Nonparametric Estimation of Interspecific Spatio-Temporal Niche Separation Between Two Lady Beetles (Coleoptera: Coccinellidae) in *Bt* Cotton Fields

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ABSTRACT Predaceous lady beetles are important natural enemies of many insect pests in agro-ecosystem. The altered agricultural practices associated with widespread adoption of *Bt* cotton may have potential effects on the spatio-temporal patterns of predaceous lady beetles, as the composition and abundance of nontarget sucking pests have been changed in *Bt* cotton fields. In the current study, the spatio-temporal patterns of two important lady beetles, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) and *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae), were surveyed in *Bt* cotton fields. A nonparametric method associated with Monte Carlo tests was used to address and test whether niche segregation occurred between *H. axyridis* and *P. japonica*. The results showed that the dominant region occupied by *P. japonica* was toward northeast across the season, whereas *H. axyridis* had higher presence to the southwest. The temporal patterns of *H. axyridis* and *P. japonica* also differed significantly, and the highest levels of each species occurred in different locations from each other on each sampling date in the same *Bt* cotton fields. In total, there were strong spatio-temporal separation patterns between these two species in *Bt* cotton fields. These spatio-temporal patterns may produce complementary impacts on prey, and this in turn could be used to strengthen the biological control of insect pests by these two lady beetles.

KEY WORDS *Harmonia axyridis*, *Propylea japonica*, intraguild predator, poisson process

Predaceous lady beetles are important natural enemies of pest species, especially whiteflies, aphids, mealybugs, scales, and mites (Hodek and Honěk 2009), and have been widely used in biological control for over a century (Obrycki and Kring 1998). In China, there are 43 species of coccinellids found in cotton fields, comprising 10% of total predators (Zhao 1984). While these coccinellids often successfully suppress outbreaks of aphids in agro-ecosystem (Obrycki et al. 2009, Liu et al. 2012), when intraguild predation and cannibalism occur between or within species, the dominant species may pose significant risks, both to the diversity of other natural enemies of Hemiptera and to their ecosystem services (Ives et al. 2005, Pell et al. 2008, Noriyuki et al. 2012, Katsanis et al. 2013, Tayeh et al. 2014). Because of this, sympatric lady beetles have evolved to differ in their habitat use or spatio-temporal activity

patterns to attack different subsets of the prey population, and this in turn strengthens the biological control of pests at higher levels of predator diversity (Schellhorn and Andow 1999, Snyder 2009, Weber and Lundgren 2009).

Harmonia axyridis (Pallas) and *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae) are two of the most important predaceous lady beetles in farmland and fruit ecosystems, and mainly prey on aphids, small caterpillars, and mites, as well as the eggs of many insects (Zhang et al. 2004, Wang et al. 2007). *H. axyridis* is native to central Asia and has been released as a biological control agent of aphids and scales in five continents (Brown et al. 2011). However, this species has begun displacing native ladybirds and threatening biodiversity in the introduced regions (Koch 2003). Declines of native coccinellids have been attributed to direct interspecific competition for resources, but are also likely to be strongly influenced by *H. axyridis*' role as an intraguild predator (Pell et al. 2008, Ware and Majerus 2008, Gardiner et al. 2011). However, in China, *H. axyridis* and *P. japonica* commonly co-occur in cotton fields (Zhang et al. 2004, Wang et al. 2007), although *H. axyridis* does prey on immature stages of *P. japonica* (Ware and Majerus 2008). *P. japonica* has a smaller body and is more tolerant of high temperatures than *H. axyridis* (Zhang et al. 2004, 2014). These factors may affect the spatio-temporal interaction patterns of *P. japonica* and *H. axyridis* when they share common

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resources. Some studies have reported that *H. axyridis* and *P. japonica* differed in their seasonal patterns in the cotton fields (Zhao 1984, Xu et al. 2003, Lv et al. 2008). However, the spatial distribution of *H. axyridis* and *P. japonica* in *Bt* cotton fields needs further study.

Transgenic *Bt* cotton (*Gossypium hirsutum* L.) expressing the insecticidal crystal proteins derived from *Bacillus thuringiensis* Berliner has been commercially grown in China since 1997, and the area planted to *Bt* cotton reached 4.2 million ha (>90% of cotton in China) in 2013 (James 2014). The widespread adoption of *Bt* cotton has effectively suppressed the cotton bollworms (Wu et al. 2008). However, the reduced pesticide usage associated with growing *Bt* cotton has also led to outbreaks of nontarget sucking pests, such as mirid bugs (Lu et al. 2010) and cotton whitefly (*Bemisia tabaci* (Gennadius); Deng et al. 2003), both of which have become key pests in Chinese cotton production regions (Luo et al. 2014). Furthermore, a fitness cost in *P. japonica* was observed when it fed on *B. tabaci* compared to consumption of aphids (Zhang et al. 2007, Liu et al. 2008). Some studies have reported that *Bt* cotton could significantly increase the population of *P. japonica*, while at the same time reducing the abundance of *H. axyridis* (Zhou et al. 2004). These changes may have profound effects on the spatio-temporal activity patterns between *H. axyridis* and *P. japonica* in *Bt* cotton fields.

In the current study, the distribution of *H. axyridis* and *P. japonica* was surveyed in the *Bt* cotton field. The method developed by Diggle et al. (2005) was used to test whether the populations of *H. axyridis* and *P. japonica* exhibited spatio-temporal niche separation under field conditions.

Materials and Methods

Study Area and Crop Management. The study was conducted at the Experiment Station of Shandong Academy of Agricultural Sciences (36.98° N, 116.98° E), located in Jiyang County, Jinan City, Shandong Province, China, in 2013. This study area is one of the China's most important grain- and cotton (*G. hirsutum*)-producing regions and was recently developed for experimental fields since 2012. Additionally, winter wheat (*Triticum aestivum* L.) and summer cotton or maize (*Zea mays* L.) were usually planted in this study area until 2012. The soil is an alkaline sandy loam.

The experiment was conducted in a large field with 140 m in length (from west to east) and 200 m width (from south to north). The *Bt* cotton (variety: Lumianyan 36), expressing the Cry1A insecticidal crystal proteins from *B. thuringiensis*, was planted during the first week of May and harvested during the second week of October in 2013. The experimental plot was surrounded by summer maize. The *Bt* cotton field was cultivated using standard agricultural management practices. No pesticides were used during the course.

Sampling Methods. The survey was conducted in August and September, as *H. axyridis* and *P. japonica* commonly co-occur and reach peak density during this period (Zhao 1984). The whole field was divided into a grid of 840 cells, with each cell being 6.5 m in length by 5 m in width. One plant in each cell was marked and visually inspected, and the number of all the life stages of *H. axyridis* and *P. japonica* were counted. A total of 840 cotton plants were therefore investigated. Sampling was conducted weekly starting 6 August and ending 17 September, for a total of seven sampling times across the season.

Statistical Analysis. Mixed-model, repeated-measures analysis of variance (ANOVA) was used for analysis of population dynamics of these two lady beetles across the season (Littel et al. 2006). The means on each sampling date were compared by Student's *t* test. The method developed by Diggle et al. (2005) was used to test whether *H. axyridis* and *P. japonica* exhibited spatio-temporal niche separation based on their presence–absence data in each cell. A multivariate pattern exhibits spatial segregation if for at least some points $j \neq i$, where the conditional intensity of type j points at x given a point of type i at x is less than the marginal intensity of type j points at x. Here, x is a location vector, while j and i represent any two point types (in our cases, occurrence of a ladybird species). The kernel function with the bandwidth was used to estimate the type-specific probabilities (Diggle et al. 2005). Monte Carlo sampling was used to test the null hypothesis of no spatial variation between pairs of different point types. We can accept or reject the null hypothesis based on the calculated *P*-value obtained from Monte Carlo simulations. In addition, the temporal changes in spatial segregation between different point types can also be tested through Monte Carlo simulations. All the statistical analysis were performed using R 3.03 (R Core Team 2013) with package "spatialkernel"(Zheng and Diggle 2013).

Results

Abundance and Population Dynamics. Overall, 1,312 individuals of *P. japonica* and 3,240 individuals of *H. axyridis* were collected from the *Bt* cotton field. The population dynamics of *P. japonica* and *H. axyridis* showed similar seasonal activity patterns (Fig. 1). However, on the first sampling date, the number of *P. japonica* significantly exceeded that of *H. axyridis* (df = 1,11746, $t = -2.89$, $P = 0.004$). From 20 August, the population of *H. axyridis* increased quickly and surpassed that of *P. japonica* until the end of sampling (3 September: df = 1,11746, $t = 11.18$, $P < 0.001$; 10 September: df = 1,11746, $t = 18.38$, $P < 0.001$; 17 September: df = 1,11746, $t = 21.25$, $P < 0.001$).

Spatial Niche Segregation. The spatial distributions (Fig. 2) of *P. japonica* and *H. axyridis*, based on presence–absence data collected, showed a strong spatial segregation between these two species (Monte Carlo test, 1,000 simulations, $P = 0.004$). *P. japonica* was more abundant toward the northeast, while *H. axyridis* was more abundant toward the southwest of the study field (Fig. 3).

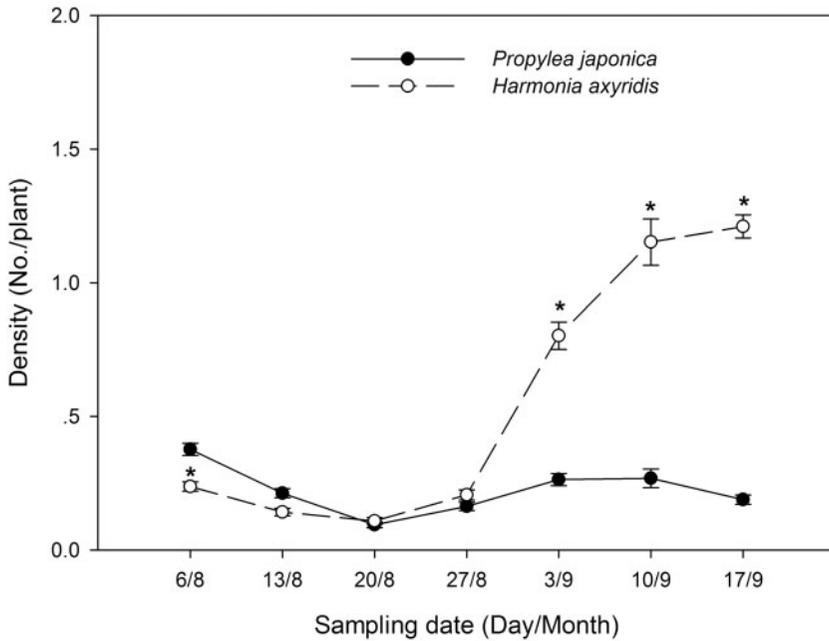**Temporal Niche Segregation.** The spatial distribution (Fig. 4) and the estimated type-specific

Fig. 1. Population dynamics of *P. japonica* and *H. axyridis* across the season in 2013. The asterisks on the *H. axyridis* represents significant difference from that of *P. japonica* on each sampling date.
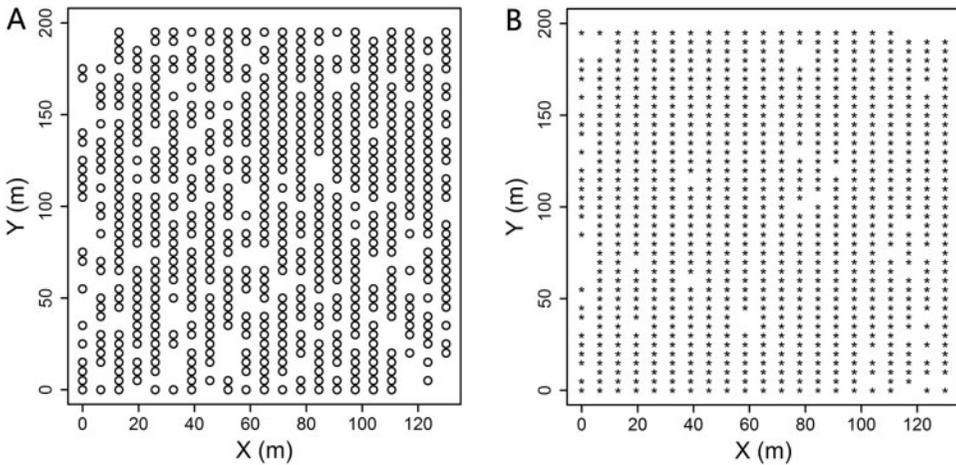

Fig. 2. Spatial distribution of *H. axyridis* and *P. japonica* over the all sampling dates in the *Bt* cotton field. (A) *P. japonica*, (B) *H. axyridis*. X axe represents field length from west to east and Y axe represents field width from south to north. The axes of following figures were alike this.

probabilities of *H. axyridis* and *P. japonica* (Fig. 5) on each sampling date suggest that *P. japonica* and *H. axyridis* showed seasonal activity patterns (for the Monte Carlo test for changes in the type-specific probability surfaces over time, $P = 0.001$, with $s = 1,000$). The regions with higher probabilities of *P. japonica* changed, from the northeast at the first three sampling dates, then northwest, northeast, and finally southeast. The regions with higher probabilities of *H. axyridis* changed from the northwest at the first and second sampling date, to the northwest, south, and finally the northwest.

Discussion

Our study provided evidence for seasonal and spatial segregation between *P. japonica* and *H. axyridis* in *Bt* cotton fields in China. *P. japonica* reached its peak abundance at the early- and mid-stage of the *Bt* cotton, while *H. axyridis* reached peak abundance at the later stage of *Bt* cotton. This phenomenon has been observed by other studies, which found that *P. japonica* reached peak abundance in mid- to late July, while *H. axyridis* reached peak abundance in mid- to late August and early September (Zhao 1984, Xu et al. 2003, Lv et al. 2008, Wang et al. 2013). The different
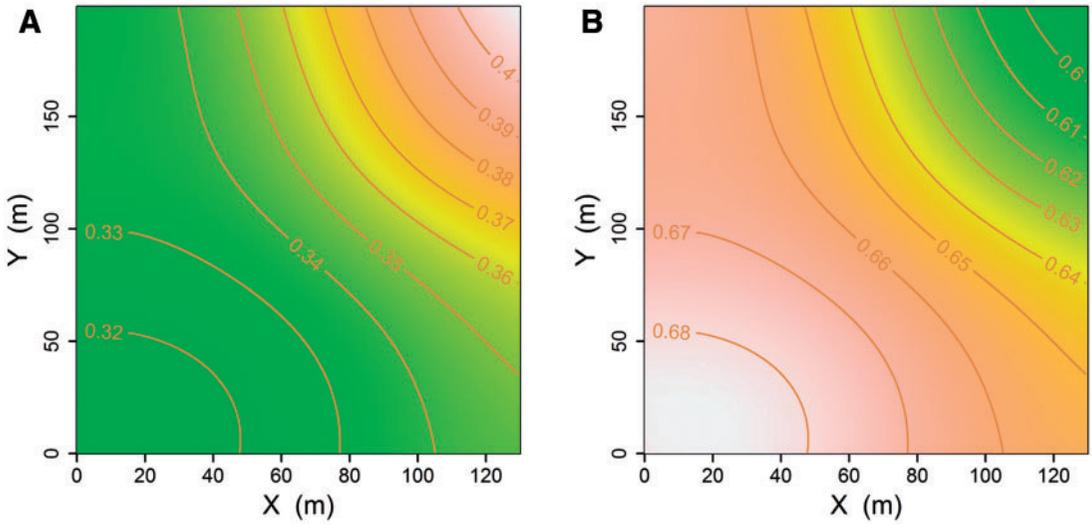
Fig. 3. The estimated type-specific probabilities of the two coccinellid species over the all sampling dates: (A) *P. japonica*, (B) *H. axyridis*.
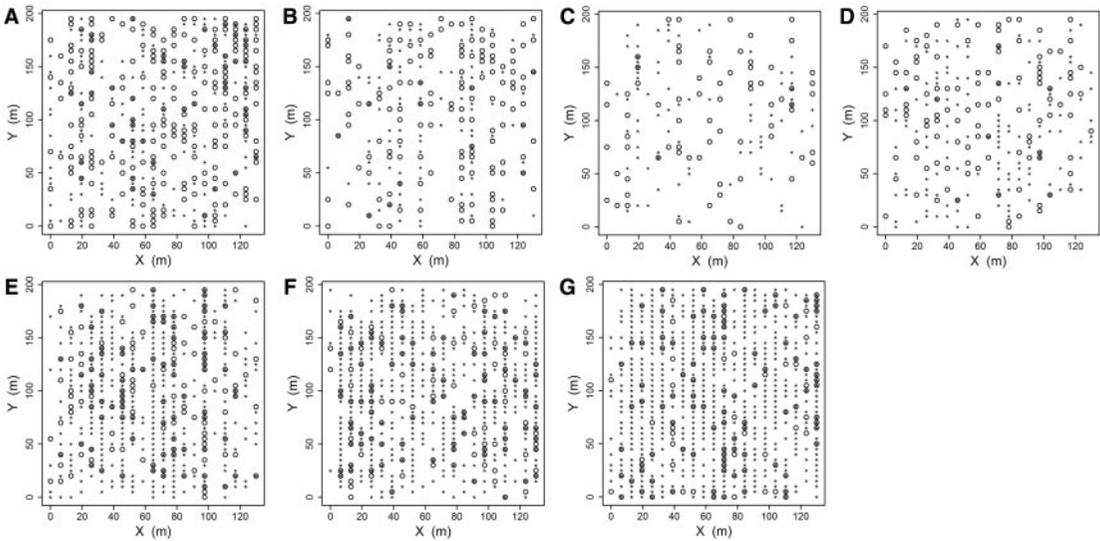

Fig. 4. Spatial distribution of *H. axyridis* and *P. japonica* on each sampling date in the *Bt* cotton field. The asterisks represent the locations of *H. axyridis*, and the black open circles represent the locations of *P. japonica*. (A) 6 August, (B) 13 August, (C) 20 August, (D) 27 August, (E) 3 September, (F) 10 September, (G) 17 September.

responses of *P. japonica* and *H. axyridis* to high temperature may partly explain this division, as temperature can affect the fitness, life history characteristics, distribution, abundance, and phenology of insects (Shi et al. 2013, Knapp 2014, Zhang et al. 2014). In China, the summer is usually very hot and temperatures can exceed 35°C in July. *P. japonica* has been found to tolerate high temperatures and its eggs can develop into adults at 36°C (Zhang et al. 2004, Cheng et al. 2007). However, at 35°C, the eggs of *H. axyridis* could not hatch, and the first-instar larvae subject to this temperature only reached the fourth instar and were unable to

develop to the adult stage (Wang et al. 2009). In addition, differences in coccinellids body size may influence their choice of prey, and coccinellids with larger body size may have requirement for high prey density (Dixon and Hemptinne 2001). Smaller body size may allow some coccinellids to thrive at relatively low aphid densities compared to larger coccinellids species (Honěk et al. 2008). Of the two species studied here, *P. japonica* is smaller, and this may allow it to move into aphid colonies relatively early in their population growth. Meanwhile, *H. axyridis*, with its larger body, arrived later when aphids abundance were higher.
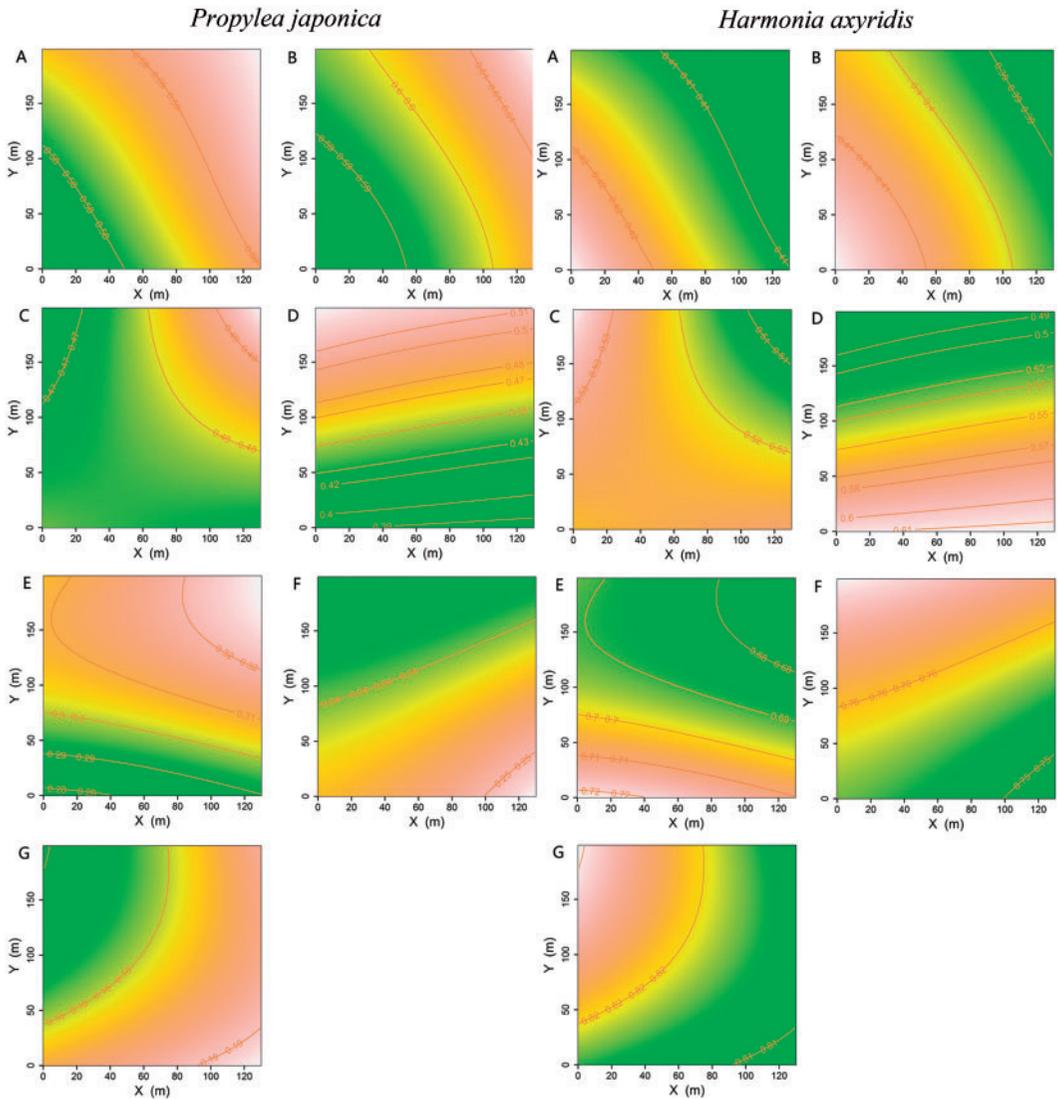
Fig. 5. The estimated type-specific probabilities of *H. axyridis* and *P. japonica* on each sampling date in the *Bt* cotton field. (A) 6 August, (B) 13 August, (C) 20 August, (D) 27 August, (E) 3 September, (F) 10 September, (G) 17 September.

Thus, high temperature and relative body size might explain the differences in temporal activity patterns between *P. japonica* and *H. axyridis*.

P. japonica and *H. axyridis* also showed different spatial patterns in *Bt* cotton fields. Cannibalism and intraguild predation between and within species may encourage each species to occupy a different habitat (Sato et al. 2003, Ware and Majerus 2008). *H. axyridis* is larger and the stronger intraguild predator, and *P. japonica* is the more frequent intraguild prey in interactions between these two species (Sato et al. 2003, Ware and Majerus 2008). When fed *P. japonica*, all fourth instars of *H. axyridis* were able to complete development (Sato et al. 2008). However, the larvae of *P. japonica* are long-legged and mobile and may be able to escape more easily in the wild (Ware and Majerus 2008). Furthermore, gravid females of *P. japonica*

reduced feeding and oviposition when exposed to either its own feces or those of *H. axyridis*, while gravid females of *H. axyridis* reduced rates of feeding and oviposition when exposed to its own feces, but not when exposed to feces of *P. japonica* (Agarwala et al. 2003), suggesting that *P. japonica* females seem to be seeking nearly enemy-free spaces that would enhance their fitness for foraging and oviposition. However, *H. axyridis* females avoid conspecific interactions but not interspecific ones in which they are most likely to prevail as intraguild predators. Also, the abundance of coccinellids in crop fields increased with the compositional and configurational heterogeneity of the landscape (Ouyang et al. 2012, Woltz et al. 2012, Wang et al. 2013, Zhao et al. 2013, Grez et al. 2014). Thus, *P. japonica* and *H. axyridis* can exchange between surrounding maize habitat and *Bt* cotton field in the present study (Ouyang

et al. 2012, Wang et al. 2013), which in turn may impact the distribution of these two lady beetles in the *Bt* cotton field.

As transgenic *Bt* cotton has altered the composition and abundance of nontarget sucking pests, whitefly and mirid bugs have became the dominat species pest insects in *Bt* cotton systems (Wu and Guo 2005, Luo et al. 2014).While *P. japonica* and *H. axyridis* can feed on whitefly nymphs, and the number of nymphs consumed by *H. axyridis* is significantly larger than that consumed by *P. japonica* (Lin et al. 2006), whiteflies are poor prey for *P. japonica*, which does not specializes on this prey group. *P. japonica* prefers aphids when feeding on a mix of aphids (*Aphis gossypii* Glover) and whitefly (*B. tabaci*). While *P. japonica* larvae can reach adulthood when fed either aphid nymphs or whitefly nymphs alone, larval survival was lower, larval development was delayed by 3 d, larval and adults fresh weight was reduced, and adults laid fewer eggs on single-species diets (Liu et al. 2008). Furthermore, when fed on *B. tabaci* eggs alone, only 6.7% of *P. japonica* larvae survived to the pupal stage and those that did developed into abnormal adults that died shortly thereafter (Zhang et al. 2007). Clearly, prey type has a range of effects on the development, survival, and reproduction of *P. japonica*. However, the impacts of whitefly as prey on the biological parameters of *H. axyridis* had been seldomly examined and need to be further conducted. Therefore, the composition and abundance of prey in *Bt* cotton field may affect the establishment and interspecies interaction of *P. japonica* and *H. axyridis*, favoring resource partitioning while decreasing direct negative interactions between species. This in turn may strengthen the biological control of insect pests, such as aphids, whitefly, mirid bugs, and thrips achieved by these two lady beetles in *Bt* cotton fields.

Acknowledgments

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