

2012

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Brust, Mathew L.; Knisley, C. Barry; Spomer, Stephen M.; and Miwa, Kentaro, "Observations of Oviposition Behavior among North American Tiger Beetle (Coleoptera: Carabidae: Cicindelinae) Species and Notes on Mass Rearing" (2012). *Papers in Entomology*. 154. <http://digitalcommons.unl.edu/entomologypapers/154>

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**OBSERVATIONS OF OVIPOSITION BEHAVIOR AMONG NORTH AMERICAN
TIGER BEETLE (COLEOPTERA: CARABIDAE: CICINDELINAE)
SPECIES AND NOTES ON MASS REARING**

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ABSTRACT

Although the larvae of a large number of North American tiger beetle species have been described, little information exists on the oviposition behavior of female tiger beetles at the species level. In this study, we found that the oviposition behavior varied widely among species, with some species utilizing more than one method. We found that, contrary to many references, several tiger beetle species did not oviposit from above the soil surface by inserting the ovipositor into the soil. Instead, several species oviposited by tunneling over 20 mm below the soil surface. In addition, we outline recently used successful protocols for rearing larvae rapidly and in large quantities.

Key Words: *Cicindela*, behavior, eggs, selection, propagation

Several sources provide some basic information on female oviposition behavior in tiger beetles (Pearson 1988; Pearson and Vogler 2001; Pearson *et al.* 2006). In this study, we examined information from the literature and made numerous observations both in the field and the laboratory.

Larval habitats of tiger beetles are extremely varied, and proximately they are most influenced by the habitat of the adult and the precise selection of an oviposition site by the female. Typical behavior involves the female biting the soil or touching the substrate with her antennae and even digging trial holes, all apparently to detect a site with suitable soil conditions (Willis 1967). Females of one species (*Cicindela marutha* Dow) may even move a considerable distance from the adult habitat to select an oviposition site (Knisley 1984). Despite this variation in larval habitats and microhabitats, most observations of oviposition are similar to those described by Willis (1967). He indicated that the female assumes an almost vertical position, extends the ovipositor and uses the gonapophyses on the ovipositor to remove small bits of soil to create a

0.5 to 1.0-cm-deep hole, and then deposits the egg (Willis 1967). The female may then rake the soil particles to cover the hole, but accumulated bits of soil may often be seen at the edge of the oviposition burrow. Hori (1982) noted similar behavior for *Cicindela japonica* Thunberg and reported the length of the entire oviposition process averaged 8.8 minutes. We recently received a video from Tim Anderson of the oviposition sequence by *Cicindela trifasciata* F. showing behavior like that described by Willis (1967). Knisley and Schultz (1997) reported a much different oviposition behavior by *Cicindela dorsalis* Say. They found that the adult female used her ovipositor to dig a large hole (2–3 cm in diameter × 5–6 cm deep) into which she then backed. Eggs have been recovered from such burrows. In this study, we document additional variations in oviposition behavior in several tiger beetle species.

MATERIAL AND METHODS

Oviposition Studies. Notes on the oviposition behavior of *Cicindela purpurea audubonii* LeConte,

Cicindela albissima Rumpff, and *Cicindela ohlone* Freitag and Kavanaugh were obtained in the field, but oviposition behavior in all other species included here was observed in the laboratory as a part of rearing studies. All rearing methodology followed the protocol explained in paragraphs to follow, except that larvae of *Cicindela denverensis* Casey, *Cicindela limbalis* Klug, *Cicindela sexguttata* F., and *Cicindela splendida* Hentz were fed a much wider variety of insect prey.

Cicindela denverensis, *Cicindela formosa formosa* Say, *C. limbalis*, *Cicindela scutellaris scutellaris* Say, *Cicindela scutellaris rugata* Vaurie, *C. sexguttata*, *C. splendida*, and *Cicindela tranquebarica tranquebarica* Herbst were reared in captivity from field-collected females in 3.8-L plastic pet aquaria with soil from the species' habitat added to a depth of 70–130 mm. Adults were fed primarily workers and pre-alates of termites, *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae), and ant, *Camponotus* spp. (Hymenoptera: Formicidae), pupae. Observations on the depth at which eggs were placed were made either by observation through the clear plastic sides of the containers or by extracting them by digging. Efforts were made to feed the adults as often as possible (ca. once every 1.5 days) to maximize egg production.

Oviposition by *Cicindela hornii hornii* Schaupp, *Cicindela nigrocoerulea nigrocoerulea* LeConte, *Cicindela obsoleta santaclarae* Bates, *Cicindela pulchra dorothea* Rumpff, *Cicindela punctulata chihuahuae* Bates, and *Cicindela viridisticta* Bates was determined from field-collected adults using different methods from those described above and detailed in Knisley and Pearson (1984). Adults of these species were fed *ad libitum* on adults and larvae of *Tribolium* sp. by dropping them into the chambers each day. Notes on oviposition in *C. denverensis*, *C. limbalis*, and *C. splendida* were obtained in another study on hybridization among these three species (Brust *et al.* 2012).

Rearing Studies. Larvae produced by field-collected adults of *C. denverensis*, *C. formosa formosa*, *C. limbalis*, *C. scutellaris scutellaris*, *C. scutellaris rugata*, *C. sexguttata*, *C. splendida*, and *C. tranquebarica tranquebarica* were fed exclusively worker and pre-alate termites. In most cases, larvae were fed by hand. The feeding apparatus consisted of a length of metal clothes hanger (ca. 15 cm long) to which a size 3 insect pin was attached with duct tape. Freshly immobilized prey could then be pierced in the thorax and held with the abdomen pointing downward. When larvae appeared at the top of the burrow, it was then relatively easy to slowly move the prey about until above them until they chose to grasp it with their mandibles, drag it into the burrow, and consume it. In some cases, a number of termites were released

into the aquaria to be captured and fed upon in a random manner.

In one part of the hybridization study, four female *C. scutellaris scutellaris* x *Cicindela scutellaris lecontei* Haldeman were crossed with three male *C. scutellaris rugata* in one aquarium, and two female *C. scutellaris rugata* were crossed with two male *C. scutellaris scutellaris* x *C. scutellaris lecontei*. The individuals were collected in spring so that they were not likely virgin; however, Knisley and Schultz (1997) have suggested that male tiger beetles may be capable of removing from females the sperm of previous males. We thus felt relatively confident that most offspring would exhibit characters of all three subspecies and this study would offer an excellent future opportunity to test this hypothesis.

In this three subspecies cross, adults were kept in the same aquarium until large numbers of first-instar burrows (>10) appeared so that the larvae would be less likely to be disturbed by the activity of the adults. The adults were then transferred to a new aquarium and the cycle continued. Notes on behavior and development time were taken. From another study, adults of *C. sexguttata* were reared from egg to adult, and notes were taken on this process.

RESULTS

Oviposition Studies. A compilation of the results of our study, work on saline tiger beetles at the University of Nebraska-Lincoln, and notes from the literature show that there is considerable variation in oviposition behavior among North American cicindelid species (Table 1). Among Nebraska saline-adapted species, *Cicindela circumscripta johnsonii* Fitch, *Cicindela nevadica lincolniana* Casey, and *Cicindela togata globicollis* Casey oviposit exclusively from the soil surface by probing the ovipositor into the soil at night (Willis 1967; Allgeier 2005), but *Cicindela fulgida fulgida* Say oviposits strictly while burrowing below the soil surface. Of the southeastern Arizona species reared in the laboratory, *C. hornii hornii*, *C. nigrocoerulea nigrocoerulea*, *C. punctulata chihuahuae*, *C. obsoleta santaclarae*, and *C. viridisticta* also oviposited only from the soil surface. Depth of egg placement was 5–10 mm for most of the species that oviposited on the surface (Table 1).

Our field observations of *C. ohlone* indicated females oviposited in the manner described by Willis (1967) (Fig. 1), the apparent norm for most *Cicindela* species. Females of *C. ohlone* produced the typical oviposition burrows with small particles of soil along the edge of the burrow created by the female ovipositor (Fig. 2). Field observations of oviposition by *C. albissima* females were like that

Table 1. Recorded oviposition behavior of North American tiger beetle species from available literature and this study. Depth is distance of egg deposition below soil surface.

Species	Oviposition behavior	Digging	Surface	Day/night	Reference
		Depth (mm)	Depth (mm)		
<i>Cicindela albissima</i>	surface and digging	50–100	6–12	day	This study
<i>Cicindela circumpecta johnsonii</i>	surface	NA	NA	night	Allgeier 2005
<i>Cicindela cursitans</i>	surface	NA	3–5	unknown	Brust and Hoback 2005
<i>Cicindela denverensis</i>	surface and digging	20–60	7–9	day	Brust et al. 2012; this study
<i>Cicindela dorsalis dorsalis</i>	surface, excavation	NA	50–80	night	Knisley and Schultz 1997
<i>Cicindela formosa formosa</i>	digging	35–60	NA	day	This study
<i>Cicindela fulgida fulgida</i>	digging	NA	NA	unknown	This study
<i>Cicindela hornii</i>	surface	NA	5–10	day	This study
<i>Cicindela limbalis</i>	surface and digging	20–60	7–9	day	Brust et al. 2012; this study
<i>Cicindela nevadica lincolniana</i>	surface	NA	NA	night	Allgeier 2005
<i>Cicindela nigrocoerulea nigrocoerulea</i>	surface	NA	5–9	day	This study
<i>Cicindela obsoleta santaclarae</i>	surface	NA	6–12	day	This study
<i>Cicindela ohlone</i>	surface	NA	5–10	day	This study
<i>Cicindela prunina</i>	surface	NA	NA	night	Spomer et al. 2008
<i>Cicindela pulchra dorothea</i>	surface and digging	90–130	6–13	day	This study
<i>Cicindela pulchra pulchra</i>	surface and digging	30–60	5–10	day	This study
<i>Cicindela punctulata chihuahuae</i>	surface	NA	5–8	day	This study
<i>Cicindela purpurea audubonii</i>	surface	NA	7–9	day	Larochelle and Lariviere 2001; this study
<i>Cicindela repanda repanda</i>	surface	NA	5–10	day	Larochelle and Lariviere 2001
<i>Cicindela scutellaris rugata</i>	digging	35–60	NA	day	This study
<i>Cicindela scutellaris scutellaris</i>	digging	35–60	NA	day	This study
<i>Cicindela sexguttata</i>	surface	NA	5–8	day	This study
<i>Cicindela splendida</i>	surface and digging	20–60	7–9	day	Brust et al. 2012; this study
<i>Cicindela togata globicollis</i>	surface	NA	NA	night	Willis 1967; Allgeier 2005
<i>Cicindela tranquebarica tranquebarica</i>	digging	20–60	NA	day	This study
<i>Cicindela viridisticta</i>	surface	NA	2–4	day	This study
<i>Tetracha virginica</i>	surface	NA	6–12	unknown	Larochelle and Lariviere 2001

in *C. ohlone*. However, we also recovered eggs from several burrows which adults dug during midday and again at night. In captivity, the females and males of some species exhibited different behaviors. In most species observed, males spent very little time digging below the surface, while females spent the majority of their time digging. The lack of oviposition holes at the surface and observation of eggs at various depths revealed that female *C. formosa*, *C. tranquebarica*, and *C. scutellaris* deposited eggs exclusively while burrowing at depths ranging from 20 to 60 mm below the surface (Table 1). Females of the closely related *C. denverensis*, *C. limbalis*, and *C. splendida*

were variable in behavior as some oviposition holes were noted on the surface, but the majority of eggs were deposited while tunneling below the surface. In such cases, the eggs appeared to be deposited in the walls of the tunnels with the tunnels then backfilled. *Cicindela pulchra* Say appeared to deposit most eggs from the surface, but some burrowing and oviposition as deep as 130 mm was noted. In such cases, a large hole was dug vertically to accommodate the female which then entered and deposited one or several eggs at the bottom of the burrow. The hole was then backfilled. In some cases, females spent a day or more in the burrow. In all of these cases,



Figs. 1–2. 1) Female *Cicindela ohlone* ovipositing. Note the abdomen is partially inserted into soil. Photo by Kevin Fielding; 2) Oviposition holes made by *C. ohlone*. Note the bits of loose soil around the holes. Photo by C. Barry Knisley.

the larvae that hatched from these eggs dug their own tunnel to the soil surface.

Exact counts of eggs were not made for most of the species, but estimates of average lifespan fecundity were around 30 to 60 eggs for *C. sexguttata* and 60 to 150 eggs for *C. scutellaris*. Direct observation of oviposition by *C. sexguttata* showed that females may deposit up to six eggs per day if well fed. Observations of patches of *C. ohlone* oviposition burrows indicated a similar daily oviposition output.

Rearing Studies. The prey used to feed both the larvae and the adults appeared to have a major impact on the lifespan of the adults. In particular, termites appeared to be an especially nutritious food, allowing females to survive much longer than their counterparts in the wild. For example, although the adult female *C. scutellaris rugata* were collected in March, they laid eggs continuously well into June. Gwiazdowski *et al.* (2011) successfully

reared several species using crickets of sizes suitable for each tiger beetle species and life stage.

A variety of behaviors was noted among larvae of the same species. Some larvae of *C. scutellaris* were seen to occasionally stash food, a behavior also observed by Leishman and Acorn (2003) for *Cicindela duodecimguttata* Dejean. In such cases, the larva would accept a hand-fed prey item and return to take another within one to two minutes. One first instar took four worker termites in less than 15 minutes. In other extreme cases, larvae would wait at the top of the burrow but would not accept food even with significant prodding. If food was then placed in the burrow, it was quickly tossed away from the burrow. In these cases, it is unknown why the larva would remain at the top of the burrow if not feeding. Observations of feeding showed that larvae will not feed if removed from the burrow. When first instars were given prey larger than themselves (worker termites), they would often macerate the prey by pushing it against the walls or bottom of the burrow while chewing with the mandibles.

We found, as did Palmer (1978), that larvae could be reared much faster in captivity than was typically required in the wild. This is no doubt the result of much greater food availability in captivity. Three adult *C. sexguttata* were obtained from eggs in less than 100 days after the date the parents were collected, and one of these reached adulthood in 79 days. Three *C. scutellaris* larvae reached the third instar within 55 days after the date the parents were collected. While mortality appeared to be relatively low in the first and second instars in captivity, it is estimated that as many as 80% of the third-instar *C. sexguttata* died prior to pupation. While the reason for this is unknown, we suspect that it is related to behavior and, potentially, diapause. Nonetheless, 22 adults were obtained from two female *C. sexguttata* within one year.

Although Gwiazdowski *et al.* (2011) found that exposing larval tiger beetles to a cool period during winter led to increased survivorship, we found that if larvae are reared to a critical minimum body mass suitable for pupation, they would pupate without having to overwinter. This suggests that flexibility exists in tiger beetle larval development, which is supported by species such as *Cicindela hirticollis* Say maturing in only 3–4 months in Virginia and Nebraska but requiring two years in Illinois (Shelford 1908).

Our results correlate well with those of Pearson and Knisley (1985) and Knisley and Juliano (1988) who found that food was a limiting resource for larvae. Our results additionally suggest that the time required for the completion of the larval stage is likely related to food availability. While our methodology for rearing differs from that of

Palmer (1979) who used Pyrex[®] tubes for individual larvae, we obtained excellent results from our rearing protocols. However, we found that most species with which we worked oviposited readily in captivity. Nevertheless, we were unable to obtain eggs from *Amblycheila cylindriformis* Say or *Cicindela nebraskana* Casey. Although our method maintains soil moisture for prolonged periods through the benefit of a large soil mass, cannibalism among larvae undoubtedly occurs. Under high density conditions, fishing out some larvae with a grass blade and transferring them to a new container appeared to reduce the effects of cannibalism.

The large number of eggs that can be obtained under heavy feeding regimes in captivity suggests that captive rearing programs for rare tiger beetle species and subspecies have great potential for success. However, based on our results of high third-instar mortality, we advise that if captive release programs are used for rare species in the future, optimum results are most likely by releasing well-fed second instars into natural habitats.

The method of hand-feeding offered some unique advantages for study. In particular, we could more accurately estimate the amount of food required to pass from one instar to the next. We estimate, for example, that *C. scutellaris* larvae required an average of 4–6 mature worker termites to molt to the second instar. However, this method may not work for species that are unusually skittish in the larval stage. Using this feeding method to rear *C. circumpecta johnsonii* from first to second instar resulted in the starvation of all larvae.

Gwiazdowski *et al.* (2011) provided further detailed information on tiger beetle rearing. Our method of rearing in small aquaria showed limitations that led to increased cannibalism, most likely because third instars were unable to dig to the depths they would in nature, resulting in burrows that occasionally intersected along the bottom of the aquaria. This suggests that rearing tubes have the advantage of minimizing cannibalism and potentially limiting the spread of disease (Gwiazdowski *et al.* 2011).

DISCUSSION

Our results show that, contrary to recent literature reviews (*e.g.*, Pearson 1988; Pearson and Vogler 2001), some North American tiger beetle species do not oviposit from above the soil surface by inserting the ovipositor into the soil. Our study suggests that these differences in oviposition behavior may be related at least in part to the soil characteristics and habitat of the species. Four of the species oviposited exclusively while tunneling beneath the soil surface and three

other species deposited the majority of their eggs by this means. Two of the species that oviposited exclusively underground were associated with dry sandy habitats (*C. formosa* and *C. scutellaris*) (Knisley and Schultz 1997; Pearson *et al.* 2006), one was found in slightly moist sandy habitats (*C. tranquebarica*) (Knisley 1984; Kippenhan 1994; Knisley and Schultz 1997; Pearson *et al.* 2006), and one was from moderately dry saline habitats (*C. fulgida*) (Pearson *et al.* 2006). Three of the six taxa that oviposited both from the surface and underground were from dry chalky or silty soils (*C. pulchra dorothea* and *C. pulchra pulchra*) or sand dunes (*C. albissima*). The other three species (*C. denverensis*, *C. limbalis*, and *C. splendida*) occur on clay or loess soils, often on steep slopes. In addition, all eight of the species observed to oviposit while tunneling were spring-fall species.

The oviposition behavior and associated depths at which eggs are deposited is likely to be related to the depth of soil moisture; however, this remains to be formally tested. Upland sand species such as *C. formosa* and *C. scutellaris* consistently oviposited in excess of 30 mm in depth. *Cicindela tranquebarica*, which prefers somewhat moister sandy habitats, also oviposited exclusively while burrowing but at a shallower depth. With the exception of *C. purpurea*, all species which we found ovipositing exclusively from the surface occur in comparatively moist habitats (Pearson *et al.* 2006). Several of these species appear to mitigate the effects of extreme temperatures by ovipositing at night (Allgeier 2005). It is unknown why *C. purpurea* and *C. ohlone* oviposit strictly on the surface, but it might be related to their habit of ovipositing in heavy soils, which retain moisture near the surface for longer periods than light, sandy soils. In many areas of the western United States, *C. purpurea* tends to be more active after rains and when soil surface is moist. *Cicindela ohlone*, a species closely related to *C. purpurea*, is active during the rainy season along the central California coast and oviposits on the surface of wet clay soils in their grassland habitat.

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(Received 28 October 2011; accepted 12 September 2012.
Publication date 20 December 2012.)