Biological aspects of *Tiracola grandirena* (Herrich-Schäffer, 1868) 
(Lepidoptera: Noctuidae): a polyphagous armyworm


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**Abstract**

We studied the biology of *Tiracola grandirena* (Herrich-Schäffer, 1868) (Lepidoptera: Noctuidae: Hadeninae) at 25 ± 1 °C, 70 ± 10% RH and 14 hours of photo phase. Three experiments, using 150 larvae each, were conducted for the larval stage. In the first, used to assess the duration and survival of all stages, insects were reared individually and fed an artificial diet (Greenee). In the second, individuals were also reared separately, but were fed leaves of 10 plants from different families. In the third, the larvae were not individualised, the food plants were rotated such as to provide three plant species every 48 hours. In the first experiment, the viability of the eggs, larvae, pupae and prepupae was 91.9, 94.7, 32.49 and 43.5%, respectively. The average duration of the egg, larvae, prepupae, pupae and adult were 6.0, 25.3, 25.7, 21.4 and 12.7 days, respectively. The prolonged prepupal period indicates that *T. grandirena* can develop larval (prepupal) diapause. The results of the experiments with different host plants showed that *T. grandirena* is polyphagous at species, population and individual level.

**Keywords:** caterpillar, developmental biology, prepupal diapause, Hadeninae.

1. **Introduction**

*Tiracola* Moore, 1881 is cosmopolitan and includes only 10 species (Poole, 1989). *Tiracola grandirena* (Herrich-Schäffer, 1868) is the most widely distributed species in the Americas, occurring in countries such as Mexico, Cuba, Jamaica, Puerto Rico, Costa Rica, Venezuela and Brazil (Todd and Poole, 1980; Specht and Corseuil, 2001; Becker, 2002; Specht et al., 2004). The species has been confused with *T. plagiata* (Walker, 1857) (e.g. Specht and Corseuil, 2001; Specht et al., 2004) because of intraspecific variation in colour, which also motivated Draudt (1924) to describe two varieties, *magniplaga* and *mediosuffusa*. In the Northern Hemisphere, the distribution of *T. grandirena* is restricted to the 20th parallel (between the towns of Jalapa, Cordoba and Misantla, Mexico) (Becker, 2002),
whereas in the Southern Hemisphere it reaches parallel 30, in Pelotas, Rio Grande do Sul, Brazil (Specht et al., 2004).

The main biological parameters of *T. grandirena* are unknown. The species has been reported on 36 host plants belonging to 19 families (Janzen and Hallwachs, 2009). Additionally, Bruner et al. (1945) reported on larvae attacking coffee in Cuba, and Specht et al. (2004), using unpublished data from Biezanko, indicated that larvae of *T. grandirena* were attacking Jasmine-Blue (*Plumbago capensis* Thunb. - Plumbaginaceae) in Pelotas.

Considering the lack of knowledge about the biology of *T. grandirena*, a polyphagous species, combined with the damage caused by *T. plagiata* on crops of economic interest such as bananas, cocoa, tobacco, orange, castor, cassava and sisal (e.g. Robinson, 1975) in the Eastern Hemisphere, this study aimed to evaluate the main biological parameters of *T. grandirena* under controlled conditions.

2. Material and Methods

Laboratory rearing started with 2,156 eggs from a female collected in Anta Gorda, state of Rio Grande do Sul, Brazil (28° 56’ 40,8” S; 52° 01’ 12,4” W; 545 m height), on October 10, 2010. All experiments were performed under controlled conditions (25 ± 1°C, 70 ± 10% RH and photo phase of 14 hours).

The main biological parameters were obtained from 150 larvae fed an artificial diet. Two other experiments, also employing 150 larvae each, assessed the species and individual polyphagy of *T. grandirena*.

2.1. Biological parameters

We evaluated the viability and duration of the embryonic period of all eggs laid by the female collected in the field. Each egg mass was individualised in a Petri dish and separated from the others by date. The bottom of the dish was lined with filter paper, which was moistened with distilled water until the larvae hatched.

The survival and duration of larval development of individuals fed an artificial diet (Greene et al., 1976) were evaluated. The following parameters were measured: duration of larval stages, in days; total duration of the larval stage were evaluated in this experiment. The average results were compared using the Tukey test with a 5% confidence level.

2.2. Evaluation of polyphagy at specific level

In order to evaluate the degree of polyphagy of *T. grandirena*, we followed the development of 15 individualised larvae which were offered ten plant species from different families. The following potential hosts were offered to the larvae: *Schinus terebenthifolium* Raddi - Anacardiaceae [St], *Musa paradisiaca* Linn. var. *sapiamentum* Huntze - Musaceae [Mp], *Nectandra megapotamica* (Spreng.) Mez. – Lauraceae [Nm], *Diospyros kaki* L. - Ebenaceae [Dk], *Schefflera arboricola* Hayata - Araliaceae [As], *Tabebuia umbellata* (Sond.) Sandwith - Bignoniaceae [Tu], *Citrus sinensis* (Linn.) Osbeck - Rutaceae [Cs], *Malus domestica* Borkhausen - Rosaceae [Md], *Ricinus communis* Linn. - Euphorbiaceae [Rc] and *Platamus acerifolia* (Aiton) Wild. - Platanaceae [Pa].

The leaves were changed daily. In order to ensure that leaves remained turgid, we immersed their petioles or basal portions in a 20 ml Erlenmeyer flask glass filled with distilled water. In the beginning of the prepupal period the larvae escaped from the glasses, looking for a place to form the pupal chamber. Most larvae hid throughout the room and died, making it impossible to continue the experiment. Consequently, only the survival and duration of the larval stage were evaluated in this experiment. The average results were compared using the Tukey test with a 5% confidence level.

2.3. Evaluation of polyphagy at individual level

In order to ascertain individual polyphagy, we evaluated the survival of larvae kept in a glass box (30 × 40 × 60cm), changing the host plants (three plant species), every two days. Host plants were offered in the following order: {St, Mp, Nm}, {Dk, As, Tu}, {Cs, Md, Re}, {Pa, St, Mp}, {Nm, Dk, The}, {Tu, Cs, Md}, {Re, Pa, St}, {Mp, Nm, Dk}, {As, You, Cs} {Md, Re, Pa}, {St, Mp, Nm}, {Dk, As, Tu}, {Cs, Md, Re}, {Pa, St, Mp}, {Nm, Dk, As}.

In this experiment, branches of each of the three plants were offered in 150 ml glass Erlenmeyer flasks, which were placed in the box, to ensure that larvae could migrate to the newly offered plants. After 24 hours, the jars with the older food-plants were removed and the larvae still on them were carefully removed and transferred to the new
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We assessed larval survival (%) only until they left their plant, indicating the beginning of the prepupal period.

The temporal and morphometric parameters were analysed using descriptive statistics with the calculation of means and standard errors. Means were compared by t-test assuming unequal variances at a significance level of 95%.

We compared the various biological parameters of T. grandirena with those of a closely-related species, T. plagiata. Data for the latter were taken from Temperley (1930) and Catley (1963), who had performed laboratory and field experiments without indicating the temperature, humidity and photoperiod. Where appropriate, our results were also compared with data from other noctuids reared under similar conditions.

3. Results

3.1. Biological parameters

The viability of eggs from females collected in the field, was high (Table 1) and the incubation period corresponded to 6.6% of the life cycle.

All larvae underwent six instars and the maximum width of the cephalic capsule and body length of 13 individuals ranged from 0.4 ± 0.00 mm and 2.7 ± 0.09 mm in the first instar to 4.1 ± 0.03 mm and 61.3 ± 1.81 mm, in last instar, respectively. The distance between the frontal setae (Table 2) revealed an average growth ratio of 1.8 from one instar to the next, with higher values in the first three. The entire larval period of T. grandirena corresponded to approximately 56% of the entire life cycle of the species. However, on average, for more than half of this period, larvae remained inactive as prepupa (Table 1). We also noted that, while the larvae remained active, there was not much variation in the duration of each instar, and in the duration of the entire period stage (22-28 days). However, the longest duration of the prepupal period (57 days) was about five times longer than the shortest (11 days).

After hatching, the larvae completely consumed the egg chorion and did not eat for up to 48 hours, observing that the first instar was longer than the other instars. However, there was a progressive increase in the duration of the instars, from the second instar until the last instar (Table 2).

Survival was high for all active larval instars of T. grandirena. However, in the prepupal period, at least 50% of the larvae died after 57 days, before metamorphosis. This period was also characterised by great variability in duration. The longest living prepupae survived 128 days and died before metamorphosis (Table 1).

The pupae stage was also characterised by low viability and it lasted nearly one quarter (23.5%) of the time required to complete the life cycle (Table 1). The length, width and

<p>| Table 1. Survival (%) and mean (± SE) duration, in days, of Tiracola grandirena individuals whose larvae were fed an artificial diet (Greene et al., 1976) under controlled conditions (25 ± 1 °C, 70 ± 10% RH and 14 hours of photo phase). |</p>
<table>
<thead>
<tr>
<th>Developmental Stage</th>
<th>Initial (N)</th>
<th>Surviving (%)</th>
<th>Mean ± S.E.</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>2156</td>
<td>1982</td>
<td>91.9</td>
<td>6.0 ± 0.00</td>
</tr>
<tr>
<td>I</td>
<td>150</td>
<td>148</td>
<td>98.7</td>
<td>5.9 ± 0.05</td>
</tr>
<tr>
<td>L</td>
<td>148</td>
<td>145</td>
<td>97.9</td>
<td>3.9 ± 0.03</td>
</tr>
<tr>
<td>A</td>
<td>145</td>
<td>145</td>
<td>100.0</td>
<td>3.1 ± 0.04</td>
</tr>
<tr>
<td>R</td>
<td>145</td>
<td>145</td>
<td>100.0</td>
<td>3.7 ± 0.04</td>
</tr>
<tr>
<td>V</td>
<td>145</td>
<td>145</td>
<td>100.0</td>
<td>4.2 ± 0.05</td>
</tr>
<tr>
<td>A</td>
<td>145</td>
<td>142</td>
<td>97.9</td>
<td>4.3 ± 0.05</td>
</tr>
<tr>
<td>E</td>
<td>142</td>
<td>46</td>
<td>43.5</td>
<td>21.3 ± 0.65</td>
</tr>
<tr>
<td>Adults***</td>
<td>20</td>
<td>---</td>
<td>---</td>
<td>12.7 ± 2.45</td>
</tr>
</tbody>
</table>

* active sixth instar larva; ** inactive sixth instar larva, in the prepupal period; *** duration considering only three virgin females.

<p>| Table 2. Averages (n= 10) of the distances between the frontal setae with the respective standard errors, growth rates and duration of each instar of Tiracola grandirena fed on artificial diet (Greene et al., 1976), under controlled conditions (25 ± 1 °C, 70 ± 10% RH and photo phase of 14 hours). |</p>
<table>
<thead>
<tr>
<th>Instar</th>
<th>Distance between frontal setae (mm) (X ± SE)</th>
<th>Growth Rate</th>
<th>Duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>0.1 ± 0.00</td>
<td>---</td>
<td>6.0 ± 0.20</td>
</tr>
<tr>
<td>II</td>
<td>0.2 ± 0.01</td>
<td>2.0</td>
<td>3.9 ± 0.13</td>
</tr>
<tr>
<td>III</td>
<td>0.4 ± 0.01</td>
<td>2.0</td>
<td>3.1 ± 0.14</td>
</tr>
<tr>
<td>IV</td>
<td>0.7 ± 0.02</td>
<td>1.7</td>
<td>3.7 ± 0.17</td>
</tr>
<tr>
<td>V</td>
<td>1.1 ± 0.02</td>
<td>1.6</td>
<td>4.2 ± 0.20</td>
</tr>
<tr>
<td>VI</td>
<td>1.9 ± 0.04</td>
<td>1.7</td>
<td>4.3 ± 0.17*</td>
</tr>
</tbody>
</table>

* Active larvae, excluding the prepupal period.
weight (Table 3) of the pupae did not differ significantly between sexes.

The average lifespan of three females of *T. grandirena* which had emerged in the laboratory (Table 1) was 12.7 days. The female of *T. grandirena* collected in the field had almost all the body scales, indicating that not much time had passed since its emergence. It oviposited in the first (n = 234), second (n = 367), eighth (n = 819), ninth (n = 402), tenth (n = 231) and eleventh days (n = 103), and died on the twelfth day after being collected. In the laboratory, *T. grandirena* eggs were laid in batches and sometimes in layers.

### 3.2. Evaluation of polyphagy at species level

As described for the larvae reared on an artificial diet, those fed different host plants also began to eat after 48 hours. Initially, larvae would just scrape the leaf surface. In subsequent instars, however, they would consume the entire leaf. Larval development was relatively uneven; there were larger and smaller larvae in all treatments. Larvae fed indiscriminately on the offered host plants, and there was practically no mortality until becoming prepupa in the sixth instar. The average larval duration was similar in all treatments without significant differences, but with very pronounced deviations (Table 4).

### 3.3. Evaluation of polyphagy at individual level

In the third experiment, in which the plants were exchanged every 48 hours, it was observed that there was almost 10% mortality within four days. However the survival rate of the larvae (active period) was 84.0%, demonstrating that *T. grandirena* larvae can easily feed on different host plants during development.

### 4. Discussion

#### 4.1. Egg stage

The high viability of this stage (Table 1) was consistent with observations made by Temperley (1930) on eggs from a *T. plagiata* female, also collected in the field. In the latter experiment, even though nearly all the eggs were fertile to begin with, adverse laboratory conditions such as low humidity and mechanical injuries during rearing prevented larvae from hatching. The observations of our study are consistent with field observations in which eggs from females collected in nature, including the first generation, are highly viable (viability percentages above 90%) (Specht et al., 2008).

The incubation period (Table 1) of *T. grandirena* was slightly shorter than that observed for *T. plagiata* reared in the laboratory (Temperley, 1930; Catley, 1963; 1963) ~ 7.9%). The duration of incubation in our experiment approximates that of other noctuids, for instance *Pseudaleitia sequax* Franclemont, 1951 (Buainain and Silva, 1988 ~ 5.9%), *Anicia infecta* (Oehsenheimer, 1816) (Teston et al. (2001) ~ 6.4%) and *Anicia mahalpa* Schaus, 1898  (Specht et al. (2008) ~ 6.9%), reared under similar conditions. The incubation periods of *T. grandirena* in this work and *T. plagiata* reared in the laboratory (Temperley, 1930; Catley, 1963) were much longer than in the field (3.5 to 4 days according to Catley (1963)).

### Table 3.

<table>
<thead>
<tr>
<th>Gender (N)</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>X ± SE</td>
<td>Range</td>
<td>X ± SE</td>
</tr>
<tr>
<td>Female (7)</td>
<td>25.5 ± 0.69</td>
<td>22.8-28.1</td>
<td>8.5 ± 0.22</td>
</tr>
<tr>
<td>Male (10)</td>
<td>24.8 ± 0.48</td>
<td>22.7-26.9</td>
<td>8.6 ± 0.19</td>
</tr>
<tr>
<td>t (p 0.05%)</td>
<td>0.47</td>
<td>0.61</td>
<td>0.67</td>
</tr>
<tr>
<td>Total</td>
<td>25.1 ± 0.61</td>
<td>22.7-28.1</td>
<td>8.6 ± 0.14</td>
</tr>
</tbody>
</table>

### Table 4.

<table>
<thead>
<tr>
<th>Host plant</th>
<th>Survival N</th>
<th>%</th>
<th>Duration (days) Mean Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Schinus terebinthifolium</em>  - Anacardiaceae</td>
<td>14</td>
<td>93.3</td>
<td>25.5 ± 0.87</td>
</tr>
<tr>
<td><em>Musa paradisiaca</em> - Musaceae</td>
<td>15</td>
<td>100.0</td>
<td>23.6 ± 1.27</td>
</tr>
<tr>
<td><em>Nectandra megapotamica</em> - Lauraceae</td>
<td>13</td>
<td>86.7</td>
<td>24.7 ± 0.85</td>
</tr>
<tr>
<td><em>Diospyros kaki</em> L. - Ebenaceae</td>
<td>13</td>
<td>86.7</td>
<td>25.5 ± 0.80</td>
</tr>
<tr>
<td><em>Schefflera arboricola</em> - Araliaceae</td>
<td>15</td>
<td>100.0</td>
<td>24.8 ± 0.79</td>
</tr>
<tr>
<td><em>Tabebuia umbellata</em> - Bignoniaceae</td>
<td>13</td>
<td>86.7</td>
<td>24.0 ± 0.79</td>
</tr>
<tr>
<td><em>Citrus sinensis</em> - Rutaceae</td>
<td>15</td>
<td>100.0</td>
<td>25.0 ± 1.03</td>
</tr>
<tr>
<td><em>Malus domestica</em> - Rosaceae</td>
<td>14</td>
<td>93.3</td>
<td>25.0 ± 0.62</td>
</tr>
<tr>
<td><em>Ricinus communis</em> - Euphorbiaceae</td>
<td>14</td>
<td>93.3</td>
<td>25.0 ± 0.79</td>
</tr>
<tr>
<td><em>Platanus acerifolia</em> - Platanaceae</td>
<td>13</td>
<td>86.7</td>
<td>24.8 ± 1.32</td>
</tr>
</tbody>
</table>
4.2. Larval stage

The results of this study (Table 2) are very similar to those obtained for T. plagiata, which also goes through six larval instars (Temperley, 1930). The average growth ratio of 1.8 from one instar to the next, with higher values in the first three was higher than that of T. plagiata (~ 1.6) using data from Temperley (1930), and also higher than in other noctuid species with six larval instars (e.g. A. infecta ~ 1.5 - Teston et al. (2001), A. mahalpa ~ 1.5 - Specht et al. (2008)). The growth rate of our subjects approximated that of the noctuid Autopliaia egena (Gueneé, 1852) (~ 1.7) (Specht et al., 2007), which goes through only five larval instars and was greater than that predicted for Lepidoptera [~ 1.4] (Dyar, 1890).

The observation that the larvae did not eat for up to 48 hours, resembles T. plagiata larvae, which do not eat for approximately 24 hours (Temperley, 1930). However, a longer first instar has also been reported for other representatives of Hadeninae, for instance Pseudaletia unipuncta (Haworth, 1809) (Guppy, 1961) and P. sequax (Buainain and Silva, 1988).

The duration of the larval stage of T. grandirena, approximately 51 days, was similar to that observed for T. plagiata in the laboratory (Temperley (1930) and Catley (1963) ~ 54 days). However, the period during which larvae of T. grandirena were active (25.3 days), in our experiment, was much shorter than that observed for T. plagiata (~ 45.7 days) by the same authors. On the other hand, the prepupal period of T. grandirena (Table 1) was much longer and variable than observed for T. plagiata (Temperley (1930) and Catley (1963) ~ 8.3 days). Catley (1963) demonstrated that, in the field, even though the life cycle of T. plagiata is reduced to a half, the proportion of the time individuals spend in each period remains unchanged: 16 days for larval development and 4 days for the prepupal period.

The long duration of the prepupal period of T. grandirena (Table 1) was similar to that observed in other noctuids which overwinter on the ground in larval (prepupae) or pupal diapause, such as Xestia c-nigrum (Linnaeus, 1758) (Honěk, 1979; Oku, 1984), Helicoverpa armigera (Hübner, [1809]) (Qureshi et al., 2000; Feng et al., 2010) and Sesamia nonagrioides (Lefebvre, 1827) (Eizaguirre et al., 2008). However, an increase in the number of larval instars was not observed for T. grandirena, contrasting with other diapausing noctuids (Esperk et al., 2007; Gadenne et al., 1997). Considering that a temperature of 25 °C used in our experiment is within the optimal range for most insects, we believe that photoperiod was involved in diapause induction, as described for several other noctuids (Qureshi et al., 2000; Feng et al., 2010). The high mortality observed in this period, despite all care taken in the experiment (Table 1) must be associated with longer duration, as observed by Eizaguirre et al. (2008), who reported very low survival rates for diapausing larvae of S. nonagrioides.

4.3. Pupal stage

The low viability of the pupal stage (Table 1), in part can be attributed to the difficulties T. grandirena has during the prepupal period. The pupal stage lasted nearly one quarter of the time required to complete the life cycle (Table 1) and less than the 29.7 days (28.3%) reported for T. plagiata in the laboratory (Temperley, 1930; Catley, 1963). Our percentage is closer to that obtained for T. plagiata in the field ~ 25% (Catley, 1963). The 13-day variation in the pupal period of T. grandirena (Table 1) was much higher than the range observed for T. plagiata (28 to 32 days) (Temperley, 1930). This variation may be an indication that T. grandirena may undergo pupal diapause under specific conditions, like other noctuids, such as H. armigera (Qureshi et al., 2000). Further studies are needed to confirm this hypothesis.

The lack of sexual dimorphism (Table 3) in the pupae is based on insufficient and very variable data, a result of the variation in the duration of the prepupal period, which gave rise to very small pupae. Additional studies should be conducted in order to ascertain possible dimorphisms, because in Hadeninae, for instance P. sequax, female pupae are significantly larger than male pupae (Buainain and Silva, 1988).

4.4. Adult stage

The average lifespan of T. grandirena females (Table 1) was very similar to that obtained for unfertilized females of T. plagiata (Temperley, 1930). The number of eggs obtained from the female of T. grandirena collected in the field was most similar to that obtained for T. grandirena (n = 2.398) (Temperley, 1930). Similarly to what has been described for T. plagiata in the laboratory (Temperley, 1930; Catley, 1963), T. grandirena eggs were laid in batches, sometimes in layers. This contrasts with field observations of T. plagiata individuals (Weddell, 1930), which distributed their eggs throughout the plant.

4.5. Larval development on several host plants

The results of the larval development on several hosts indicate that larvae of T. grandirena can feed indiscriminately on different groups of plants without having their development affected. Such information, combined with previous records of host plants (Bruner et al., 1945; Specht et al., 2004; Janzen and Hallwachs, 2009) indicates that T. grandirena is highly polyphagous, like T. plagiata (Weddell, 1930; Szent-Ivany, 1956, 1961; Szent-Ivany and Catley, 1960; Catley, 1963; Dun, 1967; Hassan, 1972; Baker, 1974; Room and Smith, 1975; Ooi 1982).

The third experiment, in which the plants were exchanged every 48 hours, demonstrated that T. grandirena larvae can easily take on different host plants during development, as described for T. plagiata. Larvae of the latter usually start out on more attractive native or cultivated host plants and then migrate to more economically important hosts such as banana, cocoa, coffee and cassava (Weddell, 1930; Catley, 1962, 1963; Dun, 1967; Hassan, 1972; Baker, 1974; Room and Smith, 1975; Ooi 1982).
According to Bernars and Singer (2002), polyphagy may occur at the species, population or individual levels. Consequently, the term polyphagous, as applied to a species of herbivorous insect, does not necessarily imply that an individual of that species will have a polyphagous habit. Our study showed that T. grandirena is polyphagous at all levels. This high degree of polyphagy makes T. grandirena and T. plagiata very interesting species for studies that evaluate different feeding patterns (Janzén, 2003), foraging tactics (Singer and Stireman, 2001; Bernars and Singer, 2002) and differences in the gut microbiota (Sittenfeld et al., 2002).

The similarities of the results obtained by us with those described for the eastern T. plagiata (Weddell, 1930; Szent-Ivany, 1956, 1961; Szent-Ivany and Catley, 1960; Catley, 1963; Dun, 1967; Hassan, 1972; Baker, 1974; Room and Smith, 1975; Ooi 1982), indicate that T. grandirena can potentially become a key pest of several crops in Brazil and other warm regions of the Americas. Although our study did not allow us to encounter natural enemies, Janzén and Hallwachs (2009) mentioned Lespesia aletiae Riley, 1879 (Tachinidae) and an unidentified species of Sarcophagidae as parasitoids of T. grandirena. However, it is expected that the number of natural enemies of T. grandirena is much higher considering that several predators are indicated for T. plagiata, such as spiders (Oxyopodidae, Salticidae), mites (Tyroglyphidae), orthopterans (Tettigoniidae), bugs (Pentatomidae, Reduviidae, Gelastocoridae), dipterans (Asilidae), hymenopterans (Vespidae, Spechidae, Formicidae), parasitoids, especially Dipterans (Tachinidae) and Hymenopterans (Braconidae, Eulophidae, Ichneumonidae) and the entomopathogenic fungus Nomuraea rileyi (Farlow) Samson (Catley, 1962).

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