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Authors: Michaud, J. P., and Grant, Angela K.

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The biology and behavior of the longhorned beetle, *Dectes texanus* on sunflower and soybean.

J.P. Michaud[1] and Angela K. Grant

[1]Kansas State University, Agricultural Research Center – Hays, 1232 240th Ave, Hays, KS, 67601, 785-625-3425.

Abstract

The biology and behavior of the longhorned beetle *Dectes texanus* LeConte (Coleoptera: Cerambycidae) was studied on two host plants that suffer economic losses from this pest; sunflower, *Helianthus annuus*, and soybean, *Glycines max*. Reciprocal crosses of *D. texanus* collected from the two plants all produced viable progeny, indicating that conspecific insects attack both crops. Pupae from soybean stalks weighed about 40% less than those from sunflower, and adults fed on soybean lived a mean of 23 days, compared to a mean of 53 days (males) and 76 days (females) for those fed sunflower. A female's larval host plant had no effect on her tendency to ovipuncture plants of either type in a greenhouse trial. A field-tested population collected exclusively from sunflower contained three types of females in similar proportions: those that laid eggs only on sunflower, those that laid only on soybean, and those that laid equally on both host plants. Females in field trials fed more on the plant they had fed on in the laboratory, but soybean-fed females fed more on soybean than did sunflower-fed females. Females fed soybean also made more ovipunctures on soybean plants in field trials than sunflower-fed females, but their responses to sunflower plants were similar. Females displayed higher total ovipositional activity when they encountered sunflower first in the field, and lower total activity when they encountered soybean first. Feeding scores were significantly correlated with ovipunctures and eggs on both plant types. We conclude that sunflower is the preferred host plant, although females will accept soybean when it is the only available food. The results suggest that *D. texanus* is still in the initial stages of a host range expansion with female host selection behavior demonstrating both genetic influences and phenotypic flexibility. Sunflower represents a nutritionally superior, ancestral host plant and relatively high fitness costs are still associated with utilization of the novel host plant, soybean, costs that may be offset by benefits such as reduced intraspecific competition. These potential benefits and their consequent implications for *D. texanus* host range evolution are hypothesized and discussed.

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Correspondence: jpmi@ksu.edu
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Introduction

The long-horned beetle *Dectes texanus* LeConte (Coleoptera: Cerambycidae) is an indigenous, univoltine species that has emerged as a serious pest of soybeans throughout the eastern, southern, and central United States over the past 40 years (Patrick, 1973, Hatchett et al., 1975, Campbell et al., 1977, Laster et al., 1981, Rogers, 1985). In soybean, yield losses due to stem boring by a single *D. texanus* larvae have been estimated at ca. 10% (Richardson, 1975), although greater losses can result from the lodging of mature plants. Pre-diapause larvae girdle the lower stalk from the interior in preparation of an overwintering chamber, causing plants to snap off at the slightest pressure. Cultivated sunflowers can also lodge because of *D. texanus* damage (Rogers, 1985), although larvae are usually unable to fully girdle larger stalks (J.P. Michaud, personal observation).

The wild host plants of *D. texanus* are all from the family Compositae and include cocklebur, *Xanthium pensylvanicum* Wallr., giant ragweed, *Ambrosia trifida* L., and wild sunflower, *Helianthus annuus* L. (Hatchett et al., 1975, Rogers, 1977). It is thus of considerable biological interest that soybean, an exotic, leguminous crop plant, should be attacked by this insect. The association between *D. texanus* and native *Helianthus* spp. is likely ancient as both the insect and plant genera are indigenous to North America. This beetle has been studied as a pest of cultivated sunflowers (Rogers, 1985) although it can be notably difficult to collect from wild *H. annuus*. Dissection of > 1000 wild sunflower stalks over several years in western Kansas has yielded only one overwintering D. texanus larva (A.K. Grant, unpublished observations), whereas a sample of 70 plants collected in the Texas panhandle in 2001 yielded 5 larva (L.D. Charlet, personal communication). In contrast, larvae of another cerambycid, *Ataxia hubbardi* Fisher, are frequently found infesting wild sunflower in western Kansas. Similarly, Rogers (1977) reported collecting the cerambycid *Mecas inornata* Say from many wild *Helianthus* spp., including *H. annuus*, *H. tuberosus*, *H. maximiliani*, *H. mollis*, and *H. salicifolius* in the rolling plains of Texas, but did not report finding larvae of *D. texanus* in any of these plants, even though it was one of the most common species he collected from cultivated *H. annuus* in the region. Although some wild hosts may be available for *D. texanus* in western Kansas (e.g. cocklebur), soybean and cultivated sunflower appear to comprise the primary host plants utilized in the region and it is not uncommon to find large fields of either crop with virtually 100% of plants infested. Both sunflower and soybean are planted as summer crops in the High Plains region with similar planting dates and maturity schedules, rendering them similar in seasonal availability for the beetles.

Although commercial farming of soybeans in the continental United States began in the 1920's, the crop did not become widely grown until the 1940's (Hymowitz, 1970) and the first reports of infestations by *D. texanus* are from North Carolina in the late 1960's (Falter, 1969). Consequently, the association between *D. texanus* and soybean is a novel one that likely evolved over the past 50-60 years within a similar number of insect generations. It is also notable that *D. texanus* has emerged as a serious soybean pest over a broad geographic region spanning North Carolina, Tennessee, Arkansas, Illinois, Missouri, Texas, Kansas and Nebraska during this short period. Since it is implausible that gene flow could have spread a single mutation across such a vast region in 60 generations or less, the observed host range expansion would appear to comprise a series of independent events that occurred in parallel in different localities, i.e. through convergent evolution in separate subpopulations. It also seems likely that the ancestral *D. texanus* population fortuitously contained substantial and widespread biological pre-adaptation to utilize soybean as a host before it ever came in contact with the plant. To be satisfactory, an evolutionary hypothesis for the *D. texanus* host transition to soybean must explain how the transition occurred in such a short evolutionary period over such a broad geographic range.

In 2003 and 2004, we undertook a series of laboratory and field experiments to compare the life history of *D. texanus* on cultivated suflower and soybean plants and address a series of questions relating to its patterns of host plant use in the agroecosystems of western Kansas. Do the insects infesting soybean and sunflower still constitute a single species? Do adult females of *D. texanus* express a preference for ovipositing in their larval host plant (the so-called 'Hopkins host selection principle')? Does the population consist entirely of polyphagous individuals, or a combination of specialists and generalists? Do females express

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phenotypic plasticity with respect to host plant acceptance, i.e. do adult experiences influence subsequent host selection behavior?

Materials and Methods

Experiments in 2003

Between 22, March and 9, April a total of 98 overwintering *D. texanus* larvae were collected from stalks of cultivated sunflower in Hays, Kansas, and a total of 110 larvae from infested soybean stubble in Garden City, Kansas, about 200 miles to the southwest. There is virtually no sunflower cultivation in the vicinity of Garden City, but both crops are commonly grown around Hays. Larvae were isolated individually in plastic Petri dishes (5.5 cm x 1.0 cm) with a circle of filter paper that was moistened once every three days with a few drops of distilled water. Larvae are highly aggressive toward conspecifics and isolation is essential to prevent mortality resulting from larval combat. The Petri dishes were individually numbered, placed on trays, and held in a climate-controlled growth chamber at 24 ± 5° C and 16:8 day length under Philips 'coolwhite' fluorescent lighting. Larvae were examined daily and their date of pupation recorded along with their pupal weight. Sex was determined on the day of pupation according to the characters described by Hatchett et al. (1975).

Adults were held in their respective labeled Petri dishes following emergence under the same environmental conditions as larvae and pupae and fed sections of greenhouse-grown sunflower stalks replaced every two days. Males and females were brought together as pairs for mating in larger Petri dishes (9.5 cm x 1.0 cm) at ages ranging from 10-12 days. Mating occurred when a male contacted a receptive female's elytra with his antennae and copula lasted anywhere from 30 minutes to several hours, often with repeated couplings. The mating behavior of *D. texanus* has been described in detail by Crook et al. (2004). A total of 12 crosses were performed for each of the four permutations of males and females from sunflower and soybean (sunflower male x sunflower female, soybean male x soybean female, sunflower male x soybean female, and soybean male x sunflower female). This yielded a total of 48 mated females that were used in oviposition experiments at 18-23 days of age.

Plants for oviposition experiments were grown from seed in plastic pots (soybean: 4 L pots, sunflower: 8 L pots) in a greenhouse. Sunflowers were an oilseed variety, Triumph 665, and soybeans were a Round–up® ready variety, Asgrow 3003. Plants were used in experiments at the 6-10 leaf stage. Cylindrical wire-frame, fabric mesh cages (30 cm diameter) were used to confine female beetles on plants (www.lucina.freeserve.co.uk/index.html). The height of the cage was adjustable from 30 – 100 cm, according to the height of the plant, by altering the numbers of slotted frame members. An elastic loop secured the bottom of the cage around the pot and a large, zippered opening permitted access for introduction and removal of insects.

Between 12, June and 18, July, 2003 a total of 48 mated females were caged individually for 48 hours on one plant, followed by 48 hours on the alternate plant, half the females receiving sunflower first, the other half receiving soybean first. Following insect exposure, plants were examined for feeding damage and oviposition punctures (hereafter 'ovipunctures') and then held for 7-10 days to permit eggs to hatch. All plants with ovipunctures were then dissected to detect the presence of larvae. Larvae recovered from plants were held in Petri dishes in a growth chamber under the same environmental conditions as the overwintered larvae and reared out on greenhouse-grown sunflower stalks replaced every 2-3 days. A paired t-test was used to analyze paired data from individual females, whereas data for female treatment groups (larval host plant, sequence of plant presentation) were compared by one-way ANOVA.

Experiments in 2004

Having demonstrated reproductive compatibility between *D. texanus* populations collected from sunflower and soybean in 2003, 326 overwintering larvae were collected from sunflower stubble in Hays in 2004 since this host plant tended to yield larger and healthier individuals. Following extraction from stalks, the insects were weighed and then held under the same environmental conditions as in 2003. Each insect was weighed again at pupation and upon emergence as an adult.

Adult beetles of both sexes were divided randomly into two treatments as they emerged, one group fed on petioles of sunflower, the other on tender green stalks of soybean. The plant food was replaced every second day. Adults were mated (as described for 2003) and mated females were used in field

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trials when they were 21 days of age, or slightly earlier if ovipunctures were observed in their food stalks.

As the quality of the greenhouse-grown plants used in 2003 was not satisfactory, oviposition trials were conducted with field grown plants in 2004. In particular, we suspected that the stalks of greenhouse-grown soybeans were too frail to be suitable for oviposition, despite the fact that females did ovipuncture in them. The same plant varieties were used as in 2003, but they were planted in the field in a small research plot fenced with chicken wire to exclude rabbits. Both sunflower and soybean plants were fully grown and in early reproductive stages when they were presented to insects, corresponding to the growth stages normally attacked by adult beetles in the field. Each field plant was given a careful visual examination prior to use in the experiment to ensure it had no pre-existing insect damage that might confound results, or possibly affect the responses of the experimental female. A sequential presentation of plants was used, rather than a simultaneous choice presentation, given the logistical difficulties of growing soybeans immediately adjacent to sunflowers (due to shading of the former by the latter) and obtaining adjacent pairs of plants that would be both in suitable stages of growth.

Field trials were conducted by caging mated females on plants using the same cages as in 2003, except that the lower edge of the fabric was buried in the soil around the base of the plant in the field. After 48 hours on one plant, the female was recovered and caged on a plant of the other type for another 48 hours. One half the females were presented with sunflower first, the other half with soybean first. Following insect exposure, each plant was uprooted and taken into the laboratory where it was trimmed of leaves. All stems and petioles were then carefully examined under a low power dissecting microscope. Each stem and leaf petiole was assessed for feeding damage on a four point scale and feeding scores were then summed for the whole plant. Unlike sunflower plants, soybean plants varied considerably in architectural complexity by virtue of dichotomous branching. Therefore, a proportional index of plant damage was also calculated for soybean plants that weighted numbers of damaged petioles/branches by the total number available for purposes of regressional analysis. All ovipunctures were counted and each was carefully dissected with a scalpel to determine the presence or absence of an egg. A paired t-test was used to analyze paired data from all females considered together and data for females grouped by treatment (adult food plant, sequence of plant presentation) were compared by one-way ANOVA. When effects were significant for dependent variables, a two-way ANOVA was performed to analyze interactions between independent variables.

Only five of the mated females fed soybean laid one or more eggs in the soybean stalks that were provided as food in the Petri dishes, but oviposition behavior was common among females provided with sunflower stalks. Therefore, the ovipuncturing and egg-laying behavior of 20 females held for their entire adult life in Petri dishes was observed and recorded with sunflower stalk segments provided fresh every two days. Upon removal, all stalks were examined for ovipuntures and dissected to determine the numbers of eggs laid. These observations provided estimates of lifetime fecundity (under laboratory conditions) and permitted regressional analyses of reproductive behavior on other life history attributes such as longevity and adult weight.

Results

2003 Experiments

Seventy-two adults were obtained from sunflower (36 females, 36 males) and 79 adults from soybean (42 females, 37 males) for survival rates of 73.5% and 71.8%, respectively. Female pupae weighed, on average, 13.7% heavier than male pupae regardless of plant source ($F = 5.331$; 1,170; $P = 0.022$). However, plant source influenced pupal weight for both males [mean ± SEM = 34.2 ± 1.4 mg (sunflower) vs. 21.0 ± 0.8 mg (soybean); $F = 77.553$; df = 1,84; $P < 0.001$] and females [mean ± SEM = 39.0 ± 1.6 mg (sunflower) vs. 23.2 ± 1.0 mg (soybean), $F = 72.812$; df = 1,84; $P < 0.001$]. Plant source had no effect on time to adult emergence calculated from the first day of spring ($F = 0.027$; df = 1,162; $P = 0.871$) and neither did sex ($F = 1.850$; df = 1,162; $P = 0.176$). Therefore, the pattern of adult emergence is depicted for all insects pooled in Fig. 1. The frequency of elytral deformities was higher among individuals maturing in soybean compared to sunflower ($F = 6.277$; df = 1,151; $P = 0.013$).

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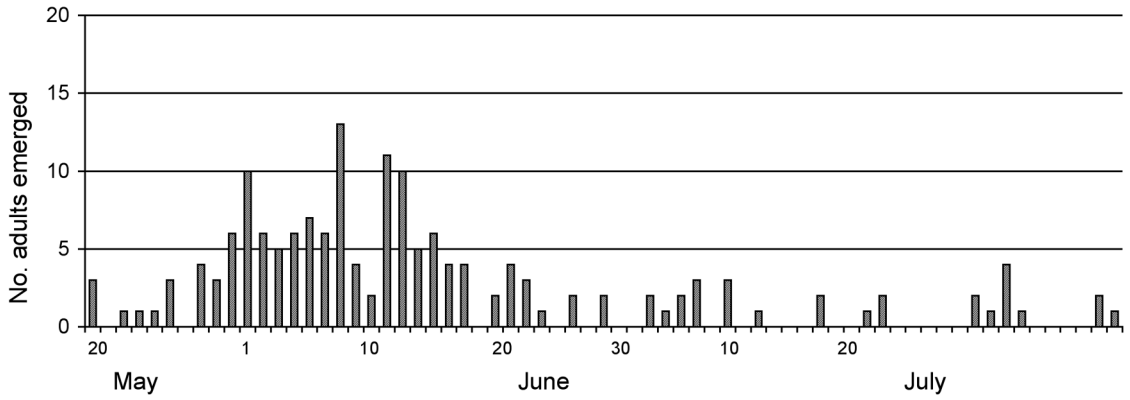
Figure 1.



Of the 48 females tested in the greenhouse oviposition experiment, 40 made at least one ovipuncture on a plant and the remaining eight were excluded from all subsequent analyses. A total of three viable larvae were recovered from plants exposed to sunflower-collected females mated to soybean-collected males and four viable larvae from plants exposed to soybean-collected females mated to sunflower-collected males. This compared to four viable larvae each recovered from plants exposed to sunflower-sunflower and soybean-soybean crosses. All larvae were recovered from sunflower plants. These larvae gave rise to 10 pupae and 9 adult beetles that emerged between 16 December 2003 and 9 April 2004. Three of these beetles were the progeny of sunflower females crossed with soybean males and two were the progeny of soybean females mated with sunflower males. Given the small numbers of larvae recovered, only numbers of ovipunctures were subjected to analysis.

Larval host plant had no effect on the number of ovipunctures females made on plants of either type as adults (sunflower; $F = 3.373$; df = 1,38; $P = 0.073$; soybean: $F = 0.303$; df = 1,38; $P = 0.585$). However, females made more ovipunctures on a plant type when it was offered first (sunflower: $F = 4.806$; df = 1,38; $P = 0.035$; soybean: $F = 5.390$; df = 1,38; $P = 0.026$). Overall, significantly more ovipunctures were made on sunflower than on soybean (mean ± SEM = 4.43 ± 0.6 vs. 0.18 ± 0.06, $t = 6.338$, df = 39, $P < 0.001$).

2004 Experiments

Development. A total of 242 adult beetles emerged from 326 overwintered larvae, 116 males and 126 females for a survival rate of 74.2 % and a sex ratio of 0.52. Female pupae averaged 60.5 ± 1.43 mg compared to 52.3 ± 52.3 mg for male pupae, 12.9 % heavier ($F = 16.529$; df = 1,240; $P < 0.001$). The mean pupation time was similar for males and females (13.6 d and 13.7 d, respectively). Male larvae lost an average of 37.6 % of their weight from time of collection to emergence as an adult; female larvae lost an average of 37.0 %.

Longevity and reproduction in the laboratory. Male beetles lived an average of 23.3 ± 1.4 d on a diet of soybean stalks, compared to an average of 75.6 ± 4.3 d on a diet of sunflower petioles ($F = 148.847$; df = 1,113; $P < 0.001$). For females, the averages were 23.2 ± 1.2 d and 52.4 ± 3.7 d, respectively ($F = 65.273$; df = 1,98; $P < 0.001$). The twenty females followed in the laboratory laid a mean (± SEM) of 33.05 ± 5.2 eggs over an average reproductive lifespan of mean (± SEM) 56.0 ± 4.5 days for an average reproductive rate of 0.57 eggs per day of reproductive life. The mean (± SEM) pre-oviposition period was 17.0 ± 0.7 days and 42.3 % of ovipunctures were associated with eggs. Female weight was positively correlated with total number of ovipunctures in linear regression ($F = 5.02$; df = 1,18; $P = 0.038$; $r^2 = 0.218$), but the effect was not significant for total number of eggs laid ($F = 1.77$; df = 1,18; $P = 0.200$). Female longevity was strongly and positively correlated with total number of ovipunctures ($F = 11.05$; df = 1,18; $P = 0.005$; $r^2 = 0.441$), but not with

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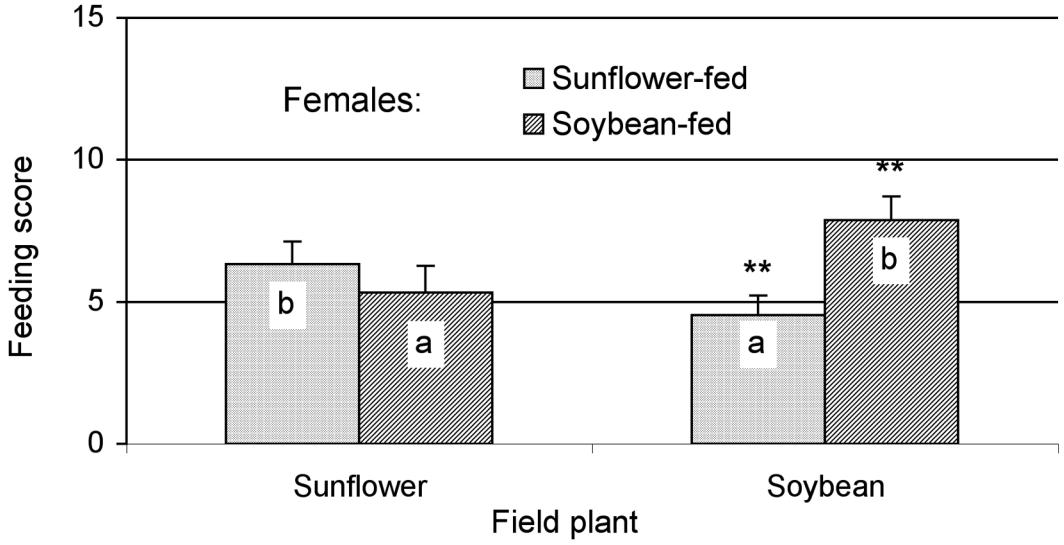
Figure 2.



total number of eggs laid (F = 2.57; df = 1,18; P = 0.131). Female longevity was negatively correlated with the proportion of ovipunctures that resulted in eggs laid (F = 5.26; df = 1,18; P = 0.038; r^2 = 0.273). Female fecundity was negatively correlated with pre-oviposition interval (F = 5.34; df =1,18; P = 0.33; r^2 = 0.229) and positively correlated with daily rate of oviposition (F = 64.21; df = 1,18; P < 0.001; r^2 =0.781).

Field trials. A total of 81 mated females were tested in the field trial, 52 fed sunflower and 29 fed soybean. These unequal samples arose because many soybean-fed females died before they were old enough to use in the experiment, some before mating and some soon thereafter. In numerous dishes we observed little or no evidence of feeding on the soybean stalks, suggesting that many adults were reluctant to consume them. Of the tested females, 27 were either lost or died in the course of their field trial and were therefore excluded from all analyses. Only data from the 54 females recovered alive at the end of their trial were used for analyses of feeding and reproductive behavior.

Feeding behavior in the field. Females fed sunflower in the laboratory had higher feeding scores on sunflower than on soybean plants in field trials (t = 2.109, df = 36, P = 0.021), whereas soybean-fed females had higher feeding scores on soybean plants (t = 1.994, df = 16, P = 0.032, Fig. 2). Comparing females by diet treatment, those fed soybean in the laboratory did more feeding on soybean in field trials than did those fed sunflower regardless of the sequence of plant presentation (F = 8.233; df = 1,52; P = 0.006), whereas both fed equally on sunflower (F = 0.593; df = 1,52; P = 0.445).

Sunflower plants sustained higher feeding scores from soybean-fed females in the field trial when they were presented first than when they were presented second (F = 5.810; df = 1,15; P = 0.029) but there was no effect of plant presentation sequence on soybean feeding scores (F = 0.005; df = 1,15; P = 0.945). Plant presentation sequence had no effect on the feeding behavior of sunflower-fed females on either sunflower (F = 1.007; df = 1,35; P = 0.323) or soybean (F = 2.989; df = 1,35; P = 0.093). A two-way ANOVA revealed no significant interactions between adult food plant and plant presentation sequence for feeding scores on either sunflower (F = 0.285; df = 1,50; P = 0.596) or soybean (F = 0.302; df = 1,50; P = 0.585).

Oviposition behavior in the field. Significantly more total ovipunctures were made (F = 10.190; df = 2,31; P < 0.001; LSD, P < 0.01) and more eggs laid (F = 9.499; df = 3,31; P = 0.001; LSD, P < 0.01) by females that accepted both plant types for oviposition (means ± SEM = 19.00 ± 3.58 and 6.00 ± 0.98, respectively) than by females that either laid only on sunflower (means ± SEM = 8.00 ± 2.12 and 3.08 ± 0.82, respectively) or only on soybean (Means ± SEM = 4.25 ± 1.10 and 1.5 ± 0.26, respectively). However, females laying eggs only on

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sunflower also made the occasional ovipuncture on soybean (mean ± SEM = 0.73 ± 0.30) and females laying eggs only on soybean also made a few ovipunctures in sunflower (mean ± SEM = 1.17 ± 0.98). Only data from the 34 females that laid one or more eggs in their field trial were included in further analyses of oviposition behavior.

On average, 32.3 and 33.2 percent of ovipunctures resulted in an oviposition in sunflower and soybean, respectively, in the field trial. The type of plant provided as adult food had no significant effect on the total number of ovipunctures made ($F = 0.661$; df = 1,52; $P = 0.420$) or the total eggs laid ($F = 1.238$; df = 1,32; $P = 0.274$). However, females fed soybean made twice as many ovipunctures on soybean plants in the field as they did on sunflower plants ($t = 2.183$, df = 16, $P = 0.044$, Fig. 3a), although the difference was not significant for numbers of eggs laid ($t = 0.537$, df = 9, $P = 0.604$, Fig. 3b). Sunflower-fed females ovipunctured sunflower and soybean plants to a similar extent ($t = 1.513$, df = 36, $P = 0.139$) and laid similar numbers of eggs in each ($t = 0.169$, df = 23, $P = 0.296$).

The sequence of plant presentation in the field affected the total number of ovipunctures made by sunflower-fed females ($F = 9.243$; df = 1,35; $P = 0.004$; Fig. 4a), although the effect was not significant for soybean-fed females ($F = 1.028$; df = 1,15; $P = 0.327$). However, the sequence of plant presentation in the field affected the total number of eggs laid by soybean-fed females ($F = 6.262$, df = 1,8; $P = 0.037$; Fig. 4b), with no significant effect for sunflower-fed females ($F = 2.534$; df = 1,22; $P = 0.126$). A two-way ANOVA revealed no significant interactions between food plant and plant presentation sequence for any reproductive activity (ovipunctures in sunflower: $F = 1.128$; df = 1,50; $P = 0.293$; ovipunctures in soybean: $F = 0.400$; df = 1,50; $P = 0.530$; total ovipunctures $F = 1.068$; df = 1,50; $P = 0.306$; eggs in sunflower: $F = 0.231$; df = 1,30; $P = 0.634$; eggs in soybean: $F = 0.001$; df = 1,30; $P = 0.983$; total eggs: $F = 0.144$; 1,30 df; $P = 0.707$). Pooling insects from both diets, females made more total ovipunctures ($F = 9.573$; df = 1,52; $P = 0.003$) and laid more total eggs ($F = 6.707$; df = 1,32; $P = 0.014$) when the plant sequence was sunflower-soybean than when it was soybean-sunflower. Thus more reproductive activity was elicited from females when sunflower was encountered first, regardless of their diet in the laboratory.

In terms of plant-specific activity, females ovipunctured more often on sunflower (5.78 ± 1.2 vs. 1.63 ± 0.57; $F = 9.910$; df = 1, 52; $P = 0.003$) and laid more eggs on sunflower (2.95 ± 0.63 vs. 0.67 ± 0.37; $F = 8.391$; df = 1, 32; $P = 0.007$) when it was presented first than when it was presented after soybean. A similar pattern was evident for ovipunctures on soybean, although the effect was only marginally significant due to a smaller sample size and large variation in female activity (4.67 ± 1.41 vs. 1.89 ± 0.57; $F = 3.334$; df = 1,52; $P = 0.074$). There was no indication that sequence of plant presentation affected the number of eggs laid in soybean ($F = 0.081$; df = 1,32; $P = 0.778$), but both female sample size and count data were even lower for eggs than for ovipunctures.

Correlations between feeding and oviposition. Feeding scores on sunflower plants were linearly correlated with both numbers of ovipunctures ($F = 93.05$; df = 52; $P < 0.001$; $r^2 = 0.642$; Fig. 5a) and numbers of eggs ($F = 39.56$; df = 52; $P < 0.001$; $r^2 = 0.432$; Fig. 6a). Similar relationships were observed between soybean feeding scores and ovipunctures ($F = 44.16$; df = 52; $P < 0.001$; $r^2 = 0.459$; Fig. 5b) and soybean feeding scores and oviposition ($F = 21.46$; df = 52; $P < 0.001$; $r^2 = 0.292$; Fig. 6b). The proportional index of feeding damage provided a better fit to the oviposition data on soybean than did the raw feeding scores ($F = 37.63$; df = 52; $P < 0.001$; $r^2 = 0.42$), but did not improve fit to the ovipuncture data ($F = 38.09$; df = 52; $P < 0.001$; $r^2 = 0.423$).

Discussion

Reproductive compatibility

The reciprocal crosses of *D. texanus* adults reared from sunflower and soybean each produced several viable progeny, indicating that the two populations comprise a single species according to the Biological Species Concept (Mayr, 1942). The fact that progeny were only recovered from sunflower plants may be of little significance. The greenhouse environment altered plant architecture and physiology considerably, especially in the case of soybeans, where leaf petioles may have been too slender to contain a pith core and permit completed oviposition. Hatchett et al. (1975) suggested that successful oviposition depended on whether or not pith was present in the stem, and whether or not the female could reach it with her ovipositor. Although we were able to compare the frequency of ovipunctures among these plants, we did not feel

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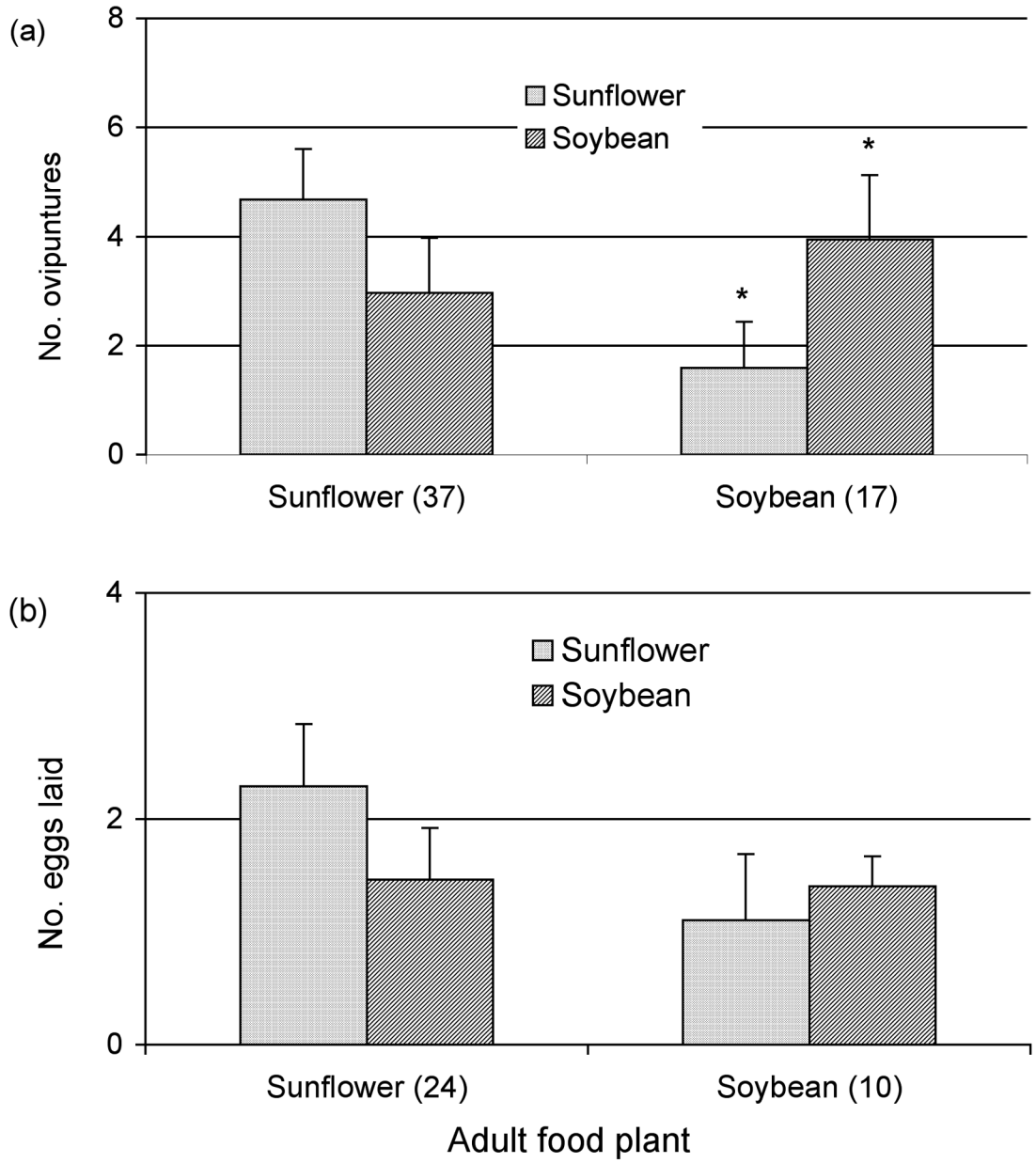
Figure 3.



that any reliable conclusions could be drawn from these data regarding the relative acceptability of the two host plants, or their suitability for larval survival. Based on these observations, we decided to perform all behavioral assays on field-grown plants the following season.

Life history consequences of host plant

Development of *D. texanus* larvae in soybean resulted in a 40% reduction in body weight compared to development in sunflower, and a higher frequency of elytral deformities. This reduction in adult weight could translate into significant reductions in beetle fitness if body size is correlated with other life history attributes that affect survival or reproductive performance in the field. For example, adult body mass could be positively correlated with ability to survive adverse physical conditions, with female fecundity, or with male mating success. The laboratory observations on reproductive females may not have had sufficient sample size to detect effects of female

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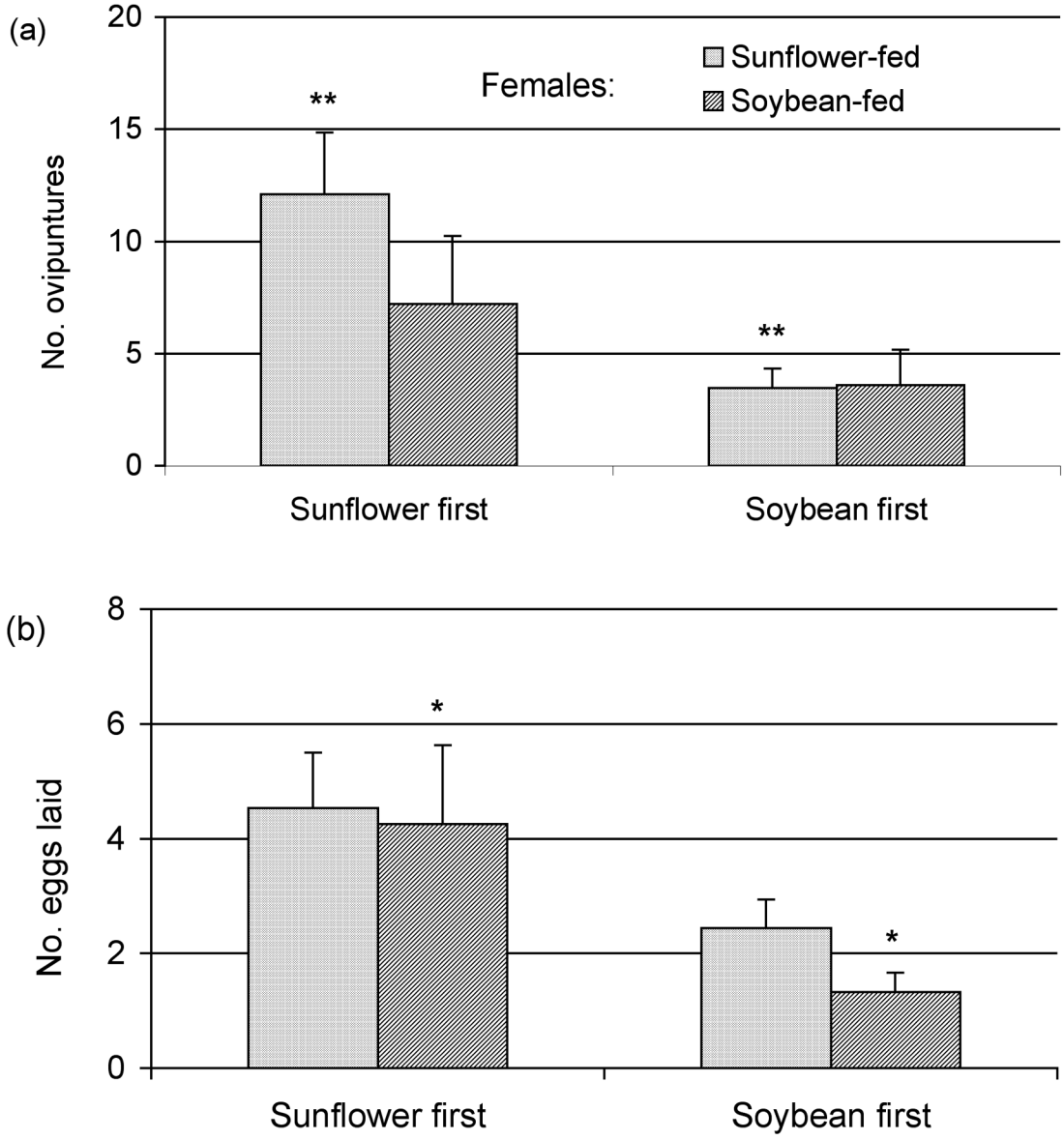
Figure 4.



weight on fecundity, but the number of ovipunctures in sunflower stalks increased significantly with female weight suggesting that larger females had greater repoductive vigor. The survival to maturity of larvae from both plant sources was similar in the laboratory, and comparable to the survival obtained by Hatchett et al. (1975) in soybean, suggesting a relatively high degree of adaptation to the novel host plant despite these apparent fitness costs.

Pupation times and emergence dates of adults in a 24° C chamber were similar for insects collected from sunflower and soybean, suggesting no effect of host plant on these life history parameters. The extended period of adult emergence (Fig. 1), combined with a female longevity of ca. two months, are probably the reasons why delayed planting dates yield limited benefits in reducing infestations in all but the most southern regions that have the largest planting window (Rogers, 1985). The fact that larvae recovered from experimental plants pupated and produced viable adults in as short a period as six months at 24° C demonstrates that diapause is facultative in this

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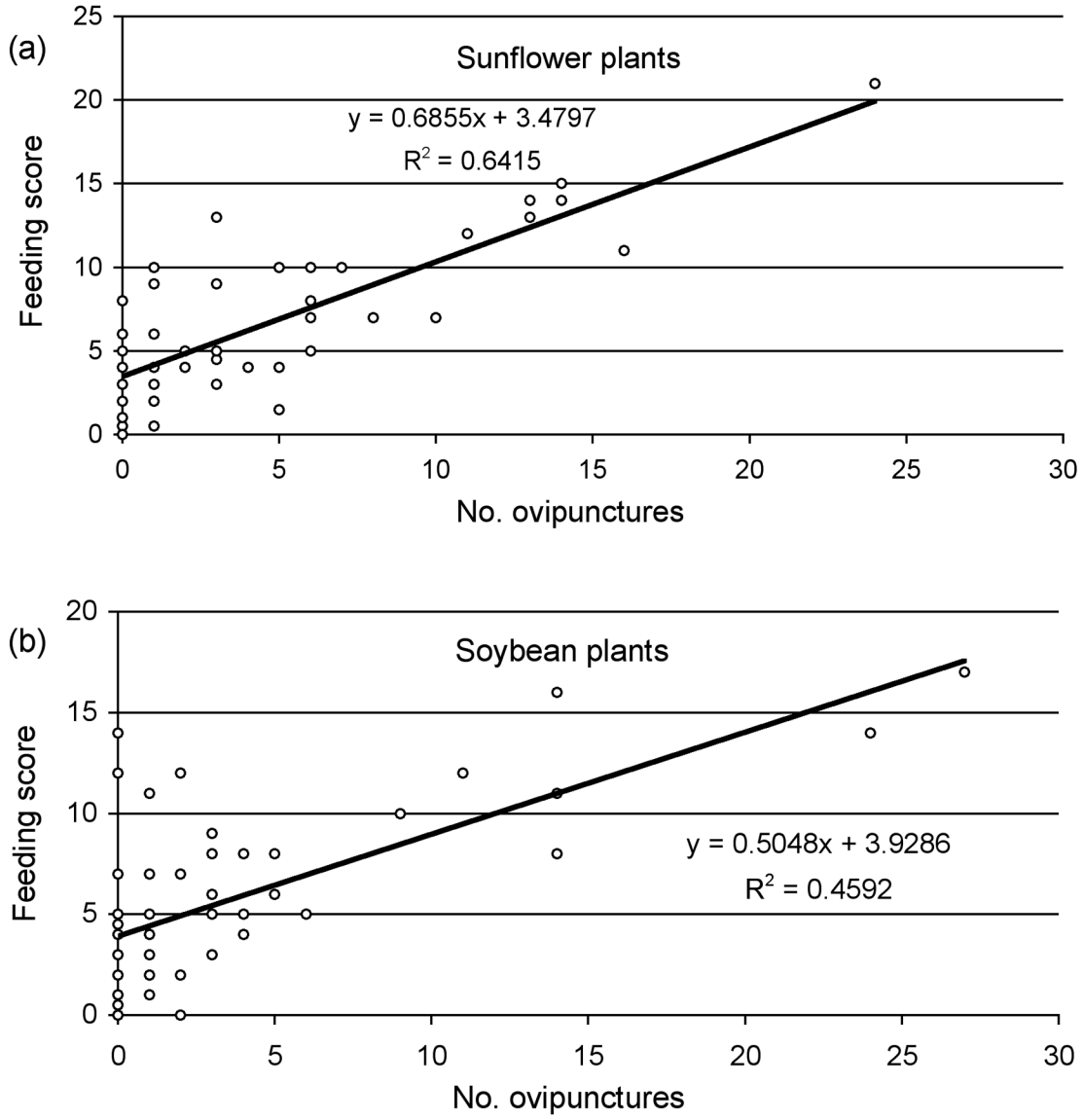
Figure 5.



species and that a cold period is not obligatory for completion of larval development.

The observed reduction in adult longevity when soybean was the exclusive adult food is consistent with soybean representing a host plant of generally lower nutritional suitability than sunflower for both feeding life stages. The significance of this effect in reducing adult longevity in natural populations will depend on the degree to which adults are limited to soybeans as a food source, or able to supplement their diet with more nutritious plants. Note also that the soybean diet did not reduce the reproductive performance of females in the field trial relative to the sunflower diet.

Feeding behavior

Females in field trials fed more on the plant they had been provided in the laboratory than on the alternative (Fig. 2), indicating that adults became conditioned to feeding on a particular plant type. When diet treatments were compared, soybean-fed females fed more on soybean in the field trial than did sunflower-fed females, whereas feeding on

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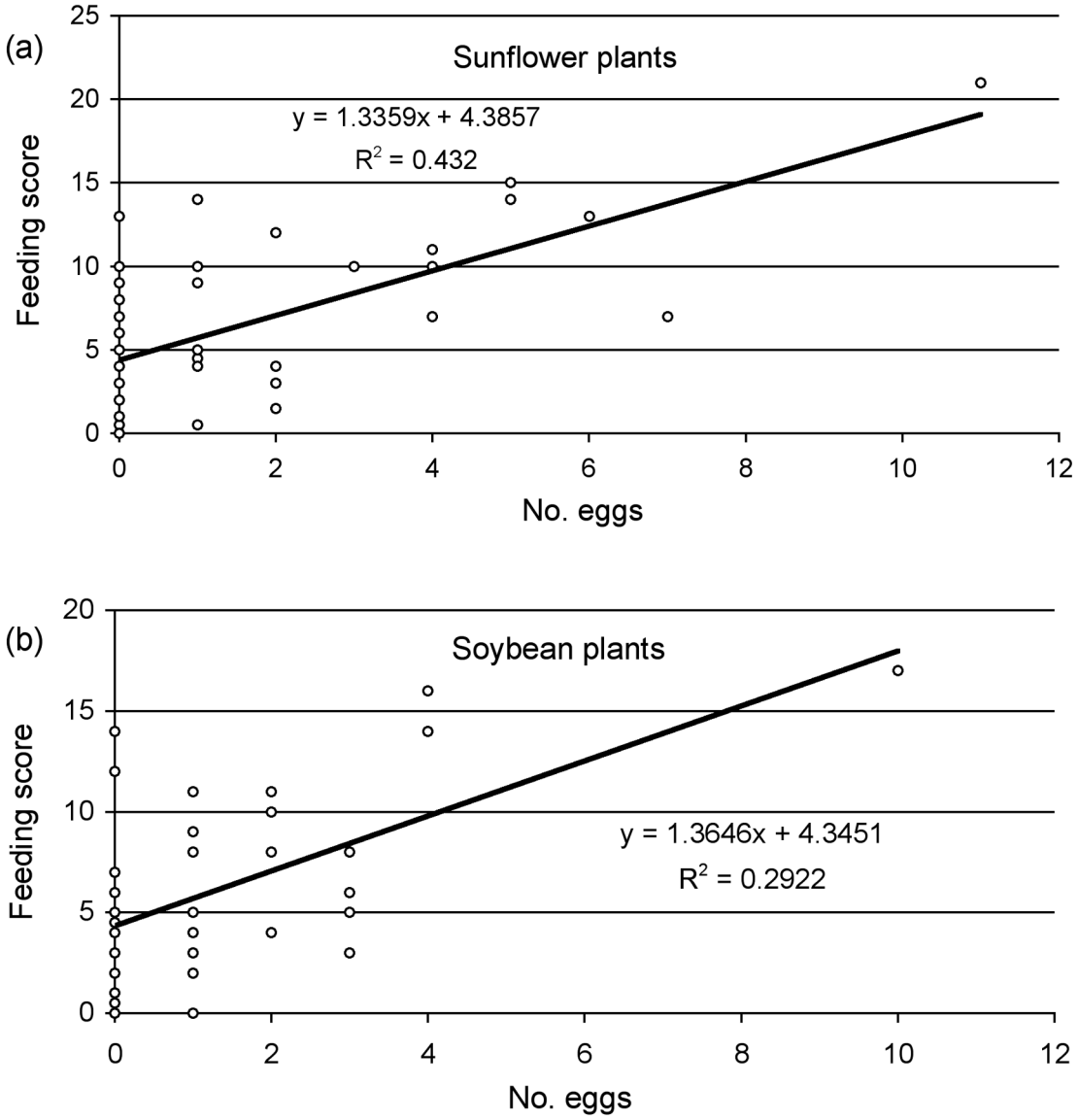
Figure 6.



sunflower was equal. Thus, the soybean feeding experience increased female acceptance of soybean as food, without reducing the acceptability of sunflower. Encounters with whole plants in the field appeared to influence female feeding behavior more than did their laboratory experience of feeding on stalk segments. Thus, soybean-fed females exhibited stronger feeding responses to sunflower plants when they were the first whole plant encountered than when they were the second. Apparently, a 48 hour encounter with a whole soybean plant reduced the feeding response to sunflower more than did three weeks of an exclusive diet of soybean stalks.

Oviposition behavior

The 2003 data did not provide any indication that the larval host plant influenced an adult female's tendency to ovipuncture plants of one type or another, the so-called 'Hopkins host selection principle'. Collectively, the 2004 data are consistent with Barron's (2001) inference that adult experiences have a greater impact on oviposition behavior than larval experiences in most phytophagous species. Approximately one third of ovipunctures resulted in an egg being laid and this was independent of host plant, suggesting that counts of ovipunctures might be used to assess host

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plant acceptance in larger scale studies without the need for time-consuming plant dissections to count eggs.

The fact that soybean-fed females made twice as many ovipunctures on soybean plants as did sunflower-fed females (Fig. 3) suggests that a female's adult feeding experience affects her reproductive response to a plant. The lower count data for eggs and the small sample size of soybean-fed females reduced our ability to detect such an effect on actual oviposition. Interestingly, a diet of sunflower did not serve to reduce the acceptability of soybean for oviposition, suggesting that no negative conditioning to soybean resulted from the sunflower diet, although positive conditioning apparently did result from the soybean diet.

It is remarkable that a female's oviposition behavior appeared more influenced by the first whole plant she encountered in the field than by the type of plant she had been fed in sections for the previous three weeks. A female's total ovipositional activity was higher when her initial encounter was with sunflower than when it was with soybean (Fig. 4), suggesting that the ancestral host plant still triggered a stronger reproductive response than the novel host plant, and one with sufficient duration to affect behavior on a subsequent plant of another species. However, the reverse effect could also be inferred, i.e. an intial encounter with soybean reduced a female's reproductive activity, not only on the soybean plant, but also on a subsequent sunflower plant. An effect of plant sequence was also noted in the greenhouse trials in 2003 in that females (all fed on sunflower in this case) made significantly more ovipunctures on the host that was presented first as a whole plant.

The description of *D. texanus* female oviposition behavior provided by Hatchett et al (1975) identifies a clear link between feeding and oviposition: almost all ovipunctures begin with a female chewing a hole through the tough, epidermal surface of plant petiole before inserting her ovipositor. The significant regressions of feeding damage on ovipunctures (Fig. 5) and eggs (Fig. 6) for both plant types support the inference of an important relationship between adult feeding and oviposition behavior. In an agricultural context, emergent adults encountering a large monoculture would be likely to feed only on plants of that type, the females ultimately accepting the same plants for oviposition. The link between adult feeding and oviposition behavior could have been an important proximal mechanism facilitating the host transition to soybean by *D. texanus*. It also suggests that sunflower, on which *D. texanus* has little if any yield impact (J.P. Michaud, unpublished data), could function as a trap crop, or companion crop, to protect soybeans. If sunflower is preferred over soybean as an adult food plant, then sunflower plants could serve to attract and retain emerging adults and subsequently serve as an oviposition sink for reproductive females. The feeding preference should result in declining gradients of infestation across soybean fields where ever they approach a border with a sunflower field, the companion crop effect. However, even better protection might be afforded the soybean crop if it were completely surrounded by sunflowers planted as a trap crop so that immigrating beetles encountered, and fed first, on the preferred host plant before encountering the less preferred.

Why a transition to soybean?

Given the significant fitness costs associated with exploitation of soybean relative to sunflower (and presumably other ancestral host plants), the potential compensatory payoffs for *D. texanus* females that decide to accept soybean for both feeding and oviposition must be examined and weighed. Various hypotheses can be considered, none mutually exclusive, and some potentially additive in effect. However, in order to be sufficient, an explanation of the selective advantage for exploiting soybean must function equally well in all the various geographic regions where host expansion has occurred.

1) The host availability hypothesis. Michaud (1990) described a series of ecological conditions that could theoretically serve to maintain, or select for, polyphagous habits in phytophagous insects. The model focused primarily on conditions that generated spatial or temporal uncertainty in the quality or availability of the preferred host plant and these were further elaborated in Michaud (1992). Soybean may have been initially accepted for feeding, and subsequently for oviposition, simply because it was readily available and abundant in circumstances where alternative host plants were not. This hypothesis seems plausible for the arid High Plains region where soybean circles under center-pivot irrigation frequently constitute 'green islands' in a virtual desert of

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parched summer vegetation. *D. texanus* ecology also conforms to the first category of cerambycids described by Hanks (1999), i.e. species that attack healthy host plants, both larvae and adults feeding on the same plant, and the adults having low dispersal tendency. Collectively, these traits are conducive to scenarios in which female beetles arrive in soybean monocultures by chance, eventually begin feeding, and finally oviposit on the plants rather than opting for dispersal. The observed link between adult feeding and oviposition also supports this scenario. However, the host availability hypothesis may function less well in regions where soybean is grown on smaller scales and without irrigation. More information on the availability of wild host pants relative to soybean in other regions of the *D. texanus* range would be useful for assessing the general applicability of the host availability hypothesis.

2) The natural enemy hypothesis. Soybean may represent a host plant that, although inferior as food for both adults and larvae, provides an effective refuge from predators, parasitoids and/or diseases that normally inflict mortality on the population in ancestral host plants. For example, Gratton & Welter (1999) showed that larvae of the agromyzid leafminer, *Lyriomyza helianthi*, subjected to an artificial host shift from *H. annuus* to other composite plants experienced a 22% reduction in rates of parasitism, consistent with the novel host plants providing 'enemy free space'. Little information exists on sources of mortality for *D. texanus* larvae in its various ancestral hosts, although the protected location of the larvae within the plant suggests little vulnerability to predation. Hatchett et al. (1975) reported one ichneumonid, two braconid, and three pteromalid parasitoids attacking *D. texanus* taken from *Ambrosia* spp. in Missouri, but none from soybean. Although moribund larvae can be found in winter stalks, we have yet to detect a single parasitoid or predator of *D. texanus* larvae in samples collected from either soybean or cultivated sunflower in western Kansas and none have been reported in the literature to our knowledge. Similarly, collections of *D. texanus* larvae from cultivated sunflowers across the High Plains made by the USDA, ARS Sunflower Insect Research Laboratory in Fargo, ND over a period of more than 20 years have yet to yield any parasitized individuals (L.D. Charlet, personal communication). Consequently, there is little evidence that natural enemies exert any significant mortality on *D. texanus* in any host plant, or in any portion of its range.

3) The interspecific competition hypothesis. Soybean might represent a refuge host plant for *D. texanus* where it can escape aggressive, superior competitors that inflict considerable larval mortality, directly or indirectly, in ancestral host plants. A great diversity of insects feeds within the stalks of sunflowers – too many to list here, but no insects have yet been reported to feed within the stalks of soybeans in the continental United States. Interspecific competition among phytophagous insects has long been thought to be a weak or insignificant evolutionary force because herbivores typically consume such a small proportion of the available primary production (Lawton et al., 1981). Whereas this may be true for many foliage feeding species, it is not necessarily true for insects that compete for more limited, high-value resources such as fruits and seeds, or in the case of *D. texanus*, for the base of the stalk, the only suitable over wintering site. There is also anecdotal evidence to indicate that *A. hubbardi* engages in 'interference competition' (Miller, 1967) with *D. texanus* within sunflower stalks in western Kansas. Larvae of the former species average three times the size of *D. texanus* and are highly aggressive toward both conspecifics and *D. texanus* larvae. *A. hubbardi* occurs in both wild and cultivated *H. annuus* in the High Plains, but does not attack soybean. A preliminary laboratory trial indicated that *A. hubbardi* larvae mutilated and killed larvae of *D. texanus* in 16 of 20 replications when two larvae of equal weight were introduced into opposing ends of the same sunflower stalk (AKG, unpublished data). Rogers (1977) reported that "there appears to be considerable competition between larvae of *A. hubbardi* and *M.* (*Mecas*) *inornata*" (another cerambycid that bores sunflower stalks) and that "larvae of *A. hubbardi* appear to have the advantage". Adults of *A. hubbardi* emerge earlier in spring than either *D. texanus* or *M. inornata* (Rogers, 1977) and the larvae typically predominate over *D. texanus* in stalks of early-planted sunflowers in our region (JPM, unpublished data). Complete information is not available on the degree to which host ranges and geographic ranges overlap for these two species, but it seems unlikely that *A. hubbardi* could represent a serious mortality factor for *D. texanus* in all its composite hosts throughout its entire geographic range, although it may contribute

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some selective pressure for soybean utilization by *D. texanus* in our particular area.

4) The intraspecific competition hypothesis. Ward (1992) put forward a model for the evolution of polyphagy in phytophagous insects that included intraspecific competition as a potential force reducing the suitability of the preferred host plant and driving the evolution of a host range expansion. *Dectes texanus* infestation rates in soybean and sunflower fields often exceed 80 or 90% of available plants. In summer, plants can be found to contain two, or even three of four larvae that are ultimately reduced through larval combat to a final victor, although occasionally two overwintering chambers may be formed. Hatchet et al. (1975) noted that "Most infested plants contained several larvae" and described larval competition occurring in two stages, the first between neonate larvae within petioles, the second between third instar and older larvae within the main stem. The unique stalk-girdling behavior of the pre-diapausing larva can also be interpreted as a defensive tactic that has evolved to foil any conspecific competitors that are late in descending to the base of the plant. In the early stages of the host transition, any viable offspring of females ovipositing in soybean would escape competition from conspecifics, although the benefits would diminish as the behavior increased in frequency in the population. There is not only strong evidence for intraspecific competition in *D. texanus* populations, but the initial benefits of reduced competition in soybean, although frequency-dependent, are quite compatible with an evolutionary scenario of multiple independent host shift events from various ancestral host plants wherever soybean has been grown. Thus, we favor intraspecific competition as the most likely force driving the host shift of *D. texanus* throughout its range, although the transition was likely re-inforced by other selective advantages for soybean exploitation that varied among localities.

Implications for the evolution of *D. texanus*. If the *D. texanus* population was uniformly polyphagous with respect to utilization of sunflower and soybean, all females would be expected to accept both host plants. However, females fell into three discrete categories of host plant acceptance with approximately equal frequency, laying eggs either only in sunflower, only in soybean, or in both plants equally. This observation is consistent with some genetic basis for host plant fidelity, and is superficially suggestive of disruptive selection if the 'both plants' category could be construed to represent heterozygotes occurring at less-than-expected frequency and the 'only one' categories, homozygotes. However, such an interpretation lacks supporting evidence as yet. An alternative, and equally plausible, hypothesis is that multiple alleles affect host plant acceptance and that the observed distribution of female 'types' in the experiment simply reflects the 'net' responses of a broad range of genotypes present in the population. Whether the basis for host plant fidelity is monogenic or polygenic, the data suggest that genes for soybean acceptance presently occur with a frequency equal to those for sunflower acceptance, at least in this particular population.

The final question is whether evolution can be expected to proceed toward specialization within subpopulations, or general polyphagy. Although the studied population contained individuals with apparent behavioral specialization, this specialization was not absolute, as evidenced by some ovipuncturing on the alternative host, and the fitness costs of feeding on soybean, for adults and larvae, remain considerable for the population as a whole. Thus it seems unlikely that disruptive selection would favor assortative mating according to host plant that would ultimately result in sympatric speciation, although this is the theoretical outcome if fitness on one host is negatively correlated with fitness on the other. An alternative evolutionary scenario, more likely in our view, is one in which particular alleles increase in the population that provide increments to fitness on soybean *without corresponding decrements to fitness on sunflower*. This scenario assumes that phenotypic plasticity for host plant acceptance yields higher average fitness for individuals over time than traits associated with specialization on either plant. Sunflower will remain the preferred host plant, but soybean will also be utilized whenever it is available, to a lesser extent when sunflower is available, and to a greater extent when it is not. The supporting rationale for this outcome encompasses both temporal and spatial components of host plant availability in the agroecosystem that now supports the vast majority of the beetle population. Agricultural crop rotations generate temporal variation in the availability of host plants, resulting in a capricious environment for the beetle population; whatever crop was present in a field in one year is the least likely to be present in the same field in a subsequent year, thus

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favoring genotypes adapted to utilize both host plants. In the High Plains, both crops are sometimes present in adjacent fields and in other cases irrigated circles are split between sunflowers and soybeans. Under these conditions, polyphagous females can 'spread risk' by placing some offspring in both host plants, and achieve potential fitness gains whenever larval mortality factors vary as a function of host plant. The *D. texanus* -soybean-sunflower system warrants continued study for many years to come as it represents a unique opportunity to test assumptions and theories of insect host range evolution in agroecosystems that are artificially simplified by monocultural practices.

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