Effect of Food Resources on Adult Glyptapanteles militaris and Meteorus communis (Hymenoptera: Braconidae), Parasitoids of Pseudaletia unipuncta (Lepidoptera: Noctuidae)

A. C. Costamagna and D. A. Landis

Department of Entomology, 204 Center for Integrated Plant Systems, Michigan State University, East Lansing, MI 48824-1311


ABSTRACT Adult parasitoids frequently require access to food and adequate microclimates to maximize host location and parasitization. Realized levels of parasitism in the field can be significantly influenced by the quantity and distribution of extra-host resources. Previous studies have demonstrated a significant effect of landscape structure on parasitism of the armyworm Pseudaletia unipuncta (Haworth) (Lepidoptera: Noctuidae). As a possible mechanism underlying this pattern, we investigated the effect of carbohydrate food sources on the longevity and fecundity of armyworm parasitoids under laboratory conditions of varying temperature, host availability, and mating status. Glyptapanteles militaris (Walsh) (Hymenoptera: Braconidae) adults lived significantly longer when provided with honey as food and when reared at 20°C versus 25°C. Meteorus communis (Cresson) (Hymenoptera: Braconidae) adults also lived significantly longer when provided with honey, although longevity was reduced when females were provided hosts. Honey-fed females of M. communis parasitized significantly more hosts because of their increased longevity, but did not differ in daily oviposition from females provided only water. Mating significantly increased parasitism by honey-fed M. communis, but not those provided water alone. These results indicate that the presence of both carbohydrate resources and moderated microclimates may significantly increase the life span and parasitism of these parasitoids. However, the greater longevity and lower daily rate of oviposition of M. communis suggest that food and microclimate resources are more critical for this species than for the shorter lived, gregarious G. militaris. These findings contribute to our understanding of how these two parasitoids respond to landscape complexity.

KEY WORDS longevity, fecundity, mating status, biological control, life history parameters

Among parasitoids, it is primarily the adult stage that finds and selects adequate resources to complete their life cycle. These resources include food, refuges from abiotic and biotic mortality factors, and hosts. The spatial distribution of these resources can limit the range of parasitoid host search (Kriván and Sirot 1997, Lewis et al. 1998). Although some adult parasitoids are able to host feed, many hymenopteran parasitoids rely on nonhost food for maintenance and to support egg production (Quicke 1997). In crop monocultures, the presence of nonhost adult food resources may be limited in time and space and may not be in synchrony with the presence of hosts in the appropriate stage (Landis and Menalled 1998, Heimpel and Jervis 2004). Many parasitoid species that attack crop pests benefit from the presence of undisturbed extra-field habitats that contain these resources, which contributes to the establishment and retention of parasitoid populations near crop fields (Landis and Marino 1999, Landis et al. 2000, Thies and Tscharntke 2000). At the landscape scale, areas that have high structural complexity and a greater proportion of undisturbed fields are most likely to have a relatively diverse and abundant community of parasitoids (Landis et al. 2000). The few studies conducted to test this hypothesis have shown a significant increase of parasitism associated with landscape complexity (Marino and Landis 1996; Menalled et al. 1999, 2003; Thies and Tscharntke 1999). However, detailed knowledge of the biology and pattern of resource utilization of different parasitoid species in any particular system is still necessary to interpret the pattern of parasitism observed at the landscape level.

Potential nonhost food sources for parasitoids include floral and extrafloral nectar, pollen, and aphid honeydew (Quicke 1997). Flowering plants are frequently visited by parasitoids (Bugg et al. 1989, Jervis et al. 1993), and consumption of floral nectar has been shown to enhance adult longevity (Heimpel and Jervis 2004). Parasitoids fed carbohydrate resources, such as honey, sucrose, glucose, fructose, and other sugars in solution, frequently show increased longevity under laboratory conditions (Jervis and Copland 1996). Accessibility of nonhost food is correlated not only with increased life span, but also with increased fecundity,
number of hosts parasitized, and proportion of time searching for hosts instead of food (Lewis et al. 1998, Tscharnkte 2000, Heimpel and Jervis 2004).

Access to food resources also could interact with other factors that affect longevity and fecundity of parasitoids. Mating status and host availability can affect adult parasitoid longevity (Godfray 1994, Michaud 1994, Lei et al. 1997, Jacob and Evans 2000), as can microclimatic conditions, especially temperature and relative humidity (Dyer and Landis 1996). High temperatures tend to reduce insect longevity, particularly under high relative humidity in which the potential for evaporative cooling is reduced (Chapman 1998). Temperatures above the species optimum reduce parasitoid longevity (Dyer and Landis 1996, Jervis and Copland 1996).

Marino and Landis (1996) and Menalled et al. (1999, 2003) demonstrated that parasitism of the armyworm, *Pseudaletia unipuncta* (Haworth) (Lepidoptera: Noctuidae), in Michigan can differ between landscapes of different structural complexity. Two braconid wasps dominate the parasitoid community of *P. unipuncta* in these studies: *Glyptapanteles militaris* (Walsh) and *Meteorus communis* (Cresson). Both are generalist, nontarget endoparasitoids that mainly attack noctuid larvae (Tower 1915, Rolim 1983, Krombein et al. 1979, West 1988, West and Miller 1989, Marino and Landis 1996, Costamagna 2002). *G. militaris* has been reported as the most important parasitoid of *P. unipuncta* in several North American studies (Breeel and 1958, Calkins and Sutter 1976, Steinkraus et al. 1993), including Michigan (Untung 1978, Rolim 1983, Costamagna 2002, Menalled et al. 2003). It is a gregarious parasitoid, producing 40–82 larvae per host on average, depending on the stage parasitized (Oliveria et al. 1999). Most studies of this species focused on determining its potential as a biological control agent, and relatively little has been reported regarding its basic biology. Fecundity of *G. militaris* under different conditions of temperature, host instar, and host diet has been reported (Calkins and Sutter 1976; Oliveria et al. 1998, 1999; Reis et al. 2003). It has also been shown that access to carbohydrates increased *G. militaris* adult longevity (Calkins and Sutter 1976), while high temperature (35°C) killed *G. militaris* larvae inside its host and reduced female fecundity (Kaya and Tanada 1969). *M. communis* is a solitary species, with most reports concerned with its field abundance (Burbutis and Stewart 1979; West and Miller 1989; Marino and Landis 1996; Menalled et al. 1999, 2003; Costamagna 2002) and immature development (West 1988, West and Miller 1989, Miller 1996). No data have been reported regarding its longevity or use of adult food resources.

The objective of this study was to determine the effect of food resources on adult *G. militaris* and *M. communis*. Specifically, we tested the effects of: 1) food resources and temperature on the longevity of male and female *G. militaris*; 2) food resources, hosts, and mating on the longevity and fecundity of female *M. communis*; and 3) food resources on the longevity of male *M. communis*.

### Materials and Methods

**Insects.** Colonies of *G. militaris* and *M. communis* were initiated from *P. unipuncta* larvae recovered from cornfields in Ingham County, Michigan, during the 2000 and 2001 growing season, respectively. Adult parasitoids were provided with solutions of 50% honey in distilled water and distilled water alone. The first laboratory generation was used for *G. militaris* experiments, and the first and second for *M. communis* experiments. A colony of *P. unipuncta* from larvae provided by the United States Department of Agriculture-Agriculture Research Service Corn Insects and Crop Genetics Research Unit (Iowa State University, Ames, IA) was maintained and used as host for each parasitoid species. *P. unipuncta* larvae were fed with an artificial diet based on pinto bean (Costamagna 2002), and occasionally provided with fresh corn leaves grown in a greenhouse. Adult moths were provided with distilled water, a sugar solution (30% beer and 20% honey in distilled water, and 7.5 g ascorbic acid per 747 ml of solution), and folded paper strips to induce oviposition. Colonies were maintained at 24°C, 60% RH, and a 16:8 (L:D)-h photoperiod.

**Effects of Food Resources, Male Presence, and Temperature on Longevity of Adult *G. militaris*.** We measured the longevity of adult females with and without males at 20 and 25°C, provided with either honey-water or water alone, or with neither food nor water (control). Containers with solitary females were included as a control for the effect of males on female longevity (Jervis and Copland 1996). Newly emerged adult *G. militaris* were placed in ventilated 500-ml plastic cups and randomly arranged in pairs of one female and one male. Ten containers with male and female pairs and 15 containers with females alone were then randomly assigned to each treatment. Food and water were offered to wasps inside the 500-ml container via 30-ml plastic cups (Solo Cup Company, Urbana, IL) with cotton wicks through their lids. To avoid fungal growth, cups with food resources were replaced once per week.

Three food resource treatments were tested. The honey-water treatment consisted of one cup filled with honey diluted in distilled water (50% by volume; hereafter honey treatment), and a second cup filled with distilled water. The water treatment consisted of two cups filled with distilled water. Finally, a control of no food or water consisted of two empty cups. Two temperature regimes were compared simultaneously in different growth chambers: 20.1 ± 0.5°C, and 25.0 ± 0.2°C (mean ± SD). Relative humidity differed slightly between temperature regimes: 62.8 ± 4.0% and 77.8 ± 4.8% (mean ± SD), at 20 and 25°C, respectively. The same photoperiod of 16:8 (L:D)-h was used in both growth chambers. Temperature and relative humidity inside the 500-ml containers were measured and compared with conditions inside the growth chamber to control for any microclimate difference among treatments. Adult survivorship was assessed twice per day, in the morning and evening. Insects
Experimental Design and Data Analysis. Microclimatic conditions of temperature and relative humidity were compared among treatments as fixed effects using a completely randomized analysis of variance (ANOVA) (PROC MIXED, SAS Institute 2001). Two separate three-way factorial ANOVA tests with fixed effects were performed (PROC MIXED, SAS Institute 2001). In the first one, we tested the effects of temperature, food, and sex on the longevity of adult couples reared in the same cage. In the second one, we tested the effects of temperature, food, and male presence on the longevity of females. Independent variables were estimated for each food treatment to avoid heterogeneity of variance effects, and the suitability of these models was assessed using the ratio likelihood test (P < 0.05, PROC MIXED, SAS Institute 2001). To meet the assumption of normality, longevity data were transformed (ln [y]) before analysis (Sokal and Rohlf 1995). Means were separated using least square means (LSM) differences (PROC MIXED, SAS Institute 2001). For all experiments, all values are reported in the original scale of measure as mean ± SE, unless otherwise indicated.

A priori predictions were that adults would live for fewer days at 25 than at 20°C, that honey provision would increase the longevity of adults under both temperature conditions, and that water would enhance adult survivorship, especially at the highest temperature. In addition, we predicted that females would live longer than males, and that the presence of males would reduce female longevity. All effects were predicted to be less pronounced in the absence of honey.

Effects of Food Resources, Host Availability, and Mating Status on Female M. communis Longevity and Fecundity. We conducted an experiment that simultaneously compared the effects of access to honey, hosts, and males on the longevity and fecundity of M. communis females. In addition, we conducted a second experiment to estimate the fraction of hosts that were parasitized, but died before parasitoid emergence. Experiments were conducted at 24°C, 60% RH, and 16:8 (L:D) photoperiod, and survivorship of adults was checked daily.

Food Resource Treatment. Newly emerged M. communis females were reared in 3.8-liter plastic containers (22 × 14 × 14 cm) with three openings closed by a fine polyester mesh no-see-um netting (Kaplan-Simon Co., Braintree, MA) to allow air interchange. After 24 h with only distilled water provided, mated and virgin females (see below) were randomly assigned to receive honey or water, following the methodology described for G. militaris. Because parasitoids are not typically water deprived in the field (Dyer and Landis 1996), the no food and no water treatment was not included to reduce the number of treatment combinations.

Host Availability Treatment. After an initial 24 h, females were randomly assigned to receive a daily provision of P. unipuncta larvae or no hosts. To estimate the effect of food resources on parasitoid fecundity, a surplus of hosts must be provided (Jervis and Copland 1996). However, no data were available concerning daily fecundity of M. communis using P. unipuncta as host. Previous studies used <10 hosts per female per day to estimate parasitism by M. communis (West 1988, Miller 1996). We provided an equal number of hosts to each female each day based on what our armyworm colony could provide. Females were provided an average of 17.8 ± 1.3 (mean ± SD) host larvae per day during the first 3–7 d of life. This rate was subsequently reduced, because our results indicated that females seldom parasitized more than 10 hosts per day (1.5% of cases). From 4–8 to 22–27 d, females were provided with 13.5 ± 1.3 hosts per day. Finally, 8.4 ± 1.7 hosts per day were provided for the rest of life. Four replicates were conducted using this protocol with females of the first laboratory generation. A second group of four replicates was conducted with the second laboratory generation of females and was provided with 8.8 ± 2.6 hosts per day all life.

Second to fourth instars were used, because previous studies indicated these were most likely to be accepted as hosts (West and Miller 1989; Marino and Landis 1996, Menalled et al. 1999, 2003). Larvae were placed on a rectangular piece (7 × 5 × 1 cm) of artificial diet in an open plastic petri dish. In addition, a piece of fresh corn leaf (9 × 5 cm) was included to provide host plant cues. Diet was replaced as needed, and the corn leaf was renewed daily. Every 24 h larvae were replaced, and those exposed to parasitoids were reared in 30-ml plastic cups with paper lids (Bio-serve, Frenchtown, NJ), containing ~10 ml of artificial diet. Larvae were checked periodically until death, pupation, or emergence of the parasitoids. Diet for larvae was replaced as needed, typically once per week. Initial attempts to rear the larvae in groups of three or two larvae per cup were substituted by individual rearing after observation of cannibalism.

Mating Status Treatment. Newly emerged females were randomly assigned to a male during the first 24 h (mating treatment) or were withheld from males (no mating treatment). M. communis mating occurs within 30 min of male contact with virgin females (West 1988), and in preliminary trials we observed that males typically copulate with females immediately after introduction into containers. However, some females that were paired with males produced only male progeny, indicating either that mating did not occur or was insufficient to allow production of fertilized eggs. Based on this post hoc information, the category of mated females was divided in two categories for analysis, resulting in a total of three mating conditions for females that had access to hosts. Females that had access to males, but produced only male offspring, were grouped in a separate category, hereafter called unsuccessfully mated. Females that had access to males and produced both male and female offspring are referred to as successfully mated. Finally, those that never contacted males are termed unmated.
Larval Mortality and Parasitism. In the previous experiment, we did not dissect dead larvae to establish the occurrence of parasitism. Therefore, we conducted a second experiment to assess the fraction of parasitized host larvae that died before parasitoid emergence. In addition, we compared the mortality of host larvae exposed to *M. communis* females versus larvae without parasitoid contact. Newly emerged females were placed in containers, as previously described, and provided water, honey-water, and two males (>1 d old). After 3–6 d, males were removed, and 20 second to third instar hosts were provided without artificial diet to minimize the potential of a physical refuge. The experiment was conducted for 72 h, and hosts were replaced daily and reared in individual cups, as previously described. The parasitism level of larvae that died before parasitoid emergence was assessed by dissection of a random sample (*n* = 98, 39% of the dead larvae). Background larval mortality was assessed by including a set of control host larvae (no wasp), randomly assigned to each block.

Experimental Design and Data Analysis. The first experiment was conducted in a complete randomized block design, using starting day as the blocking factor. Food resources, host access, and mating status were combined to produce eight treatments replicated in four blocks: 1) honey + hosts + mating, 2) water + hosts + mating, 3) honey + no host + mating, 4) water + no host + mating, 5) honey + hosts + no mating, 6) water + hosts + no mating, 7) honey + no hosts + no mating, and 8) water + no host + no mating. Treatments 1–4 were replicated in four additional blocks, for a total of eight replicates. A total of 48 *M. communis* females were reared, and 5,948 larvae of *P. unipuncta* were used as hosts.

The following responses to treatments were measured: female longevity (in days), total and daily fecundity (estimated as number of hosts parasitized), prereproductive period (number of days before first reproduction), number of days necessary to achieve half of total reproduction, and proportion male offspring. Differences in total fecundity could be caused by either: 1) differences in longevity, or 2) differences in daily fecundity. To test differences in daily fecundity, the proportion of *P. unipuncta* larvae parasitized (number of larvae parasitized/number of larvae offered) was compared among treatments. Daily fecundity was calculated for all females during the time interval in which water-fed females were alive. The use of this period avoided underestimation of honey-fed female rate of fecundity because of a decline in the rate of parasitism with female age, absent in water-fed females (Costamagna 2002). To avoid potential bias, parasitism values when less than 10 host larvae were provided were not included in the daily fecundity results, but were included in total parasitism.

We predicted an increase in longevity with honey provision and also in the absence of hosts and mating, based on the trade-off between longevity and reproduction (Roff 1992). In addition, host access was expected to decrease female longevity, under all conditions. It was also expected that mating would decrease female longevity in conditions of food absence and host availability. Honey provision was expected to increase total and daily fecundity, while the absence of carbohydrate resources and absence of mating were predicted to delay reproduction.

Effects of food resources, host access, and mating status on female longevity were compared using a three-way factorial ANOVA with fixed effects (PROC MIXED, SAS Institute 2001). Effects of food resources and mating status on total fecundity were assessed using a two-way factorial ANOVA with fixed effects (PROC MIXED, SAS Institute 2001). Daily fecundity was estimated as the proportion of *P. unipuncta* larvae parasitized per female per day, and analyzed by logistic regression using the logit link function and a binomial distribution (SAS GLIMMIX macro, Littell et al. 1996). Food resources and mating status treatments were assigned in a two-way factorial design with fixed effects. The same model was used to estimate the effects of treatments on the proportion of *P. unipuncta* larvae missing because of cannibalism and larval mortality, to establish absence of bias in the data. To avoid heteroscedasticity, independent variances were estimated for each food treatment, and the suitability of this model was assessed using the ratio likelihood test (*P* < 0.05, PROC MIXED, SAS Institute 2001), except for data of the prereproductive female period, which was previously transformed using ln ([x + 1]) (Sokal and Rohlf 1995). Nonsignificant block effects were removed from models. Significant interactions were investigated by slicing by main effects to detect significant differences between treatments at this level (Kuehl 2000). Treatments were separated within main effects by comparing the marginal means using the LSM difference (PROC MIXED, SAS Institute 2001, Kuehl 2000). The effect of the different numbers of host larvae offered on the proportion of hosts parasitized per day was assessed using simple linear regression analysis (PROC REG, SAS Institute 2001).

The experiment to determine host mortality and parasitism was conducted in completely randomized blocks, using female day of emergence as blocking factor, for a total of 15 replicates. We estimated the percentage of parasitized hosts that died before parasitoid emergence, the percentage of mortality of host larvae, and percentage of parasitism per female per day. We expected to obtain similar levels of mortality between larvae exposed to wasps and control larvae. We also predicted that parasitism would increase with time, because of wasp acclimation and/or learning. The number of hosts parasitized was compared among the 3 consecutive days using a one-way ANOVA (PROC MIXED, SAS Institute 2001).

Effect of Food Resources on Male *M. communis* Longevity. Newly emerged males were placed under conditions as described for females, and allowed access to a female (>1 d old). After 24 h, females were removed and males randomly assigned to honey or water treatments, following the same protocol as for females. Twenty-two replicates per treatment were conducted. We predicted that honey access would
extend male longevity. Longevity was contrasted between honey-fed and water-fed males using a one-way ANOVA (PROC MIXED, SAS Institute 2001).

**Results**

Effects of Food Resources, Male Presence, and Temperature on Longevity of Adult *G. militaris*. Temperature and relative humidity did not differ significantly among rearing containers provided with different food treatments (20°C growth chamber: temperature, \( F = 0.28; \text{df} = 3, 12; P = 0.84 \); RH, \( F = 0.34; \text{df} = 3, 12; P = 0.50 \)), and 25°C growth chamber: temperature, \( F = 2.01, \text{df} = 3, 11; P = 0.17 \); RH, \( F = 2.19; \text{df} = 3, 12; P = 0.14 \). Both males and females lived significantly longer at 20 than 25°C (Table 1 [temperature effects]; Fig. 1). Access to honey significantly increased longevity over the other food resources, by approximately 3-fold at 20°C (20.3 ± 4.0 d) and 2-fold at 25°C (7.7 ± 2.7, Table 1 [food resources effects]; Fig. 1). Water significantly improved the survivorship of adults over those with no resources (except for males reared at 25°C), but only by a mean increase of 1.3–0.5 d for females, and <0.5 d for males (Fig. 1). Across all treatments, females lived significantly longer than males, with female longevity approximately twice that of males when honey was available (Table 1a [sex effect]; Fig. 1). The presence of males did not affect female longevity under any food treatment or temperature condition (Table 1b [male presence effect]; Fig. 1). No significant interactions of these three main effects were found, except for temperature × food (Table 1b), because of the absence of difference in the longevity between females and solitary females provided with water (test slicing by food treatment, \( F = 2.24; \text{df} = 1, 42; P = 0.14 \)).

Effects of Food Resources, Host Availability, and Mating Status on Female *M. communis* Longevity and Fecundity. A post hoc analysis showed that cannibalism and larval mortality were not differentially associated with specific treatments. Treatments did not differ in the level of cannibalism (food resources, \( F = 0.05; \text{df} = 1, 12; P = 0.83 \); mating status, \( F = 0.04; \text{df} = 1, 12; P = 0.82 \)) or larval mortality (food resources, \( F = 0.06; \text{df} = 1, 18; P = 0.51 \); mating status, \( F = 0.00; \text{df} = 1, 18; P = 0.97 \)). In addition, the higher number of hosts provided initially in blocks 1–4 explained only 6% of the increase in parasitism (regression for larvae parasitized and number of larvae offered, \( R^2 = 0.06; F = 13.85, \text{df} = 1, 228; P < 0.01 \)). Thus, our results were robust against potential bias introduced by host larvae cannibalism and mortality, and variation in the number of hosts provided daily.

Exposure to males during the first 24 h of life did not affect female longevity nor interact with other treatments (Table 2 [mating status effect, mating status interaction terms]). Therefore, slicing by main effects was performed without mating status in the model. Access to honey significantly increased female longevity (Table 2 [food resources effect]), independent of host availability (slicing by with hosts, \( F = 103.38; \text{df} = 1, 237.7; P < 0.01 \); slicing by without hosts, \( F = 193.43; \text{df} = 1, 237.7; P < 0.01 \)) or mating status (Table 2 [food resources × mating status]; Fig. 2). In contrast, access to host larvae significantly reduced female longevity when honey was provided (Table 2 [hosts effect], slicing by honey, \( F = 7.36; \text{df} = 1, 22; P = 0.01 \)), but had no effect on females provided only water

---

**Table 1.** Results of tests for effects of three food resources (honey + distilled water, distilled water alone, and neither honey nor water) and two conditions of temperature (20 and 25°C) on *G. militaris* adult longevity

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>a) Females and males</th>
<th>b) Females with or without males</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Temperature</td>
<td>1, 25</td>
<td>9.29</td>
</tr>
<tr>
<td>Food resources</td>
<td>2, 29</td>
<td>37.51</td>
</tr>
<tr>
<td>Sex (a) or male presence (b)</td>
<td>1, 23</td>
<td>5.70</td>
</tr>
<tr>
<td>Temperature × Food</td>
<td>2, 29</td>
<td>1.84</td>
</tr>
<tr>
<td>Sex (a) or male presence (b)</td>
<td>1, 23</td>
<td>0.27</td>
</tr>
<tr>
<td>Temperature × Food × Sex (a) or male presence (b)</td>
<td>2, 27</td>
<td>1.64</td>
</tr>
</tbody>
</table>

---

**Fig. 1.** Longevity (mean ± SE) of *G. militaris* adults under three food resource treatments (honey + distilled water, distilled water alone, and control of neither honey nor water), under (A) 20°C and (B) 25°C temperature regimes. Columns with different letters differed significantly within adult category (\( P < 0.05 \), LSM difference). Males and females were reared together in pairs.
Honey increased fecundity for all mating conditions (main effect, $F = 52.15; df = 1, 10.4; P < 0.01$; slicing by successfully mated, $F = 34.85; df = 1, 9.87; P < 0.01$; slicing by unsuccessfully mated females, $F = 19.02; df = 1, 3.84; P < 0.01$), but was only marginally significant for unmated females (slicing by unmated females, $F = 4.29; df = 1, 10.4; P = 0.06$).

Honey did not increase daily fecundity, but significant differences were found among mating conditions (food resources, $F = 1.19; df = 1, 18; P = 0.29$; mating status, $F = 3.50; df = 2, 18; P = 0.05$; and food resources × mating status interaction, $F = 1.98; df = 2, 18; P = 0.17$). Successfully mated females parasitized $32.9 \pm 4.4\%$ of the hosts offered per day, and differed significantly from unmated females that only parasitized $17.0 \pm 3.4\%$ (LSM difference, $t = 2.64, P = 0.02, n = 8$), while unsuccessfully mated females showed an intermediate value of $22.1 \pm 8.1\%$ of the hosts offered per day, and did not differ from the other two.

We observed a significant delay in reproduction by females offered honey ($3.42 \pm 0.87 d$) compared with those provided water alone ($1.58 \pm 0.19 d$; $F = 3.93; df = 1, 18; P = 0.05$). Mating status did not affect this delay ($F = 0.18; df = 2, 18; P = 0.84$). Also, we did not observe a significant interaction between food resources and mating status ($F = 0.29; df = 2, 18; P = 0.75$). Successfully mated females required $18.3 \pm 2.2 d$ (0.45 of life span), unsuccessfully mated females $19.8 \pm 1.7 d$ (0.46 of life span), and unmated females $14.5 \pm 2.7 d$ (0.41 of life span) to lay half of their viable offspring, differences that were not statistically significant ($F = 0.18; df = 2, 9; P = 0.84$). Females fed exclusively with water died before becoming post-reproductive, whereas females fed with honey lived $5.5 \pm 4.8 d$ (mean ± SD) without producing viable offspring before death. Of those females initially paired with males, proportionally more fed with honey did not successfully mate ($0.625, n = 8$) than those fed with water ($0.325, n = 8$). The proportion of

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block</td>
<td>7, 13.3</td>
<td>2.94</td>
<td>&lt;0.04</td>
</tr>
<tr>
<td>Food resources</td>
<td>1, 20.3</td>
<td>238.71</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Hosts</td>
<td>1, 20.3</td>
<td>6.34</td>
<td>0.02</td>
</tr>
<tr>
<td>Food resources × hosts</td>
<td>1, 20.3</td>
<td>6.47</td>
<td>0.02</td>
</tr>
<tr>
<td>Mating status</td>
<td>1, 21.4</td>
<td>1.13</td>
<td>0.30</td>
</tr>
<tr>
<td>Food resources × mating status</td>
<td>1, 20.3</td>
<td>2.95</td>
<td>0.10</td>
</tr>
<tr>
<td>Hosts × mating status</td>
<td>1, 20.3</td>
<td>0.00</td>
<td>0.99</td>
</tr>
<tr>
<td>Food resources × hosts × mating status</td>
<td>1, 20.3</td>
<td>0.03</td>
<td>0.87</td>
</tr>
</tbody>
</table>
males produced by mated females (n = 8) did not differ significantly between females fed with honey (0.66 ± 0.18 males) and females fed with water alone (0.51 ± 0.09 males, F = 0.68; df = 1, 6; P = 0.44).

Larval Mortality and Parasitism. Seven of the 15 females tested produced offspring. Postmortem dissection of larvae that died before parasitoid emergence revealed that 11.2% were parasitized. Mortality of P. unipuncta larvae exposed to M. communis did not differ from control larvae (F = 3.33; df = 1, 7.91; P = 0.11). Female daily fecundity was highly variable and did not increase with time (F = 0.45; df = 2, 18; P = 0.64). An average of 2.7 ± 3.3 (± SD) larvae were parasitized per day, with a maximum of 11 larvae parasitized per day (4.5% of the cases). These results indicate that in the previous experiment, parasitism was likely to be only slightly underestimated (11.2% of the 3.3% that died before parasitoid emergence). That P. unipuncta larval mortality is independent of female oviposition, and that 10 hosts per day were sufficient to obtain accurate estimates of daily parasitism.

Effect of Food Resources on Male M. communis Longevity. The longevity of mated males was significantly improved by access to honey. Males provided with honey lived 26.2 ± 2.6 d in contrast to water-fed males that only lived 4.6 ± 0.6 d (F = 67.48; df = 1, 21; P < 0.01).

Discussion

Our results support the prediction of a reduction in G. militaris adult longevity at higher temperature. G. militaris adults exposed to 25°C lived half as long as those at 20°C, suggesting that the optimal temperature for this species is <25°C. This result is consistent with prior studies that showed greater longevity of G. militaris at lower temperatures (Calkins and Sutter 1976, Oliveira et al. 1998). Prevailing maximum temperatures in southern Michigan cornfields (high 20s and low 30s °C; Dyer and Landis 1996) probably are not favorable for this parasitoid species. The importance of habitats with milder conditions surrounding cornfields was demonstrated for Eriborus terebrans (Hymenoptera: Ichneumonidae), a parasitoid with similar temperature constraints as G. militaris (Dyer and Landis 1996).

The prediction that honey would increase longevity of G. militaris adults was also supported by this experiment. Calkins and Sutter (1976) reported that G. militaris females provided with fresh halved grapes as a carbohydrate source lived an average of 3 d more than those without food resources. When G. militaris was provided with 10% honey diluted in water, at 22°C, 75% RH, and a photoperiod of 16:8 (L:D) h, Reis et al. (2003) observed longevity within the range of our results. As predicted, male longevity was shorter than that of females when honey was provided, similar to the results of Reis et al. (2003). This trend has been shown for many species of Hymenoptera parasitoids (Quicke 1997).

Frequent mating can reduce life span in both male and female insects (van den Assem 1986); however, we did not observe an effect of males on G. militaris female longevity. Although G. militaris was reported to mate several times in consecutive days (Tower 1915), and we observed successful mating in our colony under similar conditions, we did not check the occurrence of mating in our experiment. Therefore, we cannot reject the possibility that the absence of an effect on female longevity was caused by an absence or reduction of mating. Previous studies with G. militaris reported a male-skewed progeny, indicating a possible mating reduction (Oliveira et al. 1998, 1999; Reis et al. 2003).

Honey dramatically increased the longevity and fecundity of M. communis. Thireau and Régnière (1995) observed similar longevities (22.0 and 23.8 d for males and females, respectively) and higher fecundity (194.2
eggs per unmated female) for *M. trachypnotus* (Vier.), which was provided with a 10% honey-water solution. Bautista et al. (2001) found a reduction in the number of eggs produced by females of the braconid *Fopius arisanus* (Sonan) deprived of honey. Similarly, females of the pteromalid *Nasonia vitripennis* (Walker) fed honey (30% honey in water) showed an increase in mature eggs 72 h after emergence (Rivero and West 2002). In our study, the proportion of hosts parasitized per day was not greater for honey-fed females, indicating the increase in total parasitism caused by honey provision was a consequence of an increase in female longevity and not in fecundity. However, because solitary braconid parasitoids are able to lay more than one egg per host (Wharton 1993), it is possible that by assessing the number of parasitized hosts we underestimated the potential fecundity of *M. communis*.

We observed accelerated oviposition in food-deprived females, in contrast to honey-fed females that exhibited more selective oviposition behavior, resulting in fewer parasitized hosts initially. Increased oviposition in response to stress has been documented for *Leptopilina heterotoma* (Hymenoptera: Eucoilidae) under conditions of low life expectancy (late in the season) and low barometric pressure (increased risk of mortality) (Roitberg et al. 1992, 1993). Olson et al. (2000) obtained similar results for sugar-starved females of *Macrocentrus grandii* (Hymenoptera: Braconidae) and suggest that the increase in the number of mature eggs as a response to low life expectancy may be a strategy that enhances opportunities for reproduction. However, because we did not measure egg load, we cannot assess whether this reduction was caused by a decrease in the production of eggs or a change in the oviposition behavior of the females.

A trade-off between female reproduction and longevity predicts a reduction in the life span of females that allocate resources to reproduction (Roff 1992). Accordingly, access to hosts significantly reduced *M. communis* female longevity. Females of the braconid *Cotesia melitaearia*um (Wilkinson) provided fresh flowers but prevented from contacting hosts, lived longer than those allowed to parasitize hosts (Lei et al. 1997). The same trend was observed for *M. trachypnotus* females (Thireau and Régnière 1995). Mating stimulates reallocation of resources from maintenance to oogenesis and egg maturation (Jacob and Evans 2000), which could lead to a reduction in female longevity under conditions of low food quality. In contrast, it may not have any effect when food quality is high, as shown for the ichneumonid *Bathyplectes curculionis* (Jacob and Evans 2000). In our study, mating did not affect *M. communis* longevity, with or without the provision of a carbohydrate resource.

Total fecundity and rate of oviposition were greater for mated than unmated *M. communis* females. Higher numbers of hosts parasitized by mated than unmated females also have been reported for several parasitoid species (Michaud 1994), such as the braconid *Cotesia glomerata* (L.). Dissections of ovaries of *C. glomerata* proved that it was a behavioral rather than a physiological change, because mated and unmated females had similar egg loads (Jervis and Copland 1996). Studies of other parasitoids, however, have not revealed differences in fecundity of mated and unmated females (Jervis and Copland 1996, Sousa and Spence 2000).

In arthropod parasites such as *G. militaris* and *M. communis*, virgin females produce only males (Quicke 1997). Berndt et al. (2002) found a decrease in the proportion of *Dolichogenidea tasmanica* (Hymenoptera: Braconidae) males in plots provided with nectar resources. In our study, the proportion of male offspring did not differ significantly in honey-fed and water-fed females, but rather showed the opposite trend, a higher proportion of male offspring from honey-fed females. Unsuccessfully mated *M. communis* females had an intermediate level of fecundity and rate of parasitization. Mated parasitoid females that receive nonviable sperm or have blocked spermathecal ducts caused by multiple matings also produce only male progeny (Godfray 1994). Therefore, one possible explanation is that females received nonviable sperm and used it as a source of energy to increase reproductive output over unmated females. Alternatively, contact with males could elicit a higher rate of oviposition, although fewer eggs were available for oviposition compared with mated females. Further research is necessary to elucidate the mechanism behind this response.

The shorter life span and gregarious reproductive strategy of *G. militaris* suggest a possible mechanism of egg limitation (Heimpel 2000). Successful reproduction of this parasitoid might be less dependent on availability of food resources in close proximity to its hosts, because it should produce high levels of parasitism in a short time. This is supported by the negative response of this parasitoid to host density under field conditions (Costamagna 2002). In addition, a recent study on the braconid *Macrocentrus grandii* indicates that sporadic (i.e., every 2–4 d) and continuous access to carbohydrate resources provides similar benefit to longevity and fecundity (Fadamiro and Heimpel 2001). Conversely, *M. communis* is a solitary species with lower daily fecundity and higher longevity, suggesting a possible host limitation mechanism (Heimpel 2000). Therefore, parasitism by this species could be affected by the presence of adult food resources in close proximity to its host larvae. Under field conditions, species parasitized proportionally more hosts in high host density patches (Costamagna 2002).

Food resources dramatically increased longevity of *G. militaris* under different temperature conditions, and longevity and fecundity of *M. communis* under varying conditions of host access and mating status. Therefore, an increase of carbohydrate resources in the field could increase the level of parasitism produced by both parasitoid species. Moreover, we can further hypothesize that an increase in habitat complexity, with its concomitant increase in food resources (Landis et al. 2000), might be more favorable to *M. communis* than to *G. militaris*. A general trend toward this pattern of association between landscape complexity and *M. communis* and *G. militaris* has been...
References Cited

Acknowledgments
We thank M. E. O’Neal, G. E. Heimpel, M. J. Brewer, and the three anonymous reviewers for their valuable comments on the manuscript. Special thanks to A. Gould, S. Clay, M. E. O’Neal, C. Hemming, M. Soto Rodriguez, K. Newhouse, D. C. Sebott, T. B. Fox, F. D. Menalled, M. Burns, and M. Smith for their assistance with the experiments. We are indebted to L. Lewis and J. Dyer, United States Department of Agriculture-Agricultural Research Service, for the provision of the armyworms used to initiate our colonies, and all the support made available to maintain the colonies throughout this study. We thank J. Luhman for providing confirmation of the identity of the parasitoid species studied. Statistical advice was provided by K. Kizilkaya and F. Cardoso (Statistical Consulting Center of the College of Agriculture and Natural Resources Biometry group, Michigan State University). Funding for this work was provided by an Instituto Nacional de Tecnologia Agropecuaria-Fulbright fellowship to A.C.C. and by the Michigan Agricultural Experiment Station.

shown by several field studies (Marino and Landis 1996; Menalled et al. 1999, 2003; Costamagna 2002).
April 2004  COSTAMAGNA AND LANDIS: FOOD RESOURCES IMPACT ARMYWORM PARASITOIDS 137


Received for publication 14 June 2003; accepted 11 October 2003.