow & Benton 2009). Taken together, our findings highlight the need to consider maternal effects on dispersal in order to understand the spatial dynamics of populations living in fragmented landscapes.

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Figures

Fig. 7.1. Effect of current feeding treatment (mean ± SE) on *Erigone dentipalpis* life-history traits. (A) Maturation latency. (B) Longevity.

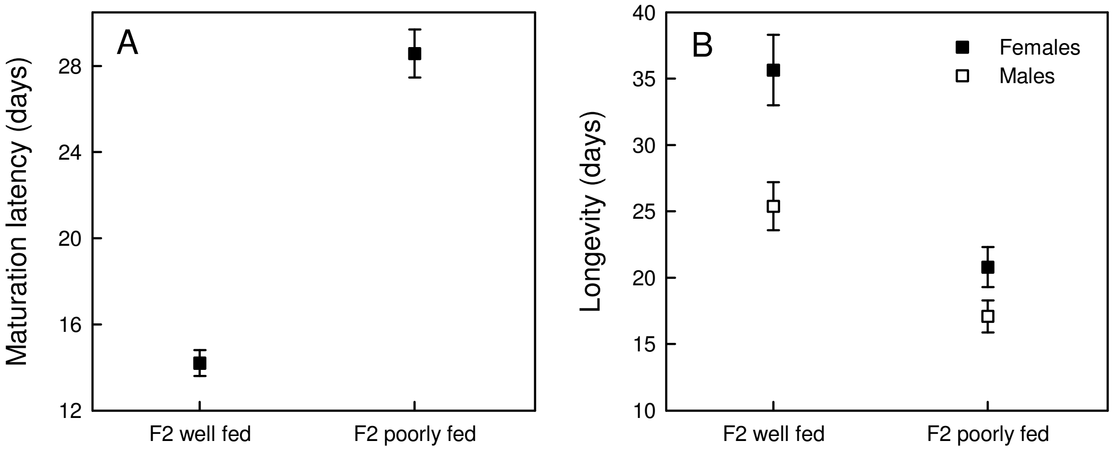
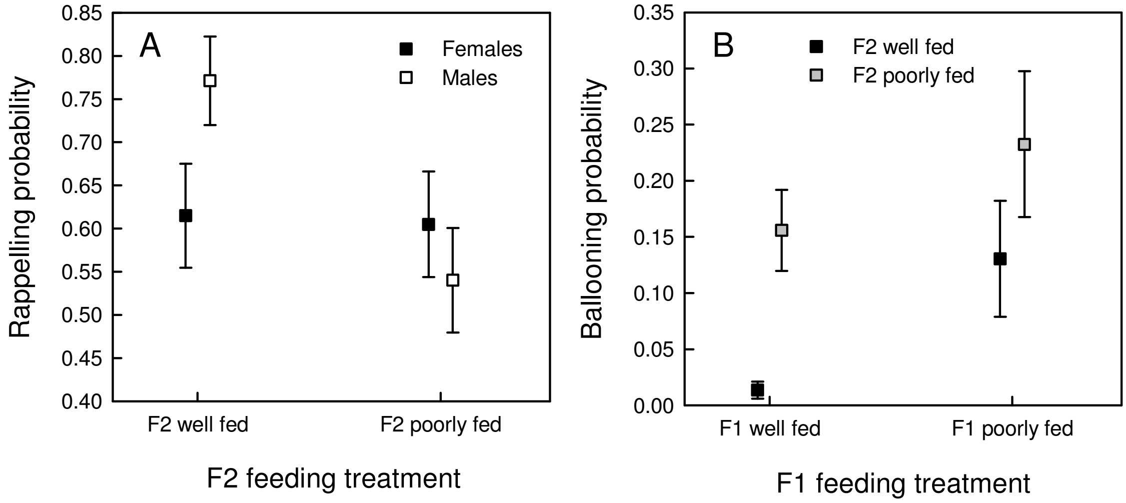


Fig. 7.2. Effect of feeding treatment (mean ± SE) on *Erigone dentipalpis* breeding dispersal propensity. (A) Effect of sex x current feeding treatment on rappelling probability. (B) Effect of current x maternal feeding treatment on ballooning probability.



8

General discussion


L. Mestre

The spider assemblage in the citrus grove

In this PhD thesis we employed various methods to sample spiders in the grove: beating trays and visual searches in the canopies, cardboard bands in the trunks, and pitfall traps in the ground. With beating trays, we sampled an area of the grove for an 8-year period (chapter 4) and another area for almost 2 years (chapter 2). We retrieved 91 spider species, the most abundant (> 5% of the total catch) being *Philodromus cespitum* (Philodromidae), *Theridion* spp. (Theridiidae), *Neoscona subfusca* (Araneidae), *Anelosimus vittatus* (Theridiidae), *Clubiona leucaspis* (Clubionidae), and *Icius hamatus* (Salticidae). We obtained 54 species using pitfall traps for nearly 2 years (chapter 2). The most abundant species were *Pardosa proxima* (Lycosidae), *Dysdera crocata* (Dysderidae), *Pelecopsis parallela* (Linyphiidae), *Pardosa hortensis* (Lycosidae), and *Zodarion styliferum* (Zodariidae). The spider fauna of the canopies and the ground barely overlapped, since only a few individuals from 14 species occurred in both layers. By contrast, using cardboard bands for 4 months (chapter 3) we sampled 30 spider species that —except two of them— we had previously found in the canopies or on the ground. The 5 most common species we retrieved represented more than 80% of the individuals: *Cheiracanthium mildei* (Miturgidae), *C. leucaspis* (Clubionidae), *I. hamatus* (Salticidae) as canopy spiders, and *Euryopis episinoides* (Theridiidae) and *Nomisia exornata* (Gnaphosidae) as ground spiders.

The dominant spider families in this grove are also common in citrus stands worldwide (Carroll 1980; Amalin et al. 2001), but the specific assemblage composition bears similarities with groves only from the Mediterranean area. In the canopies, *C. mildei* and *Theridion* sp. are the most abundant species in Israelian citrus stands (Mansour & Whitecomb 1986), whereas in Italy and the south-east of Spain, these species are *C. leucaspis* and *I. hamatus* (Benfatto et al. 1992; Barrientos et al. 2010). In the ground, the dominant species in south-eastern Spain are *P. cribata*, *Z. cesari* and *Trachyzelotes fuscipes* (Monzó et al. 2011). *C. mildei*, *Philodromus* and *Zodarion* spiders are also abundant in other types of Mediterranean groves, like almond, cotton and olive (Pérez-Guerrero et al. 2009; Benhadi-Marín et al. 2011; Cárdenas et al. in press). Comparisons between studies though, should remain at a superficial level due to the diversity of sampling methods and agricultural management practices.

Spiders in the food web of the grove

In chapter 2, a 21-month factorial exclusion of ants and birds from the tree canopies showed the much greater importance of ants relative to birds on the spider assemblage. The principal effect of ants was reducing the abundance of 4 species of the web-building families Araneidae and Theridiidae. By contrast, we did not detect any influence of birds on either canopy or ground-dwelling spiders, nor was there evidence of non-additive effects of ants and birds on spiders. However, the influence of sampling methods on the results of a study should always be kept in mind (Coddington et al. 1996; Scharff et al. 2003; Cardoso et al. 2008, 2009). Thus, in chapter 3 we studied again the effect of bird exclusion on the canopy spider assemblage, but this time we sampled the trees with visual searches and cardboard bands. The relative proportions of web-building families differed between visual searches and beating trays; particularly, Araneidae were much better represented in visual searches. Also the number of individuals per sample was twice as high with visual searches as with beating trays (unpublished). Both these differences may have allowed us to detect a negative effect of birds on Araneidae and Theridiidae numbers in the canopies. Cardboard bands also yielded different species proportions and higher numbers of individuals of hunting spiders, but no species were affected by bird predation. Finally, the method of visual searches allowed us to follow the day-night activity of araneid spiders and to show that the strength of bird predation does not differ between day- and night-active Araneidae, a possibility that had never been tested before.

Chapter 4 documents an 8-year ant exclusion experiment from the canopies and its effect on the spider assemblage. Unlike in the shorter ant-and-bird exclusion study, which ran in parallel to this experiment for the 2 last years (2008-2009), beating trays showed a clear negative effect of ants on species richness and on the abundances of not only web-building but also hunting spiders (10 species in total). Thus, the negative effects of ants patrolling in the canopies are rather widespread within the spider assemblage of this grove. However, there were also 3 ant-eating spider species that responded positively to ant presence, a result that was masked when analyzing the spider assemblage at the family level. On the other hand, the influence of ants varied considerably over time: while during the first 3 years there were no apparent effects of ants on the spider assemblage, the following year emerged a weak effect that turned strong during the last 4 years. These strikingly different outcomes within a given experiment can but emphasize the crucial importance of long-term studies in ecology, yet research on intraguild interactions mostly relies on experiments spanning less than 2 years (but see Lenoir et al. 2003; Piñol et al. 2012a).

In chapters 2, 3 and 4 we studied the effects of intraguild interference on spider assemblages at the finest taxonomic resolution (species level), except for the effect of birds on web-building canopy spiders in chapter 3 (family level). While there are many studies describing intraguild interactions between spiders and other taxa, we are not aware of any of them that examine the spider assemblage thoroughly; at most some analyse the effects of intraguild interactions on broad functional groups (Halaj et al. 1997; Mooney 2006, 2007; Mooney & Linhart 2006) or on selected families (Sanders & Van Veen 2011). But in this thesis we have shown the usefulness of species-level identifications: however demanding they are, the information they provide about the interactions taking place in the food web cannot be accurately retrieved at higher taxonomic levels. Unfortunately, there is a dramatic lack of knowledge about the faunas of spiders and other arthropods of many parts of the world, especially the tropics, where countless species are still to be described and identification resources are lacking, leaving taxonomic surrogacy as the only possible alternative (Cardoso et al. 2004, 2011).

From the more than 120 spider species present in the grove, in chapter 5 we selected the most common 25 together with other predatory and herbivorous arthropods, and we conducted stable isotope analyses to uncover the main trophic links within the arthropod food web. We found that ant exclusion from the canopies did not influence the isotopic signatures of spiders, despite the negative impact of ants on insect abundance (Piñol et al. 2012a,b) and the fact that some spider species preyed on them, as shown by the analyses. Stable isotopes also revealed that many trophic groups exist among the spider assemblage and that, once more, these bear no relationship with family or guild classifications. Moreover, spiders were usually two trophic levels above their potential herbivorous prey. Overall, the stable isotope analyses confirmed that omnivory and intraguild predation are fundamental properties of this food web. To our knowledge, there is only one other study analyzing the role of spider species in food webs, in a central European grassland ecosystem where multiple trophic levels within the spider assemblage were also found (Sanders & Platner 2007).

Resource-dependent dispersal and spider populations

In chapters 6 and 7 we showed some mechanisms by which resource availability influences dispersal in two spider species, *Cyrtophora citricola* and *Erigone dentipalpis*, that are common in arable land. We selected these as model species because we knew the types of costs of their emigration and site selection strategies, which enabled us to make explicit predictions about the changes in dispersal behaviour in response to a given factor.

Chapter 6 reports a combination of field surveys and experiments in semi-field conditions to study how prey availability influenced colony group size in the araneid *C. citricola*. We discovered that prey remains as cues of prey availability were much more important in determining site selection than actual food supply in influencing subsequent site tenacity, ultimately causing spiders to aggregate at prey-rich sites, where the size of colonies was more than 10 times as large as in prey-poor sites. The reluctance of this species to emigrate after site selection is probably due to the high energetic investment required to build a web, which indicates that indirect information about prey availability is crucial for *C. citricola* because it allows individuals to make settling decisions without spending energy on a costly structure (Pasquet et al. 1994). In Chapter 7 we assessed the importance of maternal effects as indicators of past prey availability and of current food supply on the dispersal strategies (rappelling, ballooning) of the linyphiid *E. dentipalpis*. Because rappelling is an energetically expensive means to leave a habitat, it was not surprising that rappelling frequency did not increase under food restriction. On the contrary, maternal food deprivation increased the offspring's ballooning propensity irrespective of their current feeding state, thus demonstrating that high-risk long-distance dispersal strategies depend on information of broad scope such as maternal effects (Clobert et al. 2008).

Together, our findings in chapter 6 and 7 highlight the role of indirect information of prey availability in spider dispersal and hence the need of considering them as factors influencing population dynamics. Furthermore, communities and food webs are not isolated entities but they exist within a spatial context and are interconnected by dispersing individuals of potentially interacting species (metacommunity dynamics [Wilson 1992; Leibold et al. 2004]). Indeed, dispersal plays a crucial role in modifying the properties of food webs, for instance, by altering the populations of species, thereby changing the outcome of interspecific interactions. Unfortunately, empirical knowledge about spatial food web dynamics is currently fragmented and scarce; much progress has yet to be made in quantifying dispersal traits of species and in characterizing the spatial properties of species interactions (Amarasekare 2008; Massol et al. 2011).

Future perspectives

While the field experiments we performed in chapters 2-4 reveal the nature of the intraguild interactions between spiders, ants and birds in the study system, they provide no information about the underlying mechanisms to these effects. It is commonly assumed that intraguild effects are caused by direct predatory or competitive interactions, but these effects could also arise through changes in the behaviour of one species upon detecting the presence of the other so as to avoid a harmful encounter. These behavioural changes are called "trait-mediated effects" and can sometimes be stronger than direct effects (Abrams et al. 1996; Peacor & Werner 2001; Werner & Peacor 2003; Preisser et al. 2005), thus playing a key role in food webs by modifying the species' population dynamics and inducing trophic cascades (Schmitz et al. 2004; Schmidt-Entling & Siegenthaler 2009; Hawlena et al. 2012). Most of the studies on trait-mediated effects focus on the effects of predators on herbivore prey, which change their feeding behaviour and habitat use (Preisser & Bolnick 2008; Steffan & Snyder 2010), but their importance on intraguild effects remains to be investigated. Future research should thus focus on uncovering the general significance of trait-mediated effects on intraguild interactions. Laboratory trials could be useful to determine whether individuals are able to detect the presence of intraguild species through different cues. In chapters 6-7, we showed how spiders were able to retrieve indirect information about prey availability to reach a dispersal decision (site-selection, emigration) and how this could affect spider populations. The influence of trait-mediated effects on dispersal behaviour has not yet been addressed, although given the strong reductions of spider densities caused by ants and birds, these may be important factors inducing dispersal.

The analyses of stable isotopes performed in chapter 5 gave insights on the structure of the arthropod food web, yet to know the specific diet composition of predators other methods have to be employed. DNA-based gut content analysis, which relies on the polymerase chain reaction (PCR) to amplify the DNA strands of the target prey inside the gut of predators, has been widely employed over the recent past years to study the predation rates of spiders on certain arthropod species (Agustí et al. 2003; Kuusk et al. 2008; King et al. 2011). The basic technique requires a primer for each target prey species to be developed, making it unfeasible to identify the whole range of prey of generalist predators like spiders (King et al. 2008). Ecologists have just begun to use universal primers that yield hundreds of DNA fragments that can be now sequenced fast and at reasonable costs thanks to the continuous refinement of high-throughput sequencing technologies, which will clearly revolutionize the study of food webs in the years to come (Goldberg et al. 2006; Loman et al. 2012).

Conclusions

1) Beating trays show that ants have a pervasive influence on the canopy spider assemblage of the citrus grove. However, the effect of ants on spiders varies markedly between years, highlighting the importance of long-term studies in ecology (chapters 2, 4).

2) Beating trays do not detect an effect of birds on the spider assemblage, nor do they provide evidence of non-additive effects of ants and birds on spiders (chapter 2).

3) Visual search is the only sampling method that detects an impact of birds on spiders, that is, a negative effect on the abundances of canopy-dwelling Araneidae and Theridiidae. The effect of birds, however, is not different between day-active or night-active Araneidae (chapter 3).

4) Stable isotope analyses reveal that the trophic positions of spiders are very varied and that spiders usually occupy a much higher trophic level than the most abundant prey. These results indicate that omnivory and intraguild predation are important features of the arthropod food web in the grove (chapter 5).

5) Species from the same family show very different responses to intraguild interference and have also different trophic positions in the arthropod food web. Thus, grouping species into families and guilds as surrogates of species-level identifications is not a useful strategy in community ecology studies involving spiders and, possibly, other hyperdiverse taxa (chapters 4, 5).

6) Spiders are able to modify their dispersal behaviour not only in response to food intake, but also according to indirect information on prey availability (prey remains, maternal effects) as an indicator of habitat quality. These sources of information should therefore be regarded as relevant factors shaping population dynamics (chapters 6, 7).

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