Functional responses and intraspecific competition in the ladybird Harmonia axyridis (Coleoptera: Coccinellidae) provided with Melanaphis sacchari (Homoptera: Aphididae) as prey

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Abstract. Functional responses at each developmental stage of predators and intraspecific competition associated with direct interactions among them provides insights into developing biological control strategies for pests. The functional responses of Harmonia axyridis (Pallas) at each developmental stage of Melanaphis sacchari (Zehntner) and intraspecific competition among predators were evaluated under laboratory conditions. The results showed that all stages of H. axyridis displayed a type II functional response to M. sacchari. Based on Holling’s disc equation, the instantaneous searching rates were highest (a) and handling time was shortest (T_h) of fourth instar larvae (a = 0.8818; T_h = 3.9 min) and female adults (a = 0.9881; T_h = 3.0 min) at larval and adult stages, respectively. The coefficients of mutual interference (m) assessed by the intraspecific competition equation were higher for fourth instar larvae (m = 0.4764) and female adults (m = 0.4183). The present study indicates that fourth instar and female adult were more effective stages of H. axyridis in the context of biological control but suitable predator densities need to be considered before natural enemy release.

INTRODUCTION

Melanaphis sacchari (Zehntner) (Hemiptera: Aphididae) is a perennial pest of Sorghum bicolor L. Moench and Saccharum officinarum L. which has a wide economic impact (Singh et al., 2004). Melanaphis sacchari originates from Java, Indonesia (Zehntner, 1897). In North America, M. sacchari has been recorded as a sugarcane pest in Florida (Mead, 1978; Denmark, 1988) and Louisiana (Hall, 1987; White et al., 2001). Melanaphis sacchari is initially reported on sorghum when their largely damaging populations invaded in Beaumont, Texas (Villanueva et al., 2014). Melanaphis sacchari is described as a distinct species (Blackman & Eastop, 2006), and their clones are defined by geography including Africa, China, Australia, USA and South America rather than by the host plant (Nibouche et al., 2014). Over the past several years, M. sacchari has caused measurable economic effects due to the damaged plant growth correlated with the sticky “honeydew” covering the plant. Melanaphis sacchari transmits the sugarcane yellow leaf virus causing a 25% reduction in sugarcane yields (Akbar et al., 2010). Control of M. sacchari is difficult as pesticides cannot penetrate the greater canopy of sorghum. Pre- and post-harvest restrictions exacerbate the challenge of pesticide use (Armstrong et al., 2016). Melanaphis sacchari cannot destroy sorghum in a short term period, but the large populations growing out of control lead to the chlorosis correlated with damage of plant tissues because of the rapid aphid reproduction (Colares et al., 2015). Melanaphis sacchari can continue injuring the plants at grain-filling stage and affecting their seeds both in quality and quantity (Chang & Fang, 1984; van den Berg et al., 2003). Moreover, if the M. sacchari colony has the characteristic of thermal tolerance, it could contribute significantly to its pest status under hot summer conditions.

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Studies the functional response and intraspecific competition will provide insights into the prey-predator and predator-predator interactions between *H. axyridis* and *M. sacchari*, which could result in the development of a better strategy for the biological control of *M. sacchari* using *H. axyridis*. Thus, the objectives of this study were to determine the functional response of *H. axyridis* to *M. sacchari* and intraspecific competition among *H. axyridis* under laboratory conditions.

**MATERIALS AND METHODS**

**Insect**

Colonies of *H. axyridis* and *M. sacchari* were maintained in the laboratory and a greenhouse at the experimental farm of the Florida Agricultural and Mechanical University, FL, USA. *Melanaphis sacchari* were reared and reproduced on the leaves of sorghum plants at 16L: 8D, 25°C and 40–60% RH. Approximately 20 larvae or adult *H. axyridis* were reared per plastic container (16 × 22 × 8 cm high) at 16L: 8D, 25°C and 40–60% RH. *Harmonia axyridis* were reared on the sorghum aphid *M. sacchari* from field populations. Prior to the studies, *H. axyridis* were transferred into Petri dishes (9 cm diameter) containing sorghum leaves infested with *M. sacchari*. Neonates were enclosed soon after hatching to avoid sibling cannibalism; female and male adults were also isolated. *Melanaphis sacchari* were supplied in 12 h intervals to guarantee an abundant *H. axyridis* population. For the experiment, individuals of *H. axyridis* were selected for study within 12 h of molting or eclosing. They were starved for 24 h, and then placed on wet paper discs in Petri dishes including less than 12-h-old adults of *M. sacchari*. The dishes were preserved in conditions at 16L: 8D, 25°C and 40–60% RH. Adult *M. sacchari* were not replaced during the tests and nymphs from adult *M. sacchari* were removed every 4 h by smooth brushes.

**Functional response**

To examine the functional response of *H. axyridis* at each developmental stage on *M. sacchari*, prey densities tested were 2, 4, 8, 16, 32, 64, 128 and 256 aphid adults for four instars of larvae (first, second, third, fourth instar) and adults in both sexes (male and female). The number of predation events were examined after 24 h by recording the number of aphids consumed using binocular microscopes. Each treatment was replicated 10 times simultaneously. Control treatments without predators were performed to take into account the natural mortality of *M. sacchari* adults and the amount of their newborn nymphs in order to correct *M. sacchari* consumption as a function of natural mortality. These treatments were each replicated 10 times.

**Intraspecific competition**

To evaluate the effects of intraspecific competition on the foraging behavior of *H. axyridis*, four instars of larvae (first, second, third, fourth instar) and adults in both sexes (male and female) were studied. The prey densities examined were 100, 200, 300, 400 and 500 aphid adults for 1, 2, 3, 4 and 5 predaceous coccinellids at various developmental stages in a Petri dish, respectively. The prey/predator ratio was kept at 100 for each number of coccinellids placed together in a Petri dish, with competition among predators for space increasing with the increasing number of predators placed together. The coefficients of mutual interference were calculated by counting the amount of aphids surviving after 24 h using binocular microscopes. Each treatment was replicated 5 times simultaneously.

There are 47 species of natural enemies that have been recorded as biological control agents of *M. sacchari* (Singh et al., 2004). Many studies now indicate that predators often locate their prey by using plant volatiles (Takebasyahi & Dicke, 1996; Arimura et al., 2005; Turlings & Ton, 2006). The predators search for aphids through honeydew derived from aphids (Hatano et al., 2008; Verheggen et al., 2008) and volatiles released by damaged plants (James et al., 2005; Sasso et al., 2009). Multicolored coccinellid *Harmonia axyridis* Pallas has the potential to be a biocontrol agent of aphids throughout Asia, America and Europe (Koch, 2003), and this predacious coccinellid is the effective predator of aphids in natural environments (Mogi, 1969; Choi & Kim, 1985; McClure, 1987; Hong, 1996). The primary factor to determine whether *H. axyridis* can be a suitable candidate for biological control of *M. sacchari* is their foraging capacity. Various aphidiphagous responses of *H. axyridis* have been performed in previous studies (Lou, 1987; Hu et al., 1989; He et al., 1994; Seo & Youn, 2000), but its functional response to *M. sacchari* is still unstudied. The functional response of a predator to the dynamic of prey densities depends on their instantaneous searching rate and handling time (Hassell et al., 1976). These parameters will provide a valuable reference for augmentative releases of *H. axyridis* as a biological control agent of *M. sacchari* in natural habitats. Releases of *H axyridis* eggs, larvae and adults have been studied (Tedders & Schaefer, 1994; Trouve et al., 1997; Ferran et al., 1998; Kitagami & Ohkubo, 1998; Kuroda & Miura, 2003). Growth stage of natural enemies needs to be considered as their searching rates and handling time vary with the developmental stages (Varley et al., 1973; Dixon, 2000). Complex predator-prey systems are attributed to the interactions not only between predator and prey, but also between predator individuals, especially in circumstances where competition is intense (Papanikolau et al., 2016).

Predatory coccinellids serve as biological control agents of pests in many crops (Ferran et al., 1996). Interactions among these predators, and competition for resources (prey and space), influence their impact on biological control. Our preliminary observations indicated that foraging efficiency, and hence the effectiveness of biological control, is reduced when too few or too many of these predators are present. Interactive competition is a density-dependent process including indirect and direct interactions between predators (Begon et al., 1996). Intraspecific competition occurs via direct interactions between predator individuals of same species (Hassell, 1978). Several models have been performed to quantify mutual interference using phenomenological (Hassell & Varley, 1969) or mechanistic (Bedington, 1975; DeAngelis et al., 1975; Crowley & Martin, 1989) approaches, which indicates that foraging behavior is not only prey-dependent but also a predator-dependent process. Thus, consideration of intraspecific competition is necessary during predation under both laboratory and field conditions.
**Statistical analysis**

**Functional response**

The functional responses were studied through two-stage analysis (Juliano, 2001). In the first step, cubic logistic regression analysis proportion of prey consumption as a function of initial density was performed to determine the shape (type II or type III) of functional response:

\[
N_a = \frac{aTN_0}{1 + aTN_0}
\]

where \(N_a\) and \(N_0\) are described in equation 1, \(T\) is the total time which in this case is 24 h, \(a\) is the instantaneous searching rate and \(T_h\) is the handling time. A nonlinear regression procedure (NLR) based on the Levenberg-Marquardt method was performed to estimate the parameters \(a\) and \(T_h\). The starting values of \(a\) and \(T_h\) required by the NLR procedure were found via the linear regression of 1/\(N_a\) against 1/\(N_0\). The resultant \(y\)-intercept is the initial estimate of \(T_h\) and the reciprocal of the regression coefficient is an estimate of \(a\) (Livdahl & Stiven, 1983; Watson et al., 2000).

**Intraspecific competition**

The experiment was performed to calculate the coefficients of mutual interference among predators during predation events. Nonlinear regression analysis was performed to estimate parameters of an intraspecific competition model by fitting equation 3 (Hassell & Varley, 1969):

\[
E = QP^m
\]

where \(E\) is the mean consumption, \(P\) is the predator density, \(m\) is the coefficient of mutual interference and \(Q\) is the theoretical maximum consumption rate (%). The values of \(Q\) and \(m\) were found by power-exponential regressing \(E\) and \(P\).

Descriptive statistics were given as the mean values and standard errors of the mean. Differences between natural mortality rate and 0 were examined using one sample t-test; \(P\) values < 0.05 were considered significant. Statistics were performed with SPSS 20.0 software (IBM, Armonk, NY). Regression analyses were performed using SigmaPlot 12.0 software (Systat Software Inc., San Jose).

**RESULTS**

**Functional response**

Regardless of prey density, natural mortality rates of \(M. sacchari\) were not significantly different from 0 (t-test, \(P > 0.05\)) as few newborn nymphs were produced during experiments. Thus, the mortality rates of \(M. sacchari\) and amounts of their newborn nymphs were negligible during tests. Parameter estimates from the logistic model (Eq. 1) of the proportion of \(M. sacchari\) consumed by \(H. axyridis\) over a 24 h period versus prey density are exhibited in Table 1. Estimates of the linear parameter \(P\) were significantly negative for all developmental stages (Table 1). Therefore, the logistic model analysis of all developmental stages performed a type II response to \(M. sacchari\).

The functional response data for prey consumption by \(H. axyridis\) over a 24 h period fitted the Holling’s disc model (Eq. 2) well (Table 2), confirming a type II response for all developmental stages. The amounts of \(M. sacchari\) consumed increased significantly as their densities increased, and foraging capabilities of \(H. axyridis\) increased progressively with increasing growth stages (Fig. 1). The coefficients of instantaneous searching rate (\(a\)) and handling time (\(T_h\)) indicated numerically this relationship, which had asymptotic 95% confidence intervals except 0 at vari-

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**Table 1.** Maximum likelihood estimates (+SE) of the parameters of the logistic model of the proportion of prey consumed versus initial prey density.

<table>
<thead>
<tr>
<th>Stage</th>
<th>(P_1)</th>
<th>(P_2)</th>
<th>(P_3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>First instar</td>
<td>–2.11638**</td>
<td>–0.04413**</td>
<td>0.00025*</td>
</tr>
<tr>
<td>Second instar</td>
<td>–1.40043**</td>
<td>–0.00599*</td>
<td>0.00005</td>
</tr>
<tr>
<td>Third instar</td>
<td>–0.21998*</td>
<td>–0.00736*</td>
<td>0.00004</td>
</tr>
<tr>
<td>Fourth instar</td>
<td>2.18495*</td>
<td>–0.00401*</td>
<td>0.00036</td>
</tr>
<tr>
<td>Adult male</td>
<td>2.54014**</td>
<td>–0.053385**</td>
<td>0.00041</td>
</tr>
<tr>
<td>Adult female</td>
<td>2.25384**</td>
<td>–0.0136707*</td>
<td>0.000037</td>
</tr>
</tbody>
</table>

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**Table 2.** Parameter estimates of Holling’s disc equation (Eq. 2) for \(H. axyridis\) attacking \(M. sacchari\).

<table>
<thead>
<tr>
<th>Stage</th>
<th>(R^2)</th>
<th>(E)</th>
<th>(P)</th>
<th>(T_h) (min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>First instar</td>
<td>0.969</td>
<td>189.81</td>
<td>&lt;0.001</td>
<td>740.3</td>
</tr>
<tr>
<td>Second instar</td>
<td>0.964</td>
<td>161.297</td>
<td>&lt;0.001</td>
<td>81.6</td>
</tr>
<tr>
<td>Third instar</td>
<td>0.999</td>
<td>4332.043</td>
<td>&lt;0.001</td>
<td>45.0</td>
</tr>
<tr>
<td>Fourth instar</td>
<td>0.994</td>
<td>917.564</td>
<td>&lt;0.001</td>
<td>3.9</td>
</tr>
<tr>
<td>Adult male</td>
<td>0.995</td>
<td>1230.216</td>
<td>&lt;0.001</td>
<td>5.3</td>
</tr>
<tr>
<td>Adult female</td>
<td>0.856</td>
<td>17.888</td>
<td>0.024</td>
<td>3.0</td>
</tr>
</tbody>
</table>

\(R^2\) is the coefficient of determination estimated by fitting Holling’s disc equation, \(P\) is the probability that Holling’s disc equation will yield significant parameters, \(a\) is the instantaneous searching rate and \(T_h\) is the handling time.

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ous developmental stages. The searching rates of female adults (0.9881) were highest among varied developmental stages, followed by those of male adults, fourth, third, second, and first instar larvae. The time of female adults handling a prey (3.0 min) was shortest, followed by that of fourth instar larva, adult male, third, second and first instar larvae (Table 2).

**Intraspecific competition**

When the ratio of prey/predators was kept to 100, total *M. sacchari* consumption in a Petri dish gradually increased as the introduced numbers of predators and prey increased. However, the mean consumption of ladybugs at various developmental stages decreased with increasing predator and prey density due to intraspecific competition associated with space limitation (Fig. 2). Overall, the mean consumption of ladybugs at five prey-predator densities were 53.4 (prey/predator = 100/1), 41.4 (200/2), 37.5 (300/3), 33.3 (400/4) and 25.3 (500/5). Intraspecific competition curves fitted the data at all developmental stages of *H. axyridis* with equation 3. At all developmental stages, the mean consumption at various predator densities fitted
The intraspecific competition equation well (Table 3). Theoretical maximum consumption rates ($Q$) and coefficients of mutual interference ($m$) of all developmental stages had asymptotic 95% confidence intervals that did not include 0. The order of theoretical maximum consumption rates ($Q$) were highest at the adult female stage, followed by fourth instar, adult male, third, second and first instar stages. The order of coefficients of mutual interference ($m$) were highest at the fourth instar stage, followed by adult female, adult male, and third, second and first instar stages (Table 3).

**DISCUSSION**

**Functional response**

Our study showed that all developmental stages of *H. axyridis* exhibited a type II functional response against *M. sacchari*. Type II functional response curves had been reported in previous studies on predation of *H. axyridis*. 

![Fig. 2. Intraspecific competition among individuals of *H. axyridis* when attacking *M. sacchari*. Each data point represents the mean number of individuals of *M. sacchari* consumed by an individual predator. The curve was fitted using the intraspecific competition equation (Eq. 3).](image)
Table 3. Parameter estimates of the intraspecific competition equation (Eq. 3) of prey consumption rates of H. axyridis at various predator densities.

<table>
<thead>
<tr>
<th>Stage</th>
<th>$R^2$</th>
<th>$F$</th>
<th>$P$</th>
<th>Intraspecific competition equation</th>
<th>$Q$ (%)</th>
<th>$m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>First instar</td>
<td>0.849</td>
<td>16.88</td>
<td>0.026</td>
<td>$E = 1.5236P^{0.3261}$</td>
<td>1.5236</td>
<td>0.3261</td>
</tr>
<tr>
<td>Second instar</td>
<td>0.848</td>
<td>16.752</td>
<td>0.026</td>
<td>$E = 20.1223P^{0.3275}$</td>
<td>20.1223</td>
<td>0.3275</td>
</tr>
<tr>
<td>Third instar</td>
<td>0.843</td>
<td>16.1</td>
<td>0.028</td>
<td>$E = 36.9383P^{0.3599}$</td>
<td>36.9383</td>
<td>0.3599</td>
</tr>
<tr>
<td>Fourth instar</td>
<td>0.805</td>
<td>12.377</td>
<td>0.039</td>
<td>$E = 95.8276P^{-0.4764}$</td>
<td>95.8276</td>
<td>0.4764</td>
</tr>
<tr>
<td>Male adult</td>
<td>0.94</td>
<td>47.05</td>
<td>0.006</td>
<td>$E = 78.3120P^{-0.4107}$</td>
<td>78.3120</td>
<td>0.4107</td>
</tr>
<tr>
<td>Female adult</td>
<td>0.856</td>
<td>17.888</td>
<td>0.024</td>
<td>$E = 98.6529P^{-0.4183}$</td>
<td>98.6529</td>
<td>0.4183</td>
</tr>
</tbody>
</table>

$R^2$ is the coefficient of determination estimated by fitting the intraspecific competition equation and $P$ is the probability that the intraspecific competition equation will yield significant parameters.

against different prey species, such as Rhopalosiphum prunifolii (Lou, 1987), Cinara sp. (Hu et al., 1989), Aphis craccivora Koch (Mogi, 1969), Schizaphis graminum (Hu, 1992), Lipaphis erysimi (He et al., 1994), Myzus persicae (Ma et al., 2000), Myzus nicotianae (Liu et al., 2002), Rhopalosiphum nymphaeae (Ge et al., 2006) and Danaus plexippus (Koch et al., 2003). Holling’s disc equation was the most common model to analyze the type II functional response (Fan & Pettit, 1994, 1997). Our study also showed that the prey consumption increased while the consumption rates diminished with increasing prey densities, which was predicted by Holling’s disc model. The result was consistent with past studies that Holling’s disc model was suitable to describe the predation of H. axyridis on Aphis craccivora Koch (Zhang et al., 2014), Semaphis heraclei (Zhang et al., 2015), Aphis sophoricola (Li et al., 2007) and Aphis carvines (Wang et al., 2012).

We found that low foraging success rates were detected in first instars of H. axyridis due to their smaller sizes and slower movements (Lee & Kang, 2004). The larvae in second and third instars had relatively higher M. sacchari consumption compared to the first instar larvae. Fourth instar larvae accounted for 58.2% of the total prey consumption by larvae, suggesting that fourth instar larvae are the main contributors of aphid consumption by larvae of coccinellids (Höde & Honek, 1996). Prey consumption by male and female adults of H. axyridis were 74.3% and 111.3% of that by the fourth instar larvae over a 24 h period, respectively, implying the adult and fourth instar stages were significantly higher potential maximum consumption rates and coefficients of mutual interference compared to other developmental stages. Coccinellids are digestive-limited predators, so the limitation of theoretical maximum consumption rate was shown because of predation. The coccinellids became inactive after consuming large numbers of aphids at maximum prey consumption, likely minimizing mutual interference, whereas notable time was likely to be spent on mutual interference during their foraging when the ladybugs had high satiation levels (van Gils & Piersma, 2004; Papanikolaou et al., 2016). Therefore, mature coccinellid individuals had higher coefficients of mutual interference due to higher potential maximum consumption rates.

Cannibalism was occasionally observed when multiple predators shared a Petri dish, as conspecific competitors attacked each other, resulting in injury and sometimes death. Cannibalism contributed to the sharp decline in per capita consumption as predatory density increased, which was another reason why ladybugs at these stages had more severe intraspecific competition. Cannibalism had a negative effect on the overall foraging efficiency, even though it contributed greater resources such as space and food to superior individuals (Block & Stoks, 2004; Richardson et al., 2010; Bayoumy & Michaud, 2015). Another negative effect of cannibalism was increasing disease transmission (Saito & Bjørnson, 2006) and decreasing inclusive fitness (Hamilton, 1964).

**Remaining questions and future perspectives**

Foraging capacities including instantaneous searching rates and handling time are critical for estimating the potential of predators to serve as a biocontrol agent (Lucas et al., 1997). Prey-predator dynamics can be evaluated by a mathematical model (Hassell, 1978). Thus, the dynamics could be established through the functional response curves, and...
the foraging capacity of *H. axyridis* depends on *M. sacchari* density in natural habitats. However, field studies are needed to validate the dynamics, because quantitative models built in laboratory studies appear to have limited value in assessing the foraging abilities under field conditions (Gitonga et al., 2002; Lee & Kang, 2004). A series of studies on functional responses of *Podisus maculiventris* verify that there is a distinction between laboratory and field studies (O’Neil, 1988a, b, 1990, 1997; Wiedenmann & O’Neil, 1991a, b, 1992), likely because of the difference in searching rates of predators between laboratory and field conditions (Murdoch, 1983). Spatial complexity, critical in the natural environment, cannot be recreated under simple laboratory conditions (Kareiva, 1990). Laboratory studies provide parametric analysis of predator-dependent intraspecific competition models, but they are performed only on a non-spatial scale. Thus, intraspecific competition in a spatial sense is critical to future studies as it is closer to natural conditions (Sun et al., 2008, 2014, 2015). Intraspecific competition may disrupt the foraging capacities quantified by functional response. As such, understanding not only prey-predator but also predator-predator interactions is vital for a reliable predator-based control of aphids. Functional response and intraspecific competition models describe the foraging behaviors of predators accurately and also indicate the existence of intraspecific competition impacting their foraging efficiency. Thus, a comprehensive analysis of functional response and intraspecific competition will allow further improvement of our understanding of prey-predator-predator interactions in relation to aphid biological control. Fourth instar larvae and adults of *H. axyridis* can serve as excellent biological control agents of aphids in an integrated pest management programme. Field release of third to fifth instar larvae has appeared to be economical as mass rearing to fourth instar and adult stages can be avoided (Seko & Miura, 2008). Additionally, a suitable predator density should also be considered to decrease intraspecific competition when *H. axyridis* are released in the field, as too few or too many predators released is likely to result in reduced effectiveness of the biological control agent. Moreover, it could be interesting for further studies to regard the intraguild predation in order to obtain more information on the foraging behavior of coccinellids as these interactions have been fitted by several models (de Villemereuil & López-Sepulcre, 2011; Sentis et al., 2013). Natural stochasticity needs to be considered in future field experiments on intraspecific competition among coccinellids (Papanikolaou et al., 2016). Plant characteristics also need to be considered due to their impacts on the feeding efficiency of predators (Hodek & Honék, 1996). Future field investigations associated with prey-predator dynamics are critical for effective predator release, which has the potential to reduce pesticide uses and preserve predator populations (Xue et al., 2009).

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