Effects of Temperature and Water Source on Development of *Deraeocoris nebulosus* (Uhler) (Hemiptera: Miridae), a Predacious Plant Bug[1]

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Abstract The development of *Deraeocoris nebulosus* (Uhler) was studied in relation to temperature and to water sources additional to food. Development time for *D. nebulosus* was linear between 20° and 30°C, allowing the use of a linear equation to calculate degree days. The eggs of *D. nebulosus* required 111.1 degree days over a threshold of 13.9°C to complete development. Nymphal development for males and females of *D. nebulosus* was about 1.5 times faster at 25°C than at 20°C, 1.5 times faster at 30°C than at 25°C, and almost 2.5 times faster at 30°C than at 20°C. Males developed 2 d faster than females (protandry) at 20°C, but did not develop faster at the other temperatures. This study provides the first record of temperature-regulated protandry in insects. Nymphs of *D. nebulosus* required 166.7 degree days over a threshold of 12.7°C for males and 15.2°C for females. Preoviposition period was almost 12 d at 20°C and about 6 d at 25° and 30°C. Water source (free water, sugar water, or sweet potato leaf) did not affect the development of *D. nebulosus* when fed moth eggs.

Key Words *Deraeocoris nebulosus,* temperature, Miridae, predator, development, water source

Many factors can affect the development of insects including temperature and access to and type of food and water. In developing a biological control program using predators, the system needs to promote proper development of the predators used. Insect rearing systems should be able to produce insects that are of the same quality as those found in their natural environment. Knowledge of temperature requirements and water source needs are essential for these and other applications.

The time required for nymphal development in mirids is typically inversely proportional to temperature (Wheeler 2001) and is usually linear in relation to temperature with low and high extremes excluded (Braman et al. 1984, Wheeler 2001). Data from temperature-dependent development studies can improve the efficiency of mass-rearing techniques, provide a quantitative basis for predicting natural occurrence, and be used in models to estimate insect growth, development, and reproduction (Gutierrez et al. 1981, Rodriguez-Saona and Miller 1999).

Degree-day models have been used to forecast pest development so pesticides

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can be applied more accurately at the target stage of development (e.g., Braman et al. 1992, Raupp et al. 1992, Braman and Pendley 1993). They also have been used to determine development time of predators, to improve efficiency of rearing methods, and to understand insect phenologies in the field (e.g., Nakashima and Hirose 1997, Rodriguez-Saona and Miller 1999).

Facultative plant feeding is common in the predacious Heteroptera (Coll 1998, Gillespie and McGregor 2000) and is considered advantageous to the predators, especially during times of prey scarcity (McGregor et al. 2000, Coll and Guershon 2002). Facultative phytophagy can enhance the predator's developmental time, fecundity, and survival (Gillespie and McGregor 2000, Coll and Guershon 2002). Plant feeding by heteropterans, however, can cause economic damage to crops, especially by predacious mirids (Alomar and Albajes 1996), although some predacious mirids cause no noticeable injury to the plants (Wheeler 2001).

Heteropterans obtain nutrients by using extra-oral digestion (Cohen 2000). Mechanical laceration by stylets and chemical maceration from digestive enzymes render the tissues of prey into a nutrient-rich slurry that is easily imbibed through the insect's food channel (Cohen 1990, 1998b, 2000). The addition of watery digestive enzymes not only breaks down the tissue into particles small enough to be ingested, but also reduces the viscosity of the food slurry (Cohen 2000). Reduction of viscosity is essential for tube-feeding insects because flow rate through the food canal is directly related to viscosity (Mittler 1967, Cohen 1998a). This continuous injection of dilute saliva into the prey necessitates the recycling of water. The accessory gland of the salivary gland complex, which is closely attached to the midgut (Nishijima and Sōgawa 1963), is thought to recycle water from the gut and send it back to the salivary glands (Miles 1972, Cohen 1998a).

Many prey insects are composed of high percentages of water. For example, some lepidopteran larvae are 70 to 80% water (Cohen 2000). Although most insects obtain sufficient water from their food alone (Chapman 1998), a free water supply is probably necessary for predacious heteropterans (Gillespie and McGregor 2000). *Deraeocoris nebulosus* (Uhler) has digestive enzymes (i.e., amylase, glucosidase, and pectinase) that potentially allow it to use plants for food (Boyd et al. 2002), but whether plant feeding is necessary or advantageous remains unknown.

Our objectives were to determine developmental time of *D. nebulosus* in relation to temperature, and to determine if plant feeding contributes to its development and if access to water, other than from prey, is essential. The results from temperature-related experiments were used to develop degree-day models for the life stages of this predacious mirid. These models will help develop better means of rearing this insect by providing the optimal rearing temperature and will help determine the phenology of the insect in the field. Information from the plant and water experiments will aid in determining if this insect will damage plant material and if rearing is enhanced by the addition of plant material or other water source to the colony.

Materials and Methods

Insects. A colony was established with *D. nebulosus* collected from oaks (e.g., *Quercus alba* L., *Q. stellata* Wang., and *Q. falcata* Michaux) in Greenville Co. and Pickens Co., SC, during the summer of 1999 and was maintained at 25 ± 2°C, 50 ± 10% relative humidity, and 14L:10D photoperiod. *Deraeocoris nebulosus* was reared on eggs of *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) (Beneficial Insectary, Redding CA) in 11.3-L plastic containers provided with paper towels and water in a cotton stopped 4-dram vial at the Cherry Farm Insectaries, Clemson University, Clemson, SC. Voucher specimens of *D. nebulosus* were placed in the Clemson University Arthropod Collection.

Temperature experiments. Newly-hatched first instars of *D. nebulosus* were placed singly in 100 × 25 mm Petri dishes and provided with a piece of filter paper, *E. kuehniella* eggs for food, and water via a cotton wick in a 1-dram vial. Petri dish lids had a muslin-covered, 3-cm diam hole to allow air movement. *Ephestia kuehniella* eggs were added every 2 to 3 d, and the filter paper was replaced as needed (e.g., evidence of fungus, saturation with water). Three incubators (I-30BLL, Percival Scientific, Inc., Boone, IA) were used, each set at 50 ± 10% RH and photoperiod of 14L:10D. Temperatures used were 20, 25 and 30 ± 0.5°C. Ten replicates were used in each incubator in each of three trials for a total of 30 replicates. Each incubator was used once for each temperature.

The mirids were checked every 24 h. Developmental time was determined by recording the number of days in each instar. Instar development was determined by presence of cast exuviae and by the length of the wing pads in the fourth and fifth instars (Wheeler et al. 1975). When the mirids reached adulthood, the sex was determined by the presence or absence of an ovipositor. Each female received a male and a sweet potato, *Ipomoea batatas* (L.), leaf (Jones and Snodgrass 1998). The leaf was inserted into a water-filled, 1-dram vial and held in place with Parafiln® (Pechiney Plastic Packaging, Menasha, WI) wrapped around the opening and stem. The number of days from onset of adulthood until the eggs were laid (preoviposition period) was recorded, and the number of eggs oviposited was counted each day for 5 d beginning with the first day of oviposition. The egg-incubation period was recorded as days from oviposition to egg hatch.

All individuals that reached adulthood were placed in 80% ethanol after the 5-d oviposition period. The length from the apex of the head to the end of the abdomen, the distance between the outer, lateral edges of the eyes, and the length of the left femur were measured with an eyepiece micrometer calibrated to mm.

Two-factor analysis of variance was used to determine differences of development times and all length measurements with temperature and sex as factors. Analysis of variance was used to determine differences of preoviposition time, number of eggs for 5 d, and incubation period of eggs. If differences were found using ANOVA, differences between treatments were subjected to Fisher's protected least significant difference test (PLSD) (StatView 1996).

Simple linear regression (StatView 1996) comparing the inverse of development time (in days) to temperature was used for each sex and for egg development. Each linear regression equation ($y = a + bx$) was used to determine the lower threshold estimate (-a/b) and the thermal constant (1/b), where y is the developmental rate (1/days) and x is the temperature in °C. The thermal constant is the number of degree days (DD) needed to complete development.

Water experiments. Newly-hatched first instars of *D. nebulosus* were placed singly in Petri dishes, as in temperature experiments, and were provided with a piece of filter paper, *E. kuehniella* eggs on a 1.5 × 2 cm sticky note (Highland™, Minnesota Mining and Manufacturing, St. Paul, MN), and one of four treatments: water in a cotton-wicked 1-dram vial, 0.05% w/v sugar water (table sugar) in a cotton wicked 1-dram vial, sweet potato leaf in a water-filled, 1-dram vial secured with Parafilm, or no water source. Eggs of *E. kuehniella* were replaced every 2 to 3 d.

Three incubators were used, each set at 25°C, 30% RH, and photoperiod of 14L:10D. Ten replicates of each treatment were used in each incubator. To standardize variability of location in each incubator, the position of each treatment was rotated every day during nymphal development.

The bugs were checked every 24 h. Developmental time was indicated by recording the number of days for each instar, as for temperature experiment. Seven days after the mirids reached adulthood (enough time for egg development in the females), they were placed in 80% ethanol. The sex of each bug was determined, and measurements were taken as in the temperature experiments. Females were dissected to determine reproductive condition. Females with eggs and little or no fat body were considered reproductive, and females with no eggs and extensive fat body were considered non-reproductive (Leigh 1966). The percentage of reproductive females was determined for each treatment by incubator, resulting in three replicates. Two-factor analysis of variance was used to determine differences of development times and all length measurements with temperature and sex as factors. Arcsine-square-root-transformed percentages of reproductive females were compared between treatments using analysis of variance. Significant differences between treatments were subjected to Fisher's protected least significant difference test (PLSD) (StatView 1996).

Results

Temperature. In all cases, the higher temperatures resulted in shorter development time. Nymphal development for both male and female *D. nebulosus* was about 1.5 times faster at 25°C than at 20°C, 1.5 times faster at 30°C than at 25°C, and almost 2.5 times faster at 30°C than at 20°C (Table 1). There was a significant temperature by sex interaction (F = 5.1; df = 2, 69; P = 0.0085) so we performed separate analyses between sexes for each temperature. The development times of males were significantly shorter than females at 20°C (F = 14.3; df = 1, 20; P = 0.0012), but not at 25°C (F = 0.1; df = 1, 24; P = 0.7122) or 30°C (F = 1.1; df = 1, 25; P = 0.3136).

The preoviposition period at 20°C was significantly longer than at 25 and 30°C (F = 23.7; df = 2, 21; $P < 0.0001$), but no difference was detected between the preoviposition periods at 25 and 30°C (Table 2). No difference was detected for the average number of eggs oviposited by each female for 5 d at each temperature (F = 0.6, df = 2, 20; P = 0.5425) (Table 2). The time for egg development at all three temperatures was faster at higher temperatures (F = 7106.0; df = 2, 472; $P < 0.0001$) (Table 2).

Length of mirids showed a difference among temperatures (F = 5.8; df = 2, 64; P = 0.0048) and between sexes (F = 45.3; df = 1, 64; $P < 0.0001$), but showed no interaction between temperature and sex (F = 1.9; df = 2, 64; P = 0.1565). Mirids at 20°C were larger than those at 30°C and at all temperatures the females were larger than males (Table 3). Neither femur length nor distance between the lateral edges of the eyes showed a temperature by sex interaction (F = 1.6; df = 2, 64; P = 0.2140 and F = 0.6; df = 2, 64; P = 0.5375, respectively). Neither femur length nor distance between the lateral edges of the eyes showed differences among temperatures (F = 2.1; df = 2, 64; P = 0.1318 and F = 0.4; df = 2, 64; P = 0.6738, respectively). However, the female's femur was longer than the male's (F = 4.6; df = 1, 64; P = 0.0360), and the eyes in females were wider than males (F = 6.1; df = 1, 64; P = 0.0164).

The regression equation for male rate (R) of nymphal development (1/days) by

Table 1. Mean development time (days ± SE) for all instars and total time of male and female *D. nebulosus* (from South Carolina, 1999) fed *Ephestia kuehniella* eggs, provided with water via cotton wick, and reared at three temperatures. Means within each row were all significantly different at *P* = 0.05 (Fisher's PLSD test). See text for comparisons between sexes

	Temperature in °C		
Nymphal instar	20	25	30
Males	(n = 12)	(n = 16)	(n = 12)
First	4.8 ± 0.2	2.3 ± 0.2	1.5 ± 0.2
Second	4.0 ± 0.1	2.5 ± 0.2	1.8 ± 0.2
Third	4.1 ± 0.2	2.6 ± 0.1	1.9 ± 0.1
Fourth	4.9 ± 0.1	3.0 ± 0.1	1.8 ± 0.1
Fifth	8.0 ± 0.2	4.7 ± 0.2	3.4 ± 0.2
Total	25.8 ± 0.3	15.1 ± 0.4	10.4 ± 0.2
Females	(n = 10)	(n = 10)	(n = 15)
First	5.4 ± 0.3	2.3 ± 0.2	1.3 ± 0.1
Second	4.5 ± 0.2	2.7 ± 0.3	1.9 ± 0.2
Third	4.5 ± 0.2	2.6 ± 0.2	1.8 ± 0.1
Fourth	5.0 ± 0.2	3.0 ± 0.0	1.9 ± 0.1
Fifth	8.5 ± 0.2	4.8 ± 0.3	3.1 ± 0.1
Total	27.9 ± 0.6	15.4 ± 0.7	10.1 ± 0.2

temperature (T) is R = −0.076 + 0.006(T), R^2 = 0.956. The regression equation for female rate (R) of nymphal development (1/days) by temperature (T) is R = −0.091 + 0.006(T), R^2 = 0.944. Combining the nymphal developmental data for the sexes provided the regression equation R = −0.084 + 0.006(T), R^2 = 0.947. The regression equation for egg developmental rate (R) (1/days) by temperature (T) is R = −0.125 + 0.009(T), R^2 = 0.919. The lower thresholds for temperature varied between sexes and stages, and the degree days for egg and nymphal development varied only between the life stages (Table 4).

Water. Most nymphs of *D. nebulosus* survived to adulthood in all treatments. Survival ranged from 70% in the leaf treatment to 97% in the no-water treatment. No difference in development time was detected by treatment (*F* = 0.6; df = 3, 91; *P* = 0.5936) or by sex (*F* = 0.003; df = 1, 91; *P* = 0.99) and their interaction was not significant (*F* = 2.1; df = 3, 91; *P* = 0.09). When analyzed separately the only difference in development time by sex was between males of the sugar and no-water treatments and that by only half a day (*F* = 1.7; df = 3, 60; *P* = 0.05) (Table 5).

Significant differences in body length were detected among the treatments (*F* = 4.6; df = 3, 91; *P* = 0.0048) and between the sexes (*F* = 284.7; df = 1, 91; *P* < 0.0001),

Table 2. Mean preoviposition period (days ± SE), mean number of eggs laid for 5 days (± SE) for female *D. nebulosus* (from South Carolina, 1999) and mean development time (days ± SE) for *D. nebulosus* eggs at three temperatures. Means within each column followed by the same letter are not significantly different at $P = 0.05$ (Fisher's PLSD test)

Temperature	Preovoposition period (n)	Average # eggs for 5 days (n)	Egg development time (n)
20°C	11.7 ± 0.9a (3)	7.5 ± 0.7a (3)	21.2 ± 0.1a (39)
25°C	6.7 ± 0.2b (9)	11.5 ± 2.1a (9)	11.0 ± 0.1b (167)
30°C	6.0 ± .04b (12)	10.1 ± 1.5a (11)	7.5 ± 0.0c (269)

but the interaction was not significant ($F = 0.02$; df = 3, 91; $P = 0.4316$). Females were consistently longer than males (Table 5). When analyzed separately, the body length of females offered water or sugar water was significantly longer than females offered leaves or no water ($F = 3.5$; df = 3, 31; $P < 0.05$) (Table 5).

The lengths of the left femur showed no differences among treatments ($F = 1.2$; df = 3, 91; $P = 0.2976$) but did between the sexes ($F = 24.6$; df = 1, 91; $P < 0.0001$) and there was a significant interaction between the two ($F = 3.1$; df = 3, 91; $P = 0.0314$). Analyzed by sex, females in the sugar treatment had significantly longer femur than those of females in the water and leaf treatments ($F = 3.6$; df = 3, 31; $P = 0.0245$) (Table 5).

No significant interaction was detected by treatment and sex in the width of heads ($F = 0.5$; df = 3, 91; $P = 0.6562$) and no differences were detected among treatments ($F = 0.6$; df = 3, 91; $P = 0.6053$), but between sexes there was a difference ($F = 18.9$; df = 1, 91; $P = 0.0001$) with females heads wider than males (Table 5). No significant difference was detected between any treatments for percentages of females with eggs ($F = 1.1$; df = 3, 8; $P = 0.4054$).

Table 3. Mean length (mm ± SE) of adult *D. nebulosus* males and females (from South Carolina, 1999) from the apex of the head to the end of the abdomen reared at three temperatures. At each temperature, females were significantly longer than males ($P < 0.05$, Fisher's PLSD test). Means followed by the same letter in each column are not significantly different $P = 0.05$ (Fisher's PLSD test)

	Length (mm)	
Temperature	Male (n)	Female (n)
20°C	3.523 ± 0.089a (13)	3.884 ± 0.161ab (10)
25°C	3.341 ± 0.059ab (13)	4.054 ± 0.117a (9)
30°C	3.211 ± 0.073b (11)	3.657 ± 0.052b (14)

Table 4. Lower threshold and degree days in centigrade for each life stage of *Deraeocoris nebulosus* (from South Carolina, 1999)

Developmental stage	Threshold	Degree days	R^2
Egg	13.9	111.1	0.919
Male nymph	12.7	166.7	0.956
Female nymph	15.2	166.7	0.944
Combined sexes	14.0	166.7	0.947

Discussion

Deraeocoris nebulosus develops more quickly at higher temperatures, and differing water sources do not provide much advantage to its development. Reproductive development of females is faster at higher temperatures, but various water sources did not increase reproduction potential.

Development time for *D. nebulosus* is linear for the three temperatures used in this study, allowing the use of the linear equation to calculate degree days (Metcalf and Luckmann 1994). The eggs of *D. nebulosus* require 111.1 degree days over a thresh-

Table 5. Mean total development time (days ± SE) and mean lengths (mm ± SE) of the body from tip of head to tip of abdomen, left hind femur, and distance between the lateral edges of the eyes for male and female *Deraeocoris nebulosus* (from South Carolina, 1999) provided free water, sugar water, a sweet potato leaf, or no water during development. Means followed by the same letter in each row are not significantly different at $P = 0.05$ (Fisher's PLSD test)

	Treatment			
Measurement	Water	Sugar	Leaf	None
Males	(n = 13)	(n = 16)	(n = 13)	(n = 22)
Development (d)	14.9 ± .2ab	14.5 ± .2a	14.6 ± .2ab	15.0 ± .1b
Length (mm)	3.24 ± .03a	3.27 ± .03a	3.20 ± .05a	3.19 ± .03a
Femur (mm)	1.20 ± .03a	1.18 ± .03a	1.21 ± .02a	1.21 ± .02a
Eyes (mm)	0.87 ± .01a	0.87 ± .01a	0.87 ± .01a	0.88 ± .01a
Females	(n = 10)	(n = 10)	(n = 8)	(n = 7)
Development (d)	14.6 ± .2a	14.7 ± .2a	15.1 ± .3a	14.6 ± .2a
Length (mm)	3.90 ± .04a	3.91 ± .07a	3.76 ± .03b	3.73 ± .04b
Femur (mm)	1.28 ± .03a	1.37 ± .02b	1.24 ± .03a	1.31 ± .05ab
Eyes (mm)	0.90 ± .01a	0.90 ± .01a	0.89 ± .01a	0.90 ± .01a

old of 13.9°C to complete development. The egg development of an Indian species of *Deraeocoris* at 23.7°C (11.3 d) (Kapadia and Puri 1991) is similar to the egg development of *D. nebulosus* at 25°C (11.0 d), but the egg development of *D. pallens* Reuter at 25 to 28°C (6.4 d) (Susman 1988) is considerably shorter than *D. nebulosus* at 30°C (7.5 d).

Both Wheeler et al. (1975) and Jones and Snodgrass (1998) provide nymphal develop data for *D. nebulosus* (19.8 d at 21 to 22°C and 13.3 d at 27°C, respectively) which agree with data presented here. The nymphal development of an Indian species of *Deraeocoris* (15.4 d at 23.7°C) (Kapadia and Puri 1991) and of *D. pallens* (11.1 d at 25 to 28°C) (Susman 1988) are similar to the nymphal development of *D. nebulosus.*

The mean lower development threshold level for *D. nebulosus* males is 12.7°C and for females 15.2°C (combined sexes is 14.0°C). *Deraeocoris nebulosus* might not be as effective as a biological control agent at lower temperatures as certain other heteropteran predators. At or below the lower threshold limits, the predators only need to feed to maintain homeostasis, thus reducing the number of prey eaten. An anthocorid, *Orius tantillus* (Motschulsky), has a nymphal lower-threshold level of 12.7°C (combined for sexes; male 11.9, female 13.4°C) (Nakashima and Hirose 1997). The nabids *Nabis rufusculus* Reuter, *N. americoferus* (Carayon), and *N. roseipennis* Reuter have nymphal lower-threshold levels of 11.6, 10.8, and 10.7°C, respectively (Braman et al. 1984, Braman and Yeargan 1988). The predacious pentatomid *Podisus nigrispinus* (Dallas) has a lower threshold level of 12.0°C (Torres et al. 1998).

Reproductive development of the females took almost twice as long at the lowest temperature compared with the other two temperatures, though no difference was detected between the two higher temperatures. Jones and Snodgrass (1998) showed that *D. nebulosus* started laying eggs on day 4 at 27°C, but did not lay more than 10 eggs per day until day 6. Similar trends are found in three species of *Geocoris* (Dunbar and Bacon 1972), in which preoviposition periods above 30°C were similar, but below 30°C the period increased with lower temperature. The preoviposition period of *P. nigrispinus* is higher during fluctuating periods of 25 to 35°C compared to 20 to 30°C (Torres et al. 1998), demonstrating that temperatures above a certain level can prolong preoviposition.

The average number of eggs laid for 5 d at each temperature was not significantly different, which was unexpected. However, the number of eggs laid in the first 5 d is similar to the findings of Jones and Snodgrass (1998) for the same species. Temperature affects the number of eggs laid by the tingid *Stephanitis pyrioides* (Scott) (Neal and Douglass 1988) and the predacious stink bug *P. nigrispinus* (Torres et al. 1998), but temperature does not affect the number of eggs produced by three species of *Geocoris* (Dunbar and Bacon 1972).

Temperature influences the size of *D. nebulosus.* Both males and females were larger at 20°C than at 30°C. The males are smaller than the females, and this size difference might enable the males to develop faster (Wheeler 2001). However, only at 20°C did females have a longer nymphal development time (protandry). If this development difference were “incidental protandry” (*sensu* Wiklund and Solbreck 1982), males would develop faster than females at all temperatures. Many mirids develop protandrously (Wheeler 2001), but no study has been conducted to determine if it is an adaptive trait or if it is just an incidental result by virtue of size differences (Wheeler 2001). Some studies, however, have demonstrated that sexual size dimorphism does not lead to protandry (e.g., Nylin et al. 1993). These data are the first recorded evidence that protandry can be influenced by temperature. For a general review of protandry see Wiklund and Fagerström (1977).

Access to free water and facultative phytophagy are not essential for development or survival of *D. nebulosus* at 25°C when fed eggs of *Ephestia kuehniella,* because in all treatments nymphs survived to adulthood. At higher temperatures or with lower quality food, however, the water needs of *D. nebulosus* might differ (Naranjo and Gibson 1996). Predacious Heteroptera supplemented with plant food generally develop faster and have higher nymphal survival than when provided prey only (Naranjo and Gibson 1996). For example, *Orius insidosus* (Say) (Anthocoridae) develops faster and has increased survivability when prey items are supplemented with plants (Kiman and Yeargan 1985, Bush et al. 1993). Other predacious mirids that benefit from plant feeding include *Dicyphus hesperus* Knight (Gillespie and McGregor 2000), *Campylomma livida* Reuter (Chinajariyawong and Walter 1990), and *Deraeocoris signatus* (Distant) (Chinajariyawong and Harris 1987).

Sweet potato is not a natural host plant for *D. nebulosus,* though it has been used as an oviposition substrate for rearing the insect (Jones and Snodgrass 1998, DWB unpubl. data). However, providing the mirid with leaves of one of its hosts (e.g., apple, maple, oak, pecan [see Boyd 2001 for exhaustive list]) as a water source might be beneficial, especially when this predator is fed less nutritious prey, such as aphids (Naranjo and Gibson 1996).

Males developed faster when provided sugar water than those with no water, but only by a half day. Digesting the sucrose in the sugar water would require less energy than breaking down the glycogen in the eggs, thus affording a possible slight advantage in the sugar-water treatment. This potential advantage was not observed, however, in the development time of females, but might explain why the left femur lengths were longer for females in the sugar treatment than those in the water and leaf treatments.

Females in all treatments were able to reach a reproductive state as evidenced by the presence of eggs in their abdomens. The number of eggs oviposited could not be determined without providing plant material for all the treatments, because *D. nebulosus* oviposits in leaf petioles and midveins (McCaffrey and Horsburg 1980, DWB pers. obs.). Thus, only reproductive potential could be shown to be independent of facultative phytophagy.

Knowledge of the development rate of *D. nebulosus* will aid the use of this predacious mirid as a biological control agent in the field or in greenhouse plantings. *Deraeocoris nebulosus* has been studied as a biological control agent for pests of pecans (Ellington et al. 1998) and cotton (Jones and Snodgrass 1998), and its use as a biological control agent in ornamental plants has been suggested (Wheeler et al. 1975). The degree-day model developed here for *D. nebulosus* can be used in conjunction with known predation rates (Snodgrass 1991) to estimate the effectiveness of the mirid as a biological control agent in the field or greenhouse. The degree-day model also can be used to determine the best temperature at which to rear this plant bug.

Plant feeding by some predacious Heteroptera is beneficial by providing a food source during prey scarcity or by providing essential nutrients not found in prey (Naranjo and Gibson 1996). Some predators, however, feed and injure the plant when prey are scarce and can cause economic damage (Alomar and Albajes 1996). *Deraeocoris nebulosus* has an advantage as a biological control agent because it can survive without feeding on plants. The potential for *D. nebulosus* to feed facultatively on plants, however, is indicated by the presence of amylase and pectinase in its salivary secretions, however these enzymes might be used to digest glycogen from prey and to aid in oviposition, respectively (Boyd et al. 2002). Further studies using *D. nebulosus* in greenhouse or agricultural crops might demonstrate that *D. nebulosus* is beneficial in reducing pest populations without damaging the plants.

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References Cited

Alomar, O. and R. Albajes. 1996. Greenhouse whitefly (Homoptera: Aleyrodidae) predation and tomato fruit injury by the zoophytophagous predator *Dicyphus tamaninii* (Heteroptera: Miridae), Pp. 155-177. *In* O. Alomar and R. N. Wiedenmann (eds.), Zoophytophagous Heteroptera: implications for life history and integrated pest management. Thomas Say Publications in Entomology. Entomological Society of America, Lanham, MD.

Boyd, D. W., Jr. 2001. *Deraeocoris nebulosus* (Uhler) (Hemiptera: Miridae): a potential biological control agent. Ph.D. Diss., Clemson Univ., Clemson, SC.

Boyd, D. W., Jr., A. C. Cohen and D. R. Alverson. 2002. Digestive enzymes and stylet morphology of *Deraeocoris nebulosus* (Uhler) (Hemiptera: Miridae), a predacious plant bug. Ann. Entomol. Soc. Am. 95: 395-401.

Braman, S. K. and K. V. Yeargan. 1988. Comparison of developmental and reproductive rates of *Nabis americoferus, N. roseipennis,* and *N. rufusculus* (Hemiptera: Nabidae). Ann. Entomol. Soc. Am. 81: 923-930.

Braman, S. K. and A. F. Pendley. 1993. Temperature, photoperiod, and aggregation effects on development, diapause, reproduction, and survival in *Corythucha cydoniae* (Heteroptera: Tingidae). J. Entomol. Sci. 28: 417-426.

Braman, S. K., P. E. Sloderbeck and K. V. Yeargan. 1984. Effects of temperature on the development and survival of *Nabis americoferus* and *N. roseipennis* (Hemiptera: Nabidae). Ann. Entomol. Soc. Am. 77: 592-596.

Braman, S. K., A. F. Pendley, B. Sparks and W. G. Hudson. 1992. Thermal requirements for development, population trends, and parasitism of azalea lace bug (Heteroptera: Tingidae). J. Econ. Entomol. 85: 870-877.

Bush, L., T. J. Kring and J. R. Ruberson. 1993. Suitability of greenbugs, cotton aphids, and *Heliothis virescens* eggs for development and reproduction of *Orius insidiosus.* Entomol. Exp. Appl. 67: 217-222.

Chapman, R. F. 1998. The insects: structure and function. 4th edition. Cambridge University Press, Cambridge, UK.

Chinajariyawong, A. and V. E. Harris. 1987. Inability of *Deraeocoris signatus* (Distant) (Hemiptera: Miridae) to survive and reproduce on cotton without prey. J. Aust. Entomol. Soc. 26: 37-40.

Chinajariyawang, A. and G. H. Walter. 1990. Feeding biology of *Campylomma livida* Reuter (Hemiptera: Miridae) on cotton, and some host plant records. J. Aust. Entomol. Soc. 29: 177-181.

Cohen, A. C. 1990. Feeding adaptations of some predaceous Hemiptera. Ann. Entomol. Soc. Am. 83: 1215-1223.

1998a. Biochemical and morphological dynamics and predatory feeding habits in terrestrial Heteroptera, Pp. 1-8. *In* J. R. Ruberson and M. Coll (eds.), Predaceous Heteroptera: implications for biological control. Thomas Say Publications in Entomology. Entomological Society of America, Lanham, MD.

1998b. Solid-to-liquid feeding: the inside(s) story of extra-oral digestion in predaceous Arthropoda. Am. Entomol. 44: 103-117.

2000. How carnivorous bugs feed, Pp. 563-570. *In* C. W. Schaefer and A. R. Panizzi (eds.), Heteroptera of economic importance. CRC Press, Boca Raton, FL.

Coll, M. 1998. Living and feeding on plants in predatory Heteroptera, Pp. 89-129. *In* M. Coll and J. R. Ruberson (eds.), Predatory Heteroptera: their ecology and use in biological control. Thomas Say Publications in Entomology. Entomological Society of America, Lanham, MD.

Coll, M. and M. Guershon. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. Annu. Rev. Entomol. 47: 267-97.

Dunbar, D. M. and O. G. Bacon. 1972. Influence of temperature on development and reproduction of *Geocoris atricolor, G. pallens,* and *G. punctipes* (Heteroptera: Lygaeidae) from California. Environ. Entomol. 1: 596-599.

Ellington, J., D. Richman, S. Meeks, T. Carillo, S. Liesnac and S. Bell. 1998. Biological control of insect pests in pecans. Annual Report, New Mexico State University.

Gillespie, D. R. and R. R. McGregor. 2000. The functions of plant feeding in the omnivorous predator *Dicyphus hesperus:* water places limits on predation. Ecol. Entomol. 25: 380-386.

Gutierrez, A. P., J. U. Baumgaertner and K. S. Hagen. 1981. A conceptual model for growth, development, and reproduction in the ladybird beetle, *Hippodamia convergens* (Coleoptera: Coccinellidae). Can. Entomol. 113: 21-33.

Jones, W. A. and G. L. Snodgrass. 1998. Development and fecundity of *Deraeocoris nebulosus* (Heteroptera: Miridae) on *Bemisia argentifolii* (Homoptera: Aleyrodidae). Florida Entomol. 81: 345-350.

Kapadia, M. N. and S. N. Puri. 1991. Biology and comparative predation efficacy of three heteropteran species recorded as predators of *Bemisia tabaci* in Maharashtra. Entomophaga 36: 555-559.

Kiman, Z. B. and K. V. Yeargan. 1985. Development and reproduction of the predator *Orius insidiosus* (Hemiptera: Anthocoridae) reared on diets of selected plant material and arthropod prey. Ann. Entomol. Soc. Am. 78: 464-467.

Leigh, T. F. 1966. A reproductive diapause in *Lygus hesperus* Knight. J. Econ. Entomol. 59: 1280-1281.

McCaffrey, J. P. and R. L. Horsburgh. 1980. The egg and oviposition site of *Deraeocoris nebulosus* (Hemiptera: Miridae) on apple trees. Can. Entomol. 112: 527-528.

McGregor, R. R., D. R. Gillespie, C. G. Park, D. M. J. Quiring and M. R. J. Foisy. 2000. Leaves or fruit? The potential for damage to tomato fruits by the omnivorous predator, *Dicyphus hesperus.* Entomol. Exp. Appl. 95: 325-328.

Metcalf, R. L. and W. H. Luckmann. 1994. Introduction to insect pest management. 3rd edition. John Wiley & Sons, New York.

Miles, P. W. 1972. The saliva of Hemiptera. Adv. Insect Physiol. 9: 183-255.

Mittler, T. E. 1967. Flow relationships for hemipterous stylets. Ann. Entomol. Soc. Am. 60: 1112-1114.

Nakashima, Y. and Y. Hirose. 1997. Temperature effects on development of *Orius tantillus* (Het.: Anthocoridae), a predator of *Thrips palmi* (Thys.: Thripidae). Entomophaga 42: 337-342.

Naranjo, S. E. and R. L. Gibson. 1996. Phytophagy in predaceous Heteroptera: effects on life history and population dynamics, Pp. 57-93. *In* O. Alomar and R. N. Wiedenmann (eds.), Zoophytophagous Heteroptera: implications for life history and integrated pest management. Thomas Say Publications in Entomology. Entomological Society of America, Lanham, MD.

Neal, J. W., Jr. and L. W. Douglass. 1988. Development, oviposition rate, longevity, and voltinism of *Stephanitis pyrioides* (Heteroptera: Tingidae), an adventive pest of azalea, at three temperatures. Environ. Entomol. 17: 827-831.

Nishijima, Y. and K. Sōgawa. 1963. Morphological studies on the salivary glands of Hemiptera I. Heteroptera. Res. Bull. Obihiro Univ. Ser. I. 3: 512-521.

Nylin, S., C. Wiklund and P.-O. Wickman. 1993. Absence of trade-offs between sexual size dimorphism and early male emergence in a butterfly. Ecology 74: 1414-1427.

Raupp, M. J., C. S. Koehler and J. A. Davidson. 1992. Advances in implementing integrated pest management for woody landscape plants. Annu. Rev. Entomol. 37: 561-585.

Rodriquez-Saona, C. and J. C. Miller. 1999. Temperature-dependent effects on development, mortality, and growth of *Hippodamia convergens* (Coleoptera: Coccinellidae). Environ. Entomol. 28: 518-522.

Snodgrass, G. L. 1991. *Deraecoris* (sic) *nebulosus* (Heteroptera: Miridae): little known predator in cotton in the Mississippi Delta. Florida Entomol. 74: 340-344.

StatView. 1996. StatView reference. Abacus Concepts, Inc., Berkeley, CA.

Susman, I. 1988. The cotton insects of Israel and aspects of the biology of *Deraeocoris pallens* Reuter (Heteroptera: Miridae). M.S. Thesis. Tel-Aviv Univ., Israel (in Hebrew, English summary).

Torres, J. B., J. C. Zanuncio and H. N. de Oliveira. 1998. Nymphal development and adult reproduction of the stinkbug predator *Podisus nigrispinus* (Het., Pentatomidae) under fluctuating temperatures. J. Appl. Entomol. 122: 509-514.

Wheeler, A. G., Jr. 2001. Biology of the plant bugs (Hemiptera: Miridae): pests, predators, opportunists. Cornell Univ. Press, Ithaca, NY.

Wheeler, A. G., Jr., B. R. Stinner and T. J. Henry. 1975. Biology and nymphal stages of *Deraeocoris nebulosus* (Hemiptera: Miridae), a predator of arthropod pests on ornamentals. Ann. Entomol. Soc. Am. 68: 1063-1068.

Wiklund, C. and T. Fagerström. 1977. Why do males emerge before females? A hypothesis to explain the incidence of protandry in butterflies. Oecologia 31: 153-158.

Wiklund, C. and C. Solbreck. 1982. Adaptive versus incidental explanations for the occurrence of protandry in a butterfly, *Leptidea sinapis* L. Evolution 36: 56-62.