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Suitability of pollen sources for the development and reproduction of *Coleomegilla maculata* (Coleoptera: Coccinellidae) under simulated drought conditions.

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Running Head: SUITABILITY OF POLLEN FOR COLEMEGILLA

Abstract

Laboratory experiments compared the nutritive value of various pollen sources for the development of *Coleomegilla maculata* DeGeer under conditions of continuous water availability and simulated drought. When water was continuously available, larval survival was not different from 100% on diets of frozen eggs of *Ephestia kuehniella* Zeller, corn pollen, sorghum pollen, or pulverized bee pollen, whereas survival of larvae was significantly reduced on the latter three diets in the simulated drought treatment. Pollen of cultivated sunflower, *Helianthus annus* L., proved fatal to both larvae and adults; its surface structure caused clumping and accumulation on the insect cuticle that led to death from exhaustion/desiccation in Petri dishes. The *Ephestia* egg diet yielded shorter developmental times and heavier adult weights than any pollen diet in both treatments. The drought treatment increased developmental time on all diets with a significant treatment-diet interaction. Drought reduced the adult weight of females on the sorghum pollen diet, and that of both sexes on the bee pollen diet, again with a significant treatment-diet interaction. Initial water content was highest in corn pollen (36.8 %), followed by *Ephestia* eggs (29.2 %), sorghum pollen (25.3 %), sunflower pollen (8.7 %), and bee pollen (4.6 %), but did not appear correlated with *C. maculata* larval survival on pollen sources under drought conditions. Reproductive adult females that received corn or sorghum pollen as a supplement to *Ephestia* eggs did not differ in fecundity or fertility from those fed only *Ephestia* eggs.

Key Words: Coleomegilla maculata*, development, drought, *Helianthus annus*, pollen, reproduction, *Sorghum bicolor*, *Zea mays

1. Introduction

Agriculture in the High Plains of the United States is dominated by cereal crops such as wheat, *Triticum aestivum* L., corn, *Zea mays* L., and sorghum, *Sorghum bicolor* (L.). Of secondary importance are oilseed crops such as soybeans and sunflowers. The primary pests of cereal crops are aphids, including the greenbug, *Schizaphis graminum* Rondani, the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) and the bird cherry-oat aphid, *Rhopalosiphum padi* (L). Recently, the soybean aphid, *Aphis glycines* Matsumura, has emerged as an adventive pest of soybeans in the American Midwest, renewing interest in biological control of aphids in oilseed crops (Fox and Landis, 2003). Suppression of aphid populations by natural enemies is especially important in these crops because their relatively low market value renders most control tactics non-economic. Biological control is typically provided by a complex of parasitoids (Aphidiidae, Aphelinidae), and predators (mostly Chrysopidae, Coccinellidae and Syrphidae).

The twelve-spotted ladybeetle, *Coleomegilla maculata* DeGeer, is a native coccinellid species that, along with other species such as *Hippodamia convergens* Guerin and *Coccinella septempunctata* L., contributes significantly to biological control of cereal aphids in the High Plains (Elliott and Kieckhefer, 1990). *Coleomegilla maculata* is renowned for its polyphagous habits (Hodek and Honek, 1996) and the ability of the larvae to develop successfully on an exclusive diet of pollen (Hodek et al., 1978). However, pollen may have relatively low water content compared with insect prey, especially aphids, raising the question of how a pollen diet might affect the water requirements of larval stages in an arid environment such as the High Plains.

It has been noted that the abundance of *C. maculata* in sweet corn tends to peak around the time of anthesis (Groden et al., 1990). Ostrom et al. (1997) used analysis of stable isotopes to demonstrate that *C. maculata* adults field-collected in California had obtained a large portion of the their carbon and nitrogen budget from pollen sources, primarily alfalfa and corn. However, whether pollen availability improves or decreases the efficacy of *C. maculata* as a biological control agent has been the subject of some debate. The availability of pollen may serve to attract adult *C. maculata* into a crop, potentially improving biological control if beetles or their progeny remain beyond flowering to feed on insect prey. However, if beetles focus on pollen consumption at the expense of insect prey, the impact of predation on pest populations may be reduced. For example, Pfannenstiel and Yeargan (2002) concluded that the availability of sweet corn pollen during anthesis reduced predation of *Helicoverpa zea* eggs by *C. maculata*, similar to the conclusion of Cottrell and Yeargan (1998). On the other hand, the presence of pollen as an alternative food source has been postulated to ameliorate intraguild predation between *C. maculata* and *Harmonia axyridis* Pallas and promote their co-existence in corn fields, presumably facilitating improved biological control (Musser and Shelton, 2003).

Much of the research on *C. maculata* pollen consumption has focused on corn, especially since it was discovered that the *Bacillus thuringensis* endotoxin can be expressed in the pollen of certain transgenic maize cultivars such as event MON863 (Wold et al., 2001; Duan et al., 2002; Lundgren and Weidenmann 2002). In western Kansas, *C. maculata* is known to be a important component of the predator guild that contributes to biological control of greenbug (Rice and Wilde, 1988). Adult *C. maculata* and other coccinellid species enter sorghum fields in early summer when plants are in the whorl stage to feed on colonies of *Rhopalosiphum maidis* (Fitch) (Kring and Gilstrap, 1986; J.P. Michaud, pers. observation). Although these aphid colonies normally disappear prior to flowering, *C. maculata* adults can also be found in flowering sorghum fields consuming pollen. Thus, both corn leaf aphids and sorghum pollen could serve to retain *C. maculata* adults within this crop and facilitate subsequent functional and numerical responses to greenbugs that can develop large and damaging colonies on sorghum plants in later stages of development. *Coleomegilla maculata* can also be found in multispecies aggregations of adult coccinellids on juvenile sunflower plants where they appear to ingest the exudates of leaf hairs, although they are rarely present on the sunflower blooms despite their production of abundant pollen (J.P. Michaud, unpublished data).

Given the potentially important role of pollen in the life history of *C. maculata* on the High Plains, and the ephemeral availability of different types of crop pollen seasonally, we conducted a series of experiments to assess the relative suitability of various pollen types for *C. maculata* larval development and adult reproduction. We compared the development of larvae raised on exclusive diets of the various pollen types to maximize resolution of nutritional differences and compare development to that obtained on a standardized diet of animal protein (eggs of *Ephestia kuehniella* Zeller). Since the High Plains is an arid region, we examined larval development on pollen under regimes of both limited and unlimited access to water, as some pollen sources can have relatively low water content relative to insect prey.

Adults also engage in pollen consumption, raising the question of how feeding on various pollen sources might affect reproductive performance. It has been shown that *C. maculata* fecundity is greater when animal protein is provided in addition to pollen (Riddick and Barbosa, 1998). However, pollen might serve as a dietary supplement that improves adult reproductive performance if available insect prey are of low nutritional value. Alternatively, if pollen feeding diminishes the consumption of more nutritious insect protein sources, adult reproduction could be adversely affected. Since adult beetles are capable of dispersal over considerable distances and unlikely to feed exclusively on pollen without access to animal protein, we provided three different crop pollens to ovipositing females as dietary supplements in addition to *Ephestia* eggs and assessed their reproductive performance.

2. Materials and methods

2.1. Insects

Adults of *C. maculata* were collected in Hays, KS in April, 2003 and used to initiate a stock colony that was maintained on a diet of frozen *Ephestia* eggs (Beneficial Insectary, Oak Run, California) supplemented with bee pollen. All insects in stock colonies and experiments were held in a climate-controlled growth chamber at a constant temperature of 24 ± 2 ºC under 'cool-white' fluorescent lights set to 18 h day length. Relative humidity averaged 42 ± 5 % throughout the course of experiments. Ovipositing females were isolated in plastic Petri dishes (5.5 cm x 1.0 cm), provisioned with food (as above) and water on a cube of sponge, and their eggs collected daily. Eggs hatched in about four days under these conditions and newly eclosed larvae were reared four or five per Petri dish on the same diet as adults. When adults emerged from pupae, they were transferred to 1 L glass mason jars filled with shredded wax paper for harborage, up to 100 beetles per jar. *Ephestia* eggs were added to each jar daily and water was provided on cotton wick.

2.2. Pollen collection

Tassels of sweet corn were covered with brown paper pollination bags secured with staples and the pollen collected by carefully inverting and removing the bags 24 h later. Sorghum pollen was collected by shaking anthesis flowers upside down into paper bags. Sunflower pollen was collected directly from the faces of anthesis flowers by brushing anthers over a large plastic funnel placed on top of a plastic collection vial. Back at the laboratory, all field-collected pollen was sifted through a fine mesh stainless steel sieve to remove miscellaneous insects and plant debris and then funneled into 5 dram glass screw-top vials and stored in a freezer at -20 °C. Bee pollen, presumed to constitute a blend of wild flower pollens, was purchased from a local health food store and pulverized with a mortar and pestle before provisioning to the insects. Samples (approx. 50 mg.) of each pollen type and the frozen *Ephestia* eggs were weighed on a microbalance and then dried in an oven at 50 ºC for 48 h before re-weighing to estimate moisture content.

2.3. Larval development assays

A preliminary experiment was conducted to determine the relative suitability of the *Ephestia* egg diet for *C. maculata* larval development. This was accomplished by isolating 40 newly-eclosed larvae in Petri dishes (as above), provisioning them with conspecific eggs during their first day of life, and then dividing them randomly into two groups. One group completed the remainder of their development on an exclusive diet of conspecific eggs, while the other was fed *Ephestia* eggs. Egg cannibalism on the first day of life has been shown to enhance development of coccinellid larvae and even improve their survival if the subsequent larval diet is inferior (Michaud and Grant, 2004). However, an exclusive diet of conspecific eggs for the complete duration of development serves as reference against which the quality of other diets can be measured. A highly suitable diet will yield faster development and heavier adult weight than an exclusive diet of conspecific eggs, whereas the reverse is true in the case of an inferior diet (Michaud, 2003). Developmental time was tallied as the number of days from eclosion to formation of a prepupa. Upon emergence, teneral adults were allowed to harden and then placed in individual screw-cap glass vials, labeled, and dried in an oven at 50 ºC for three days before weighing on an analytical balance.

Hatching larvae were isolated in individual plastic Petri dishes (as above) within several hours of eclosion and then divided into five different treatment groups (n = 25 - 40 larvae per treatment). The control group was fed frozen *Ephestia* eggs, whereas larvae in each of the other groups received corn, sorghum, sunflower, or pulverized bee pollen that was placed in a heap on a small square of filter paper. All food was provided fresh daily *ad libitum*. In one series of treatments, water was continuously available on small cubes of sponge placed in each dish and moistened daily (= ‘watered treatment’). Larvae in the second series had opportunity to drink to satiation once every third day from a single drop of water (approx. 0.1 - 0.2 ml) placed on a small cluster of polymer beads (each 2 -3 mm in diameter) in each dish (= 'drought treatment'). Water adhering to the surface of the beads evaporated completely within 1-2 h in the chamber. This presentation was designed to be analogous to the ephemeral availability of morning dew in a prairie habitat. Larval development times were tallied as above and emerging adults were placed in labeled glass vials and frozen. Upon completion of the experiment, adults were defrosted individually and carefully dissected to determine sex. All were then returned to their respective vials and dried and weighed as above.

Larval survival in each of the various treatments was tested for significant deviation from 100% using a Chi-square, goodness of fit test. Single factor ANOVAS were performed separately for males and females to compare effects of diet within treatment, and treatment within diet, and means were separated using the LSD test ($\alpha = 0.05$; Statsoft 2000). Data for developmental time and adult dry weight were then analyzed by three-way ANOVA with 'treatment', 'food' and 'gender' as independent variables (Statsoft 2000) to identify any significant interaction terms among independent variables.

2.4. Female reproduction assay

Pre-reproductive adults between two and three weeks of age were removed from mason jars and placed as male-female pairs in individual Petri dishes (as above). Pairs were provided with an *ad libitum* diet of *Ephestia* eggs freshened every second day, and water on a cube of sponge. When a female began to oviposit, she was isolated in a Petri dish and assigned to one of four treatments. Females in the control treatment (n = 18) were fed frozen *Ephestia* eggs only, whereas females in other three treatments received frozen *Ephestia* eggs supplemented with either corn (n = 16), sorghum (n = 17), or sunflower pollen (n = 6). Food and water was provided fresh daily to ovipositing females and all eggs were harvested at this time. Petri dishes with eggs were labeled with the date, female number, and number of eggs. The number of eggs hatching was tallied for each female-day of reproduction after an appropriate period of incubation (4 -5 d). A total of 13 days egg batches were collected from each female. The first day's reproduction for each female was excluded from analysis since treatments were imposed on the day following first oviposition. Data on numbers of eggs laid, numbers of eggs hatching, and the period required to obtain 13 days of oviposition were analyzed by one-way ANOVA.

3. Results

The water content of the various foods was estimated on a per-weight basis as follows: *Ephestia* eggs, 29.2 %; sunflower pollen, 8.7 %; corn pollen 36.8 %; sorghum pollen, 25.3 % and; bee pollen, 4.6 %.

3.1 Larval development assays

Larvae allowed to cannibalize eggs on their first day of life and then complete development on *Ephestia* eggs developed significantly slower (mean ± SEM = 12.9 ± 0.17 d vs. 12.3 ± 0.15 d; F = 7.571; 1,34 df; P = 0.009) and weighed significantly less (mean ± SEM = 38.2 ± 0.94 mg vs. 41.5 ± 1.14 mg; F = 4.807; 1,34 df; P = 0.035) than did those completing their development exclusively as egg cannibals. Nineteen of 20 egg cannibals survived to adulthood, compared to 16 of 20 non-cannibals.

Only one of 30 larvae fed sunflower pollen yielded a viable adult male in the watered treatment (Fig. 1), although six reached the pupal stage. None of the forty larvae fed sunflower pollen in the drought treatment pupated. Larvae fed sunflower pollen with continuous access to water lived significantly longer than those in the drought treatment (mean ± SEM = 16.1 ± 0.9 days vs. 8.9 ± 0.8 days; F = 26.101, 1,58 df; P < 0.001). The sunflower pollen treatment was excluded from subsequent analyses of developmental time and adult weight because of insufficient data. Larval survival on the other pollen diets was significantly reduced in the drought treatment, but never significantly less than

100% when adequate water was available. Only the *Ephestia* egg diet yielded survival not significantly different from 100% in both treatments.

3.1.1. Developmental time

The factors 'Treatment' and 'Diet' both had singular effects on developmental time, whereas 'Gender' did not (Table 1). There was a significant 'Treatment – Diet' interaction. Drought increased developmental time significantly on all diets (*Ephestia* eggs: $F = 84.334$; 1,66 df; $P < 0.001$; corn pollen: $F = 192.393$; 1,39 df; $P < 0.001$; sorghum pollen: $F = 238.213$; 1,38 df; $P < 0.001$; bee pollen: $F = 192.005$; 1,53 df; $P < 0.001$; Fig. 2). Development was faster on the *Ephestia* egg diet than on the pollen diets in both watered and drought treatments.

3.1.2. Adult dry weight

The factors 'Treatment', 'Diet' and 'Gender' all had singular effects on adult weight, but only the 'Treatment – Diet' interaction was significant (Table 1). Drought did not decrease the adult weight of either males or females on either the *Ephestia* egg or corn pollen diets (one way ANOVA, $P > 0.05$ in all cases, Fig. 3), but it reduced female weight on the sorghum pollen diet ($F = 14.953$; 1,17 df; $P = 0.001$) and the weight of both males and females on the bee pollen diet ($F = 21.284$; 1,29 df; $P < 0.001$ and $F = 35.054$; 1,22 df; $P < 0.001$, respectively).

3.2. Female reproduction assay

When exposure to sunflower pollen resulted in the death of six reproductive females within a 3 d period this treatment was terminated as reproductive females were in short supply. Females became coated with the pollen and typically died upside down with their elytra spread. Supplementation of the *Ephestia* egg diet with corn or sorghum pollen did not affect the mean number of eggs laid over 12 d of reproduction, the period required to obtain 13 batches of eggs, or the proportion of these eggs that hatched (Table 2).

4. Discussion

4.1. Larval development

Larvae of *C. maculata* that cannibalized eggs on their first day of life but completed development on *Ephestia* eggs had slower development and lower adults weight relative to those reared on an exclusive diet of conspecific eggs. Since only optimal diets tend to yield faster development and larger adult size relative to a diet of conspecific eggs (Michaud, 2003; Michaud and Grant, 2004) *Ephestia* eggs can be considered an adequate, but sub-optimal, diet for *C. maculata* development, given that survival to adult was not significantly different from 100 percent. Similarly, all pollen sources except sunflower proved adequate provided water was continuously available, but under simulated drought conditions became marginal (i.e. yielded survival significantly less than 100 percent). Only the *Ephestia* eggs remained an adequate diet under drought-stressed conditions, although developmental time was extended by about two and one half days. Although *Ephestia* eggs are a very suitable diet for *C. maculata*, they likely have a substantially lower water content than aphids.

Larvae in the drought treatment were frequently observed to drink continuously for 30 - 40 sec following addition of water to the polymer beads, consistent with expectation for insects experiencing water-deficit. The fact that corn pollen actually contained more water than the *Ephestia* eggs suggests that food water content was not solely responsible for the patterns of survival observed in the drought treatment. This inference is further supported by the significant treatment-diet interactions for both developmental time and adult weight. However, we only measured initial water content and it is conceivable that rates of water loss from the various foods varied significantly over a 24 h period under these experimental conditions.

Direct access to some form of water appears to be an important factor affecting development when *C. maculata* larvae are restricted to feeding on pollen, or even animal prey items such as the eggs of Lepidoptera, that may be significantly lower in water content than aphids. Examinations of aphid species suitability for coccinellids typically do not involve the provision of a water source, and it has been inferred that supplemental water is not necessary on aphid diets because of their high water content (Hodek and Honek 1996). However, the results of the present study suggest that water availability might be worthy of addressing in other studies of aphidophagous coccinellids that seek to evaluate the suitability of non-aphid prey.

We were intrigued by the finding that sunflower was the only pollen type that did not support completed development in *C. maculata*. Examination of sunflower pollen at 100 - 200x magnification under a compound microscope revealed that individual grains were spherical in shape and covered with a regular array of small spines. In contrast, both corn and sorghum pollen grains had smooth, convex surfaces. We observed that the spines on the surface of sunflower pollen grains promoted adhesion to the insect cuticle and clumping of the pollen itself, resulting in considerable accumulation of pollen grains on the insects. Thus, larval death appeared to result from the physical structure of the pollen grains, rather than any nutritional inadequacy *per se*. That sunflower pollen was not devoid of nutritional value was evidenced by the successful formation of six pupae in the watered treatment, one of which produced a small but viable adult male. However, larvae that became coated with sunflower pollen were effectively immobilized and appeared to succumb to a combination of desiccation and exhaustion as they struggled in vain to gain purchase on the smooth surface of the Petri dishes. Larvae fed sunflower pollen with access to water lived almost twice as long, on average, as did those in the drought treatment, supporting the inference that desiccation exacerbated mortality on this diet.

4.2. Female reproduction

Adult females were directly observed consuming the various pollens provided as supplements to the *Ephestia* eggs, with the possible exception of sunflower pollen which may or may not have been consumed in small amounts. Six reproductive females died in the sunflower pollen within a period of 3-4 days following first exposure, and without laying any further eggs. Again, death appeared to be associated with pollen clumping and adhesion to the insect cuticle. However, as with larvae, mortality under these conditions may have been exacerbated by the smooth surface of the Petri dishes.

Consumption of corn and sorghum pollen by adult females in conjunction with *Ephestia* eggs did not produce any measurable effects on adult female reproduction (Table 1). Thus, under the conditons of these experiments, pollen consumption neither diminished female reproductive performance via reduced consumption of animal protein, nor did it appear to supplement female nutrition beyond that provided by the *Ephestia* eggs.

4.3. Conclusions

Coccinellids reared on aphid prey are not known to require a supplementary source of water, likely because aphid tissues have a high water content. The findings of this study indicate that the relative suitability of various pollen sources for *C. maculata* development depends to a substantial degree on the availability of a water source, a factor that could be especially important for *C. maculata* populations inhabiting arid regions such as the High Plains. However, the lack of any detectable effects of pollen consumption by adult females on their fecundity or fertility suggests that this behavior is unlikely to have any direct impact on the potential numerical response of *C. maculata* to aphid populations that may be present in corn or sorghum fields.

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Table 1. Three-way ANOVA of Treatment (watered / drought), Diet (*Ephestia* eggs / corn pollen / sorghum pollen / bee pollen) and Gender (male / female) on *Coleomegilla maculata* developmental time and adult weight.

		Developmental time		Adult weight	
Effect	df	*F*	*P*	*F*	*P*
Treatment	1	733.09	0.000	37.80	0.000
Diet	3	239.49	0.000	314.29	0.000
Gender	1	0.54	0.465	30.34	0.000
Treatment - Diet	3	58.31	0.000	3.77	0.012
Treatment - Gender	1	0.52	0.471	0.37	0.544
Diet - Gender	3	2.92	0.035	1.83	0.144
Treatment - Diet - Gender	3	2.07	0.106	0.60	0.618

Table 2. Mean (± SEM) numbers of eggs laid in 12 days of reproduction by female *Coleomegilla maculata* fed three different diets. Fertility = mean (± SEM) proportion of eggs hatching. Analysis of fertility was performed on actual numbers of eggs hatching. Period = mean (± SEM) number of days required to obtain 12 clutches of eggs, excluding the first day of reproduction.

Food	Total eggs	Fertility	Period
Ephestia eggs	153.9 ± 9.6	0.401 ± 0.03	20.8 ± 2.6
Ephestia eggs + corn pollen	155.2 ± 8.5	0.403 ± 0.03	21.3 ± 2.1
Ephestia eggs + sorghum pollen	162.1 ± 7.6	0.387 ± 0.04	18.8 ± 1.3
F	0.258	0.07	0.423
d.f.	2,47	2,47	2,47
P	0.774	0.932	0.658

Fig. 1. Percentages of *Coleomegilla maculata* larvae surviving to adulthood on five different diets with either unlimited access to water (Watered) or with brief access once every three days (Drought). Asterisks indicate treatments with survival significantly less than 100% (Chi-square, goodness-of-fit test, α = 0.05).

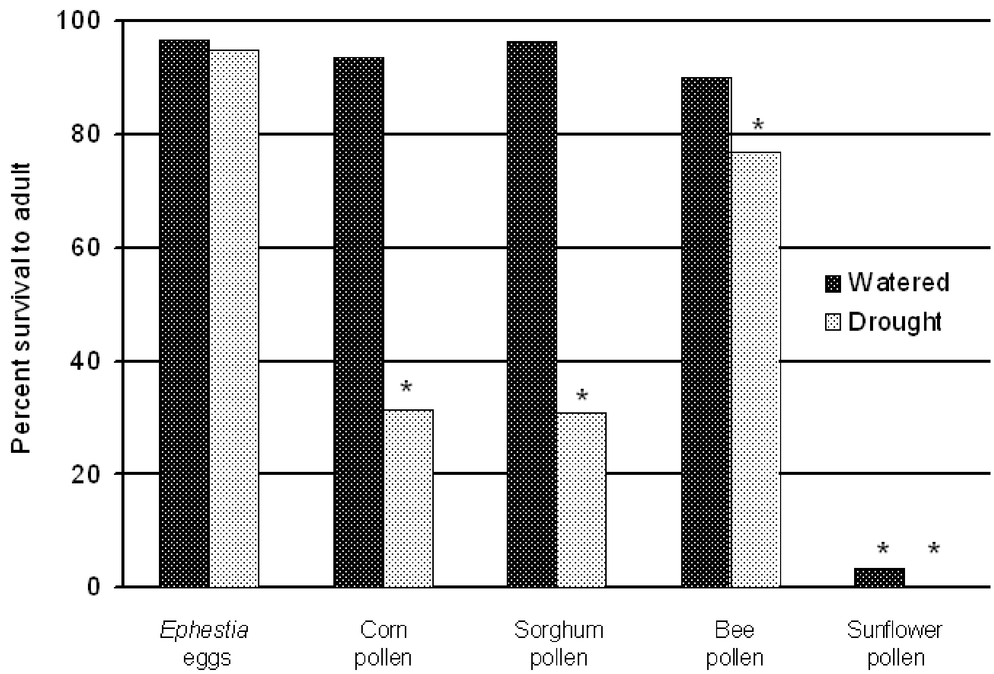

Fig. 2. Mean (+ SEM) developmental time (days) of male and female *Coleomegilla maculata* larvae fed various diets under conditions of limited and unlimited access to water. Bars bearing the same lower case letters were not significantly different ($P > 0.05$) among diets within treatments for males; those bearing the same upper case letters, females. Numbers on bars indicate sample sizes. No differences between males and females were significant for any diet. The drought treatment resulted in significant longer developmental times ($P < 0.001$ in all cases) than did the watered treatment for all diets.

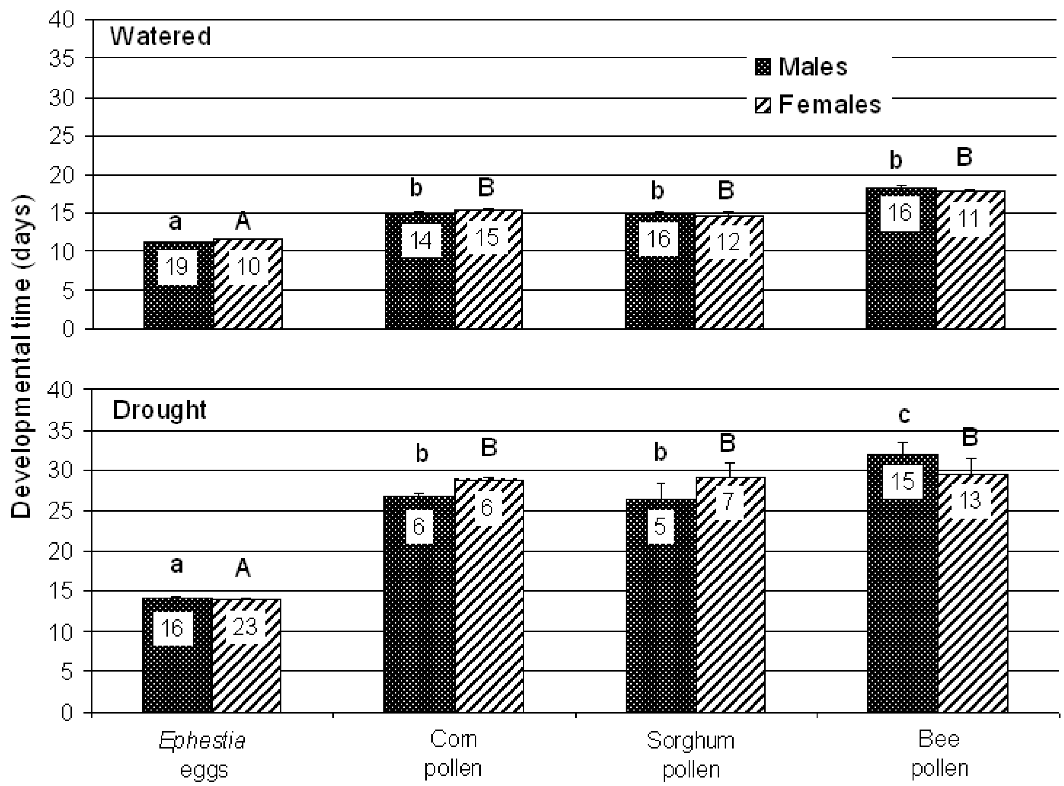

Fig. 3. Mean (+ SEM) adult dry weight (mg) of male and female *Coleomegilla maculata* larvae fed various diets under conditions of limited and unlimited access to water. Bars bearing the same lower case letters were not significantly different ($P > 0.05$) among diets for males; those bearing the same upper case letters, females. Numbers on bars indicate sample sizes. Females were significantly heavier than males ($P < 0.05$) on all diets except watered/corn pollen and drought/sorghum pollen. Asterisks indicate gender-specific differences ($P \leq 0.001$ in all cases) between watered and drought treatments for a given diet.