Seasonal, spatial and diel partitioning of *Acyrthosiphon pisum* (Hemiptera: Aphididae) predators and predation in alfalfa fields

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HIGHLIGHTS

- *Acyrthosiphon pisum* was used as sentinel prey in alfalfa to study predators segregation.
- A seasonal, day–night and foliage–ground segregation of predators was observed.
- Coccinellids were the main predators, with daytime activity mainly in spring and summer.
- Syphids were the main nighttime predators in spring and summer.
- More predatory activity was observed on the foliage than on the ground.

GRAPHICAL ABSTRACT
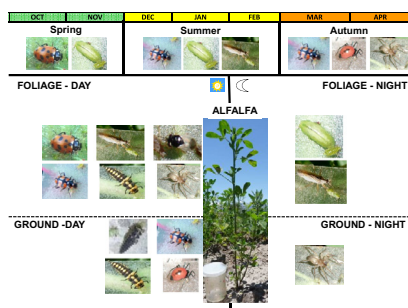
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ABSTRACT

Predators are important natural enemies, often responsible for preventing pest population outbreaks of in many crops. Complementarity in resource use involves spatial or temporal segregation of predators, which can result in better biological control when several species of natural enemies share a prey. In this study, we investigated the seasonal, spatial and diel segregation of *Acyrthosiphon pisum* predators and its predation in alfalfa fields, by setting out cards with sentinel aphids, and making observations every 3 h for a 24 h period. A temporal and spatial segregation of predators was observed. Coccinellids were the most abundant predators, representing 51% of the total observations, followed by syrphid larvae. Coccinellids were also responsible for high levels of predation throughout the year, although the species responsible varied from spring to summer and autumn. On the other hand, syrphids were only found in spring and summer, while spiders only in autumn. Predator species also differed on their preferred sites for predation, with Heteropterans and syrphids found on the foliage, the spider *Neomaso articeps* only on the ground, and coccinellid and Anyphaenidae species on both sites. The two main predator groups also showed distinct diel patterns, with coccinellids observed only during day and syrphids only during night. This predatory activity corresponded with aphid predation, observing more predation in spring, on the foliage and during the day time. The proportion of predators observed preying on cards in the different seasons did not corresponded tightly with their field abundance, particularly in the case of coccinellids, which maintained high levels of predation in spite of great variations in its field abundance. Our results support the hypothesis of a spatio-temporal segregation of the predators associated with *A. pisum* in alfalfa, which might be beneficial for the outcome of biological control of this pest.

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1. Introduction

Predators are important natural enemies of pests in many crops and are often responsible for preventing outbreaks of pest populations. The relationship between the diversity of natural enemies' assemblages and the efficiency of biological control has been largely discussed (Snyder et al., 2005, 2006; Casula et al., 2006; Letourneau et al., 2009; Straub et al., 2008; Snyder, 2009). Although neutral or negative effects might occur if mechanisms like functional redundancy or intraguild predation occur (Casula et al., 2006; Straub et al., 2008), frequently a higher diversity of consumer communities may lead to greater total prey consumption via a sampling effect (i.e., more species are more likely to include particularly efficient predators) or species complementarity in resource use (i.e., natural enemies with different feeding niches) (Loreau and Hector, 2001; Casula et al., 2006; Snyder et al., 2006; Straub et al., 2008; Letourneau et al., 2009; Northfield et al., 2010).

Theoretical and empirical evidence suggest that natural enemy species with similar traits, such as microhabitat use and phenology, may result in strong competition for resources (Straub et al., 2008). On the other hand variation in how, where and when enemies attack prey, may yield complementary prey suppression (Snyder et al., 2006). Therefore studying if predators in a given system have different traits regarding spatial (microhabitat) and temporal (season, time of day) predatory activity, is the first step to identify the natural enemies functional groups present and how they might be potentially partitioning a resource (Straub et al., 2008; Snyder, 2009). Spatial prey partitioning can occur when a single pest species have more than one feeding place, and different predators can specialize on these different places, without directly interfering with each other, thereby complementing prey predation (Losey and Denno, 1998a, 1998b; Grez et al., 2007; Straub and Snyder, 2008; Northfield et al., 2010). Seasonal prey partitioning occurs when different species of natural enemies colonize the crop and reach their highest abundance in different times of the year, either as a response of predators to prey density or by complementary phenology, with some species appearing only early or late in the season, preying when other predator species are not present (Roy et al., 2005). Diel partitioning takes place when predators forage at different times of the day, resulting in ensembles that differ greatly between day and night. This segregation makes less likely that predators encounter each other, and thus, may lower direct antagonistic interactions, like intraguild predation. This segregation mechanism has been poorly explored in resource partitioning studies (Pfannenstiel and Yeargan, 2002; Nakashima and Akashi, 2005; Lucas, 2005, 2012). The spatiotemporal activity observed for predators might be an active choice or the result of biological constraints, which in turn could be modulated by biotic and/or abiotic factors (e.g. Gable et al., 2012). Therefore the patterns observed may change under varying conditions but limited by the extent of the species plastic behaviour.

Alfalfa (Medicago sativa L.) is a widely distributed crop around the world that harbours a high diversity of insects, including herbivores and their natural enemies (Flint and Dreistadt, 1998; Gerding and Devotto, 2000; Pons et al., 2005; Rakhshani et al., 2009). Among them, the pea aphid, Acyrthosiphon pisum (Harris) (Hemiptera: Aphididae) is one of its most important pests all over the world (Summers, 1976; Nakashima and Akashi, 2005; Rakhshani et al., 2009). This aphid, and others present in alfalfa, is preyed upon by a variety of aphidofagous predators like carabids, coccinellids, syrphids, nabids, anthocorids, geocorids, chrysopids and spiders (Wheeler, 1977; Gerding and Devotto, 2000; Lucas, 2005; Grez et al., 2007, 2010). In alfalfa fields many of these predators coexist, but it is not known if they, and their predation activity,

partition either in space or time. In this study, we aimed to determine the seasonal, spatial and diel activity of A. pisum predators and aphid predation patterns in alfalfa fields in central Chile. We hypothesized that the predatory activity of the aphidophagous species found in alfalfa differs in space, season and time, and consequently the spatiotemporal pattern of aphid predation.

2. Materials and methods

2.1. Field sites

The experiments were carried out in alfalfa fields (cultivar WL903 WL-Agvance S.A.) at the Agricultural Experimental Research Station, of the Pontificia Universidad Católica de Chile, located in Pirque – Chile (33°40′09S, 70°36′31W), from October 2009 to April 2010. No pesticides were used, and observations were made when alfalfa was between 50 and 70 cm height. Temperature was measured during the experiments with Hobo® Weather Station data logger (Pro series Onset Computer Corporation, USA).

2.2. Aphid predation and predator activity

To determine aphid predation and the predators responsible for it, six live A. pisum (4th instar nymphs and adults) were mounted in transparent plastic cards (5.5 × 1.5 cm) using a glue spray (Spray-Mount, 3M, USA). Aphids were obtained from a laboratory colony on broad bean (Vicia faba L.). Cards were randomly placed near the centre of the fields, separated at least by 4 m, in 42–63 sampling points. In each sampling point, two cards were set, one fixed at the ground level with a cocktail stick, and the other on the foliage, 20–30 cm above the ground, attached to the plant with a wire (Fig. 1). Cards were placed in the field at mid morning, and then monitored at 3 h intervals for the next 24 h. Therefore, there were four observations during the day (10:00, 13:00, 16:00 and 19:00 h), and four during the night (22:00, 1:00, 4:00, and 7:00 h). The 7:00 am time was considered part of the night time observations because it represented predation that occurred between 4:00 and 7:00 am, although in summer at this time it was already clear. In each observation time, the number of aphid preyed upon on each card was noted, and cards were replaced when 50% or more aphids were consumed. Additionally, when

Fig. 1. Sentinel aphids on cards positioned at (A) foliage and (B) ground level.

predators were observed feeding upon aphids on the cards they were identified to species level when possible. Observations were done in spring (October 28, November 5, 19 and 25), summer (December 10, January 12 and 20) and autumn (April 8 and 13), during 2009–2010 season.

2.3. Predators and aphids abundance in the fields

Because the method used to asses predatory activity could be biased for or against certain species, predator's abundance in the fields were estimated parallel to the above observations. Aphid predators were sampled by taking 12 sweep net samples (10 sweeps each, with a 30 cm diameter net) in the area. Samples were taken every six hours, at 13:00, 19:00, 1:00 and 7:00, and then pooled for the analysis. Additionally, aphid abundance was measured by randomly sampling 50 alfalfa stems, and the number of aphids present was counted in the laboratory.

2.4. Data analysis

To analyse the diel patterns of predator activity and of aphid predation (proportion of cards with predation in each 3 h observation period) circular statistics was used. This type of analysis is appropriate when data is collected in a circular interval scale, like time of day, where there is no true zero point and designation of high or low values is arbitrary (Zar, 1999). In this method, units are divided in 360 equal intervals (degrees) and data are described by its angular direction. Statistical procedures are then carried out using the sine and cosine of the angles, instead of the raw angle measures (Fisher, 1993; Zar, 1999). For the circular statistics analyses we pooled all the observations within a season and recorded the frequency of occurrence in each observation period. Analyses were run by season (spring, summer, autumn) for predator activity, considering those taxa that had more than 15 observations in a season, and by season and position (foliage or ground) in the case of aphid predation. To determine if observations of predatory activity and predation were uniformly distributed during the 24 h period, a Rayleigh uniformity test was run (Fisher, 1993; Zar, 1999) using Oriana software (Rockware, 2010).

To determine the effect of season and position on aphid predation we calculated the percentage of cards with aphids preyed upon (cards with 1 or more aphids preyed upon/total numbers of cards deployed) as a measure of predation incidence. We also estimated of the percentage of aphids preyed upon (aphids preyed upon /total aphids offered) and in a 24 h as a measure of predation intensity. Data was arcsine [square root (X)] transformed and were analyzed with two way ANOVA, with means differences separated by Tukey HSD test ($p < 0.05$). Differences in field predator and aphid abundance between seasons were analysed by ANOVA, with each sampling date representing a replicate, and means differences separated by Tukey HSD test ($p < 0.05$).

3. Results

3.1. Predator activity

A total of 302 observations of predators feeding on cards were recorded in the whole experiment (Table 1). Coccinellids were the most abundant predators, representing 51% of the total observations, with *Eriopis connexa* Goeze being the most frequent species, both as adult and larvae. The second most frequent predator was *Allograpta exotica* Weidenmann (Diptera: Syrphidae), with 28% of the total observations. Other predators were hemipterans, mainly *Nabis punctipennis* Blanchard (Nabidae) and *Geocoris sobrinus* (Blanchard) (Lygaeidae), with 8% and 2%, respectively, and the

Table 1
Predator activity on cards (occurrences) with *Acyrthosiphon pisum* as a sentinel prey, by season and position (G = ground; F = foliage).

		Spring		Summer		Autumn		Total	
		G	F	G	F	G	F	G	F
Coccinellidae									
E. connexa	Adults	1	8	14	46	8	13	23	67
	Larvae	1	4	5	2	9	7	15	13
H. variegata	Adults	0	5	0	6	0	4	0	15
	Larvae	8	8	1	1	0	0	9	9
H. convergens	Adults	0	2	0	0	0	0	0	2
A. bipunctata	Adults	0	1	0	0	0	0	0	1
Syrphidae									
A. exotica	Larvae	4	31	1	47	0	0	5	78
Nabidae									
Nabis spp.		0	1	0	22	0	1	0	24
Lygaeidae									
G. sobrinus		0	0	0	2	0	5	0	7
Aranae									
Anyphaenidae		0	0	0	2	10	7	10	9
N. articeps		0	0	2	0	13	0	15	0
Total		14	60	23	128	40	37	77	225

spiders *Neomaso articeps* Millidge (Lyniphiidae) and species of Anyphaenidae, with 5% and 6%, respectively.

The frequency of the different predators observed on cards varied with season (chi^2 = 142.6; $p < 0.0001$; Table 1). In spring and summer, by far the most frequent predators were syrphids and coccinellids, with *Hippodamia variegata* Hofmann being the most frequent coccinellid species observed in spring and *E. connexa* in summer. Other predators were also found in summer, particularly nabids ($\sim$15%; Table 1). In autumn, *E. connexa* was still the most common coccinellid species, but no syrphids were observed. At this time of the year spiders were more commonly observed preying on the cards ($\sim$40%; Table 1).

In general, there was more predatory activity on the foliage than on the ground (74% vs 26%), but this differed between seasons (chi^2 = 35.6; $p < 0.0001$; Table 1). However there were different patterns among the species (chi^2 = 76.3; $p < 0.0001$). The Heteropterans, *Nabis* spp. and *Geocoris* spp. were found only on foliage, and *Allograpta exotica* larvae were found more on foliage than on the ground (94% vs 6%). The place of coccinellid foraging depended mainly on life stage. Adults were observed preying on the foliage, except for *E. connexa* where 26% were observed on the ground. Larvae were found preying equally on the ground and foliage. The foraging location of spiders varied with taxa. *Neomaso articeps* was observed preying only on the ground, while Anyphaenidae species were found on the foliage and on the ground.

Different diel activity of predators on the cards was observed (Fig. 2). The two main predator groups, Coccinellids and Syrphids (*A. exotica*), showed distinct diel patterns (Rayleigh uniformity test, $p < 0.0001$ for all species and seasons). Coccinellids were observed only during the day, with a mean vector time around 14:00 pm in all seasons. In summer, much less Coccinellids were observed in the midday, when temperatures were close to 30 °C. *Allograpta exotica* larvae were observed preying only during the night, with mean vector time at 1:30 am during the spring and 3:00 am during summer, and it was not observed in autumn (Fig. 2). Nabids in summer were observed during the 24 h cycle with no statistical deviation from uniformity (Fig. 2, Rayleigh test $p = 0.28$) and a peak at 22:00 pm. Spiders were mostly found in autumn, when species of Anyphaenidae foraged at night, with a mean vector time at 22:41 pm (Rayleigh test, $p < 0.001$). On the contrary, *N. articeps* showed a day time foraging activity, similar to Coccinellids, with a mean vector time at 13:00 (Fig. 2, Rayleigh test, $p < 0.001$). In this period, temperatures during night were below 0 °C in some days.
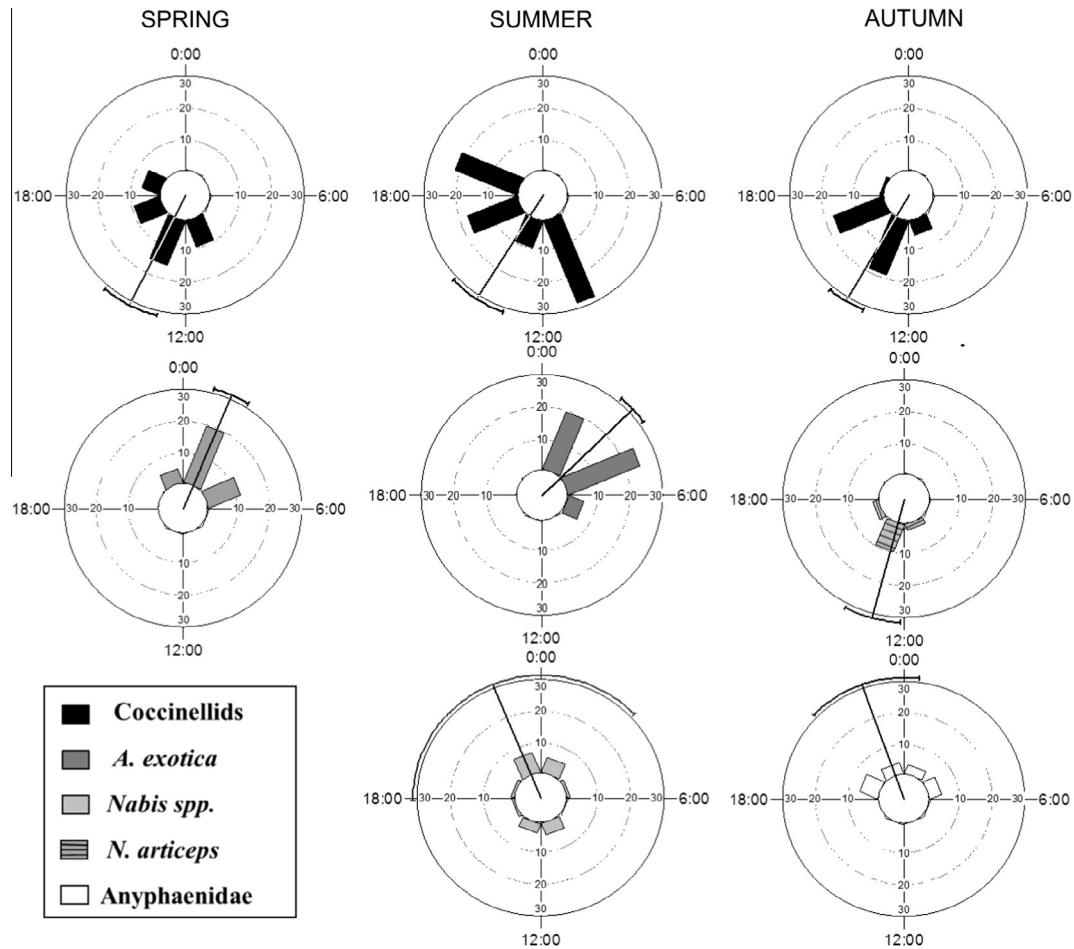
Fig. 2. Diel activity patterns of aphid predators on sentinel cards, presented in columns according to season. Each circular graph represents the activity pattern for one predator type. Bars in the circular graphs present the frequency of occurrence by time of day, with 00:00 as midnight. Numbers on axis indicate numbers of sightings. The line running from the center of the diagram to the outer edge and arc represents the mean time vector (μ) and 95% confidence interval respectively.
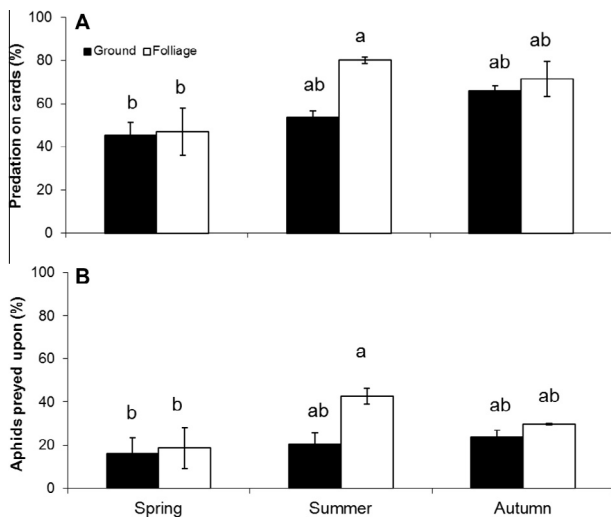
Fig. 3. (A) Percentage of cards with aphid preyed upon, and (B) percentage of aphids preyed upon in a 24 h period in each season (mean of 3 replicates for spring and summer and 2 for autumn ± 1 se) on ground and foliage. Letters above bars denote significant differences (ANOVA, Tukey HSD on transformed data).
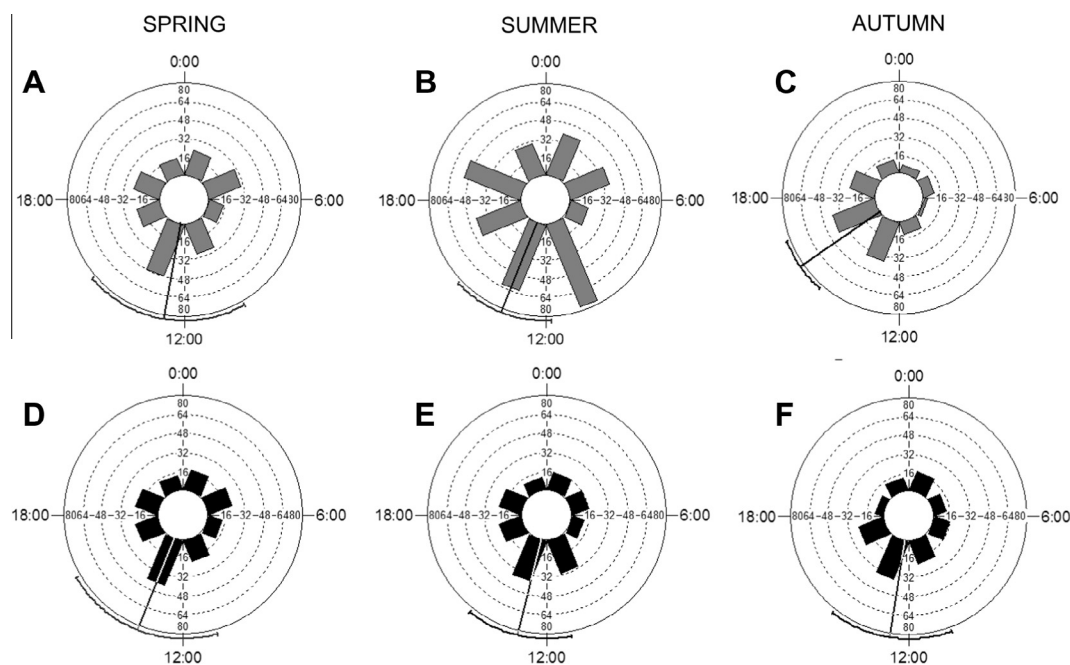
3.2. Aphid predation

There was a significant effect of season ($F_{2, 12} = 6.18$, $P = 0.014$) on the percentage of cards with aphid preyed upon in a 24 h

period, with a lower proportion of cards preyed upon in spring than summer and autumn (Fig. 3A). On a 24 h period, around 67% of the cards showed some predation in summer and autumn, while in spring was only 46%. There was a trend to higher predation on the foliage than on the ground (66% vs 55%), but this was not significant ($F_{1, 12} = 3.36$, $P = 0.091$, Fig. 3A), and no interaction (season x position) effect was found ($F_{2, 12} = 1.85$, $P = 0.200$). There was a significant effect of season ($F_{2, 12} = 6.23$, $P = 0.014$) and position ($F_{1, 12} = 6.25$, $P = 0.028$) on the percentage of aphid preyed upon in a 24 h period, but no significant effect on the interaction of these factors ($F_{1, 12} = 2.41$, $P = 0.131$) (Fig. 3B). A significantly larger proportion of aphids were consumed in summer (32%) than in spring (17%), with autumn having intermediate levels of predation (27%). A larger proportion of aphids were preyed upon the foliage than on ground (30% vs 20%), particularly in summer (Fig. 3B).

Predation was not uniform during the 24 h period, for all seasons and both positions (Rayleigh Test, $p < 0.02$ for all; Fig. 4). Mean vector time for predation was between 12:30 pm and 13:30 pm, except on foliage in autumn, when it was at 15:40 pm (Fig. 4).

3.3. Aphid and predator abundance in the field

Few aphids were found on the stem samplings in the fields. The largest numbers were found in the first samples, but drop to 0 by the end of spring, with a mean for spring of 4.7 ± 2.0 aphids per stem. In summer no aphids were found, and in autumn the mean

Fig. 4. Diel patterns of aphid predation on cards by season (spring = A, D; summer = B, E; autumn = C, F) and position (foliage = A, B, C; ground = D, E, F). Bars in the circular graphs present the frequency of occurrence by time of day, with 00:00 as midnight. Numbers on axis indicate numbers of cards with signs of aphid predation in a 24 h period. The line running from the center of the diagram to the outer edge and arc represents the mean time vector (μ) and 95% confidence interval respectively.

was 0.4 ± 0.2 aphid per stem. However, aphidophagous predators were abundant throughout the seasons. A total of 2527 predators were captured with the sweep nets, with Coccinellids, representing 41% of the total, followed by Hemipterans (34.2%), spiders (14%) and syrphids (10.6%) (Table 2). Summer was the season with more predators captured in nets (9.1 ± 0.2 predators per sample), which was significantly larger than autumn (4.9 ± 0.6), with spring having intermediate values (7.7 ± 1.4) ($F_{2, 6}$ = 8.56, P = 0.036).

4. Discussion

In this study, we found clear evidence for seasonal, spatial and diel segregation of *A. pisum* predators in alfalfa. Regarding seasonal segregation, although coccinellids were observed preying on aphids in similar frequencies throughout the year, other groups showed a marked seasonal segregation, with syrphids present in

Table 2
Abundance of aphid predators in the fields by season (mean per sweep sample, ± 1 se), and total numbers captured in the study. Means followed by different letters in a row denote significant differences (Tukey HSD, α = 0.05).

		Spring	Summer	Autumn	Total
Coccinellidae	Total	5.86 ± 1.43a	2.94 ± 0.72ab	0.56 ± 0.13b	1041
E. connexa	Adults	1.74 ± 0.28a	1.32 ± 0.45a	0.33 ± 0.13a	389
H. variegata	Adults	2.83 ± 0.58a	1.35 ± 0.35ab	0.13 ± 0.04b	479
H. convergens	Adults	0.13 ± 0.06a	0.04 ± 0.03a	0.01 ± 0.01a	19
Several spp.	larvae	1.17 ± 1.06a	0.23 ± 0.07a	0.09 ± 0.05a	154
Syrphidae	Total	1.14 ± 0.14a	1.08 ± 0.71a	0.05 ± 0.03a	269
A. exotica	Adults	0.56 ± 0.04a	0.86 ± 0.60a	0.05 ± 0.03a	183
	Larvae	0.57 ± 0.09a	0.22 ± 0.11ab	0.00 ± 0.00b	86
Nabidae					
Nabis spp.		0.46 ± 0.10a	3.36 ± 0.96a	0.39 ± 0.09a	565
Lygaeidae					
G. sobrinus		0.06 ± 0.06a	0.44 ± 0.26a	0.95 ± 0.01a	161
Anthocoridae		0.16 ± 0.03a	0.75 ± 0.21a	0.10 ± 0.06a	133
Aranae					
Several spp.		0.10 ± 0.08b	0.52 ± 0.24b	2.81 ± 0.27a	355
Total		7.78 ± 1.45ab	9.10 ± 0.19a	4.86 ± 0.57b	2524

spring and summer, nabids mainly in summer and spiders in autumn. A similar seasonal change of predator populations in alfalfa have been also demonstrated in USA (Summers, 1976; Wheeler, 1977), Iran (Rakhshani et al., 2009), Japan (Nakashima and Akashi, 2005) and Chile (Apablaza and Stevenson, 1995; Zaviezo et al., 2004; Grez et al., 2010), and might be related to species phenology or response to prey abundance (Rakhshani et al., 2009). In central Chile, aphid populations have two peaks, one in summer and the other in late autumn. Therefore, the early colonization of alfalfa fields by syrphids in spring and late of spiders in autumn may result in a temporal partitioning of the prey and potentially leading to complementary impact on the aphid populations, a mechanism that has been pointed out by Straub et al. (2008).

Regarding spatial segregation, the predatory species of this guild distributed differentially on foliage and ground. Co-existence of natural enemies of aphids on the same host plant is facilitated by them occupying different strata within the plant (Honěk, 2012). Among the coccinellids, *H. variegata* adults only fed on the foliage, while *E. connexa* adults and larvae of both species foraged on foliage and ground. Syrphid larvae, nabids and geocorids were only found feeding on aphids on the foliage, while the spider *N. articeps* was found preying only on the ground and Anyphenidae spp. were found both on ground and foliage. Spatial segregation has also been observed in other aphidophagous guilds in alfalfa and other crops (Musser and Shelton, 2003; Hoogendoorn and Heimpel, 2004; Nakashima and Akashi, 2005). In our case, although most species foraged preferentially on the plant, some of them were able to exploit the aphids on the ground, like *E. connexa*, *N. articeps* and probably also carabids, although the latter were not observed in this study. This phenomenon may represent what naturally occurs when *A. pisum* drops to the ground to escape from foliage foraging predators (Losey and Denno, 1998a, 1998b; Grez et al., 2007; Francke et al., 2008), likely resulting in complementarity in resource use by predators while lowering the probability of intraguild predation. On the other hand, those species that share the same feeding place, like coccinellid species, may more often engage in intraguild predation or other antagonistic interactions (Grez et al., 2007, 2012), which may interfere with an efficient biological control.
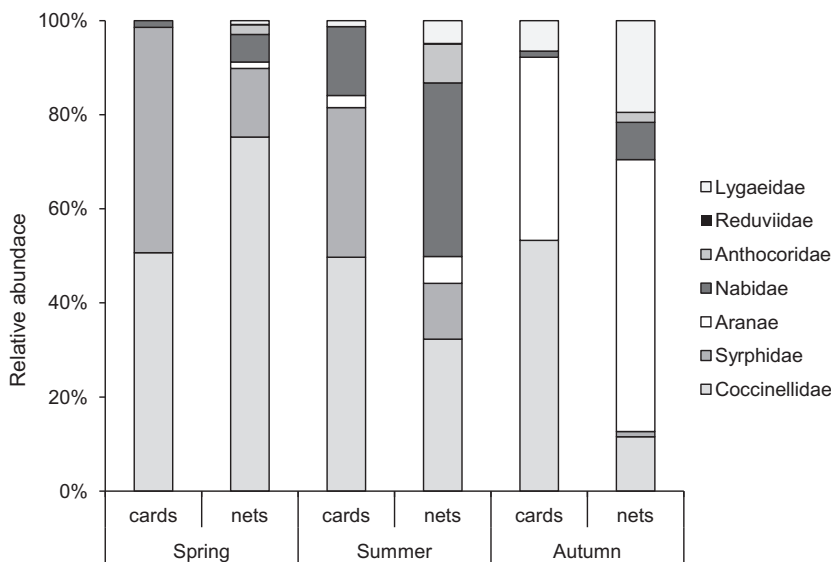
Fig. 5. Relative abundance of aphidophagous predators found preying on cards and in the field according to sweep nets, per season.

Diel segregation was also found among the aphidophagous species in alfalfa. Coccinellids, geocorids and *N. articeps* preyed only during the day, while the syrphid larvae preyed only during night. Nabids and Anyphaenidae spp. didn't have a clear diel pattern. The distinct diel segregation of the predators would decrease the encounter probability of syrphids with most of the other predators of the guild, potentially providing a temporal refuge from intra-guild predation, which is common among species of this guild (Hindayana et al., 2001; Putra et al., 2009). Nevertheless, some species might still be encountered and preyed upon while resting or in a sheltered place.

Predation also varied with season, space and time of the day, being higher in summer and autumn, in the foliage and during day-time, matching the general patterns of predatory activity. The seasonal pattern of predation observed might be influenced by the availability of predators and aphids in the field. The low predation in spring most probably was due to the low abundance of predators and a high availability of aphids in the field, which may have diluted the arrival of the few predators to the sentinel prey. Consequently, the high predation in summer could be the result of the large abundance of predators (1.2 times the amount in spring and 1.9 times the number in autumn) and almost nil abundance of aphids in the field, making the sentinel aphids more prone to be attacked by the natural enemies.

Using sentinel prey, or placed-out prey, showed to be valuable in assessing aphid predation and the species responsible for it. Nevertheless this technique could have made aphids more prone to predation, particularly because pea aphids have developed several behaviours to defend from predators. Thus the relative impact of the various predator species observed here might differ under natural conditions. Additionally, this technique could have been biased for or against certain predators and some of the reasons why this might happen were described by Kidd and Jervis, 1996. Comparing the predatory activity on cards with field abundance according to sweep nets, can give some indication if this was happening in our study. Most of the predatory groups described to be common aphid predators in alfalfa were observed feeding on the sentinel aphids, with the exception of carabids, lacewings, reduviids and anthocorids. Of these, the first two groups (carabids and lacewings) were not captured in sweep nets in this study, nor in a subsequent study carried out in the same fields and using additional sampling techniques (yellow sticky cards and pitfall traps) (Andrade, 2013), suggesting that they were very rare or not present

in the study site. In the case of reduviids, even though they were captured in nets in spring and summer, they represented less than 0.5% of the insects sampled, suggesting that this group was also very rare in the fields (Table 2). On the other hand, anthocorids were sampled with nets throughout the seasons, being between 2% and 8% of the captures, but never observed preying upon the sentinel aphids. Thus, anthocorids could have been missed in the observations because of several reasons: aphids were not a pre-ferred prey, glued aphids were not attractive, and/or they fed too fast lowering the probability of being observed. For the other pred-atory groups, their predatory activity observed on cards approxi-mately corresponded with its relative abundance in sweep nets through the seasons, with Syrphids being relatively better repre-sented on cards than in swept nets, while the opposite happened for Nabids and spiders (Table 1 and 2, Fig. 5). One exception were coccinellids, that varied greatly in abundance through the seasons (10 times more abundant in spring than autumn), but always ac-counted for nearly 50% of the predatory activity (Fig. 5). These re-sults highlight the importance of carrying out direct observations in combination with sampling field abundance in studies that aim to assess the impact that the different predators of a guild have on a pest.

In summary, our results support the hypothesis of a spatio-tem-poral segregation of the predators associated with *A. pisum* in alfa-fa, which may favour resource partitioning while decreasing direct negative interactions among them. This could explain the rich nat-ural enemy guild associated with aphids in alfalfa that might com-plementary impact the outcome of biological control. Nevertheless, manipulative experiments are needed to better understand the mechanisms operating in this system and corroborate this hypothesis.

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