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Movement of *Cicindela hirticollis* Say Larvae in Response to Moisture and Flooding

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Abstract

The larvae of the tiger beetle, *Cicindela hirticollis* Say, inhabit sandy shoreline areas that flood periodically. This species has declined over much of its range and at least one subspecies is near extinction, possibly as a result of human alteration of waterways. In addition to physiological tolerance for anoxia, the larvae have physical and behavioral adaptations to avoid drowning. We hypothesized that *C. hirticollis* larvae would exhibit behavioral responses to soil moisture change and flooding because, unlike most other tiger beetles, they frequently relocate their burrows. Our laboratory studies demonstrated that larvae select surface soil moisture levels of 7–50% saturation in which to dig new burrows. Within 96 h of immersion, most larvae abandon burrows and larvae do not form new burrows in darkness. Larvae may relocate when flooded, suggesting a previously undocumented mechanism for dispersal; however, dams often eliminate suitable habitat areas downstream, suggesting that this behavior may be detrimental in riverine populations. Because larvae move during daylight hours, they also are likely to suffer mortality from trampling due to human recreational activity.

Keywords: tiger beetle, flooding, behavior, conservation

Introduction

The larval stages of most tiger beetle species are soil-dwelling, long-lived, and sedentary (Knisley and Hill, 1992; Pearson and Vogler, 2001). Females are specific in choosing oviposition sites (Knisley and Schultz, 1997; Hoback *et al.*, 2000a,b), and the larvae of most species spend their entire life in the same location, enlarging the diameter and depth of the burrow with each of three successive instars (Knisley and Pearson, 1984; Knisley and Schultz, 1997; Pearson and Vogler, 2001). Habitats used by tiger beetles in the temperate zones typically have areas that are sparsely vegetated or devoid of vegetation. Such habitats include stream and pond edges, dunes and blowouts, seashores, salt flats, and open areas in grasslands (Pearson, 1988; Laroche and Lariviere, 2001). Larvae often co-occur with adults (Knisley and Schultz, 1997), but in some cases the two life-stages occur in different microhabitats (Knisley and Pearson, 1984).

Because they are adapted to specific environments, many tiger beetle species are sensitive to habitat changes and may be especially vulnerable to the effects of hydrologic change or excessive disturbance. Several water-edge tiger beetle species have experienced sharp declines in both abundance and distribution over the past century (Nagano, 1980; Shook, 1981; Knisley and Schultz, 1997; Laroche and Lariviere, 2001). The most geographically widespread of these declining species is *Cicindela hirticollis* Say (Laroche and Lariviere, 2001).

Cicindela hirticollis occurs across much of North America with populations found along rivers, large lakes, and seashores from Florida to California north to Labrador, the southern edge of Nunavut, and British Columbia. Despite its broad range, it is apparently lacking from the Great Basin and much of the Appalachian region. The regions where *C. hirticollis* does not occur either lack permanent streams or the streams tend to be of high gradient and lack the soft sandy substrates utilized by this species (Graves *et al.*, 1988).

Of the eleven subspecies of *C. hirticollis* currently recognized, at least three have decreased dramatically in the last 30 years (Nagano, 1980; Dunn, 1981; Graves *et al.*, 1988; Laroche and Lariviere, 2001; Knisley, 2003). Human-induced changes, including hydrologic alterations, dams, and compaction from human activity, are believed to be the primary cause of the decline. Beach trampling was apparently responsible for the decline of two subspecies (Nagano, 1980; Dunn, 1981). *Cicindela hirticollis gravida* LeConte is extinct over most of its former range in the southern half of California (Nagano, 1980). *Cicindela hirticollis rhodensis* Calder is threatened in much of its former range in New England (Dunn, 1981; Laroche and Lariviere, 2001) and has disappeared from many historic sites near the Great Lakes. This beetle

has been eliminated from heavily used state parks on the western shoreline of Lake Michigan (M. L. Brust, unpublished).

Unlike most other tiger beetle species, the larvae of *Cicindela hirticollis* relocate their burrows and are often observed crawling on the sand surface (Shelford, 1908; Knisley and Schultz, 1997). Although the reasons for this movement are not clearly understood, Shelford (1908) found that *C. hirticollis* larvae would abandon old burrows and dig new ones in response to slight changes in soil moisture. Disturbance of habitat can change moisture gradients within the soil, leading to larval desiccation, and may trigger relocation (Wilson, 1970; Stamatov, 1972; Nagano, 1980; Schultz, 1988; Knisley and Hill, 1992). Shelford (1908) found that movement exposed larvae to mortality from diurnal predators. Although larvae are often observed moving during the day (Knisley and Schultz, 1997), we suspect that larvae also relocate at night, when risks of predation and desiccation are lower.

Our recent studies have demonstrated *C. hirticollis* larvae have poor immersion tolerance (Brust *et al.*, 2005). We hypothesized that larvae may exhibit behavioral responses that increase survival in frequently flooded water edge habitats. To test this and to determine if larvae use moisture cues to select new burrow locations, we conducted laboratory experiments and made field observations of larval habitat. We also determined whether flooded larvae move in light and darkness.

Materials and Methods

Organisms for Laboratory Tests

Our laboratory experiments used larvae of *Cicindela hirticollis hirticollis* Say that were collected along the Chesapeake Bay, from Northampton County, Virginia, 6 km NNE of Reedville. This subspecies was chosen because larvae are abundant and widespread, occurring both on the coast and along eastern rivers and lakes. Information in the literature (Graves *et al.*, 1988) and our experience indicates that all subspecies of *C. hirticollis* are similar in biology and behavior. Larvae were collected in July, August, and September of 2003 by waiting for larvae to appear at the top of the burrow and then using a trowel to block larval retreat.

Selection of Burrow Location

To quantify larval selection of habitats with different soil moistures, three arrays of four 13.2-L aquaria (3.5 gallon) were connected along two of their

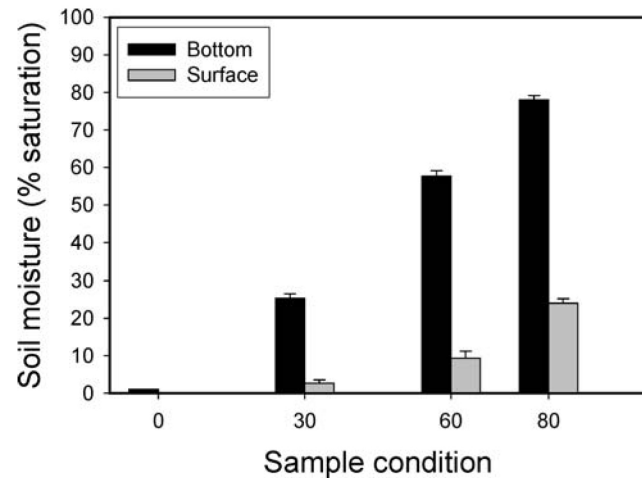


Figure 1. Mean (\pm standard error) soil moisture (%) at the bottom and surface of experimental arrays used to test larval burrow selection.

sides with duct-tape. A plastic barrier was secured around the top of each array to prevent escape by larvae. Each aquarium was filled with sand until the sand was flush with the top. As each was filled, an Aquapro™ sample tube was placed in the center of the aquarium so that soil moisture could be measured throughout the soil column. With the soil moisture probe in the tube, water was added until one of four pre-assigned moisture levels (0, 30, 60, and 80% saturation) was achieved at the bottom. Soil moisture was recorded at the bottom and top of each aquarium (Figure 1). The arrays were then allowed to stabilize for 1 day and moisture levels were re-measured before larvae were introduced. The arrays were kept in the laboratory at room temperature (measured at 21.5°C).

Individual third instars were placed on an 8 by 8 cm card in the middle of the array (overlapping the edge of all four aquaria). The procedure was repeated after each larva left the note card until 12 larvae were released in each array. The larvae were allowed 24 h to dig a burrow in their desired location, and the number selecting each moisture level was recorded.

Larval Response to Flooding

To test larval responses to flooding, water was first added to the dry (0%) aquarium in each array to produce 60% soil moisture. After waiting 24 h to test for larval dispersal from existing burrows (as control), the 60 and 80%

soil moisture aquaria containing *C. hirticollis* larvae were flooded to 100% saturation (standing water). Larvae that emerged from flooded burrows could then choose between the original 30% saturated aquarium or the new 60% saturated aquarium, and we recorded new burrow locations after 24, 48, and 72 h. Data were analyzed with analysis of variance followed by a Bonferroni test to separate means.

In a second test, sand was added to 7.5-L (2 gallon) plastic containers (32.5 cm long \times 20.3 cm wide \times 20.3 cm high) to simulate a sloped beach, with depths from 2.5 cm at one end to 20 cm at the other end. The sand was then thoroughly wetted. Four third instars were placed individually on the sand in a row across a line where it was 15 cm deep and covered with a vial until they dug a burrow. The test was replicated ten times, and chambers were kept in the laboratory at room temperature. For each replicate, a new set of four larvae was used. After 5 days of acclimation to burrows and one to two feedings, the trial was begun by adding brackish water from the Chesapeake Bay to cover the sand in the chambers on the following schedule: one-third of sand covered at 0800 h; two-thirds of sand covered at 1000 h; and sand completely covered at 1200 h. After the sand was completely covered, larval activity was recorded at 12, 24, 36, 48, 60, 72, and 96 h. Visible larvae were recorded as out of the burrow and then categorized as floating, sunk, or dead.

Effect of Light on Post-Flooding Larval Activity

The effects of light on movement and burrowing behavior were tested by connecting two 1.25-L plastic containers side by side with duct tape and creating a barrier around the two connected containers by folding the duct tape over itself. The area connecting the two containers was left without a barrier. Four of these two-container arrays were created. Sand was added to each container until it was flush with the top. In each array, one container was left dry, while water was added to the other to approximately 50% soil moisture. The containers were allowed to stabilize for 24 h. After 24 h, a cardboard barrier was inserted between the two connected containers. Six third instars were then released one by one into the moist container. Approximately 5 min were allowed between releases to minimize cannibalism and no more than four larvae were allowed to be searching for a larval burrow location at one time.

Once all larvae had established burrows, the cardboard barrier was removed and water was added to the previously dry container until soil moisture reached approximately 50%. Two arrays were placed in a lighted envi-

ronmental chamber at 16.5°C and two were placed in a dark environmental chamber at 16.5°C. The room containing the unlighted environmental chamber was also unlit. In each replication, the orientation of the two arrays was opposite and both were placed along the same wall of the environmental chamber to reduce potential uncontrolled variables. The arrays were checked after 24 h to ensure that no larval movement had occurred prior to flooding of established burrows. The container with established larvae was then flooded until standing water was present, and the arrays were placed back in the environmental chambers in their original orientation. The arrays were checked at 2, 4, 6, 8, 10, 20, 26, and 30 h for movement of larvae and establishment of new larval burrows in the container that was not flooded.

Results

Selection of Burrow Location

In the experiment to test habitat selection based on soil moisture, 28 of 36 larvae dug burrows. The remaining larvae were cannibalized or apparently drowned. The majority of larvae were observed circling the treatment arrays numerous times before choosing a site, and thus most larvae experienced every test condition. Compared to moister conditions, larvae avoided the 0% (dry) and 30% soil moisture conditions (ANOVA, $P < 0.05$). Approximately equal numbers of larvae established burrows in the 60% soil moisture ($N=13$), and 80% soil moisture ($N=15$) conditions and there were no significant differences ($P=0.67$). Larvae presumably chose burrow locations based on surface moisture content, which related to subsurface moisture (Figure 1). As they sought locations to dig burrows, larvae encountered all conditions; however, no larva probed the surface or attempted to dig a burrow in the 0% or 30% treatments. When the dry condition (0% soil moisture) was increased to 60% soil moisture, none of the larvae in the other conditions moved during the 24-h observation period prior to immersion of established burrows.

Larval Response to Flooding

Upon flooding, larvae (24 of 28) moved to the new 60% saturated treatment. Four larvae drowned and were recovered after the experiment. All surviving larvae established new burrows within 72 h. In the second test, which simulated flooded beach conditions, larvae gradually left flooded burrows. Within 12 h, 25% had left flooded burrows, and all had emerged within 96 h

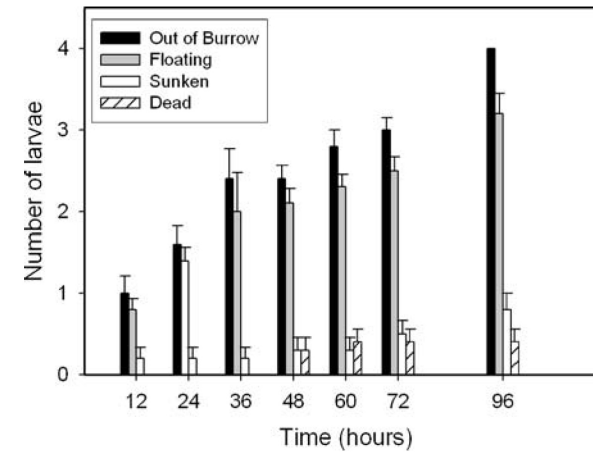


Figure 2. Activity of third instars under simulated flooded beach conditions. Bars represent mean (\pm standard error) number of larvae exhibiting each activity (10 replicates).

(Figure 2). Because no dry habitat was available in the chambers, larvae could not escape, and floating larvae gradually sank. Approximately 12% of these larvae were dead after 96 h.

Effect of Light on Post-Flooding Larval Activity

No movement occurred during the 24-h period prior to flooding of the established burrows in the two-container arrays. Thirty hours post-flooding, 9 of 12 larvae under lighted conditions left the flooded container and established new burrows, whereas none of the larvae under dark conditions dug burrows. During the first three observation periods, larvae under dark conditions were noted crawling on the sand of the 50% moisture condition, but at later times all visible larvae were floating in the flooded containers. Under lighted conditions, all larvae observed crawling on the moist sand had established new burrows within 10 h (Figure 3).

Discussion

The females of most tiger beetle species are specific in choosing oviposition sites (Hoback *et al.*, 2000a,b), and larvae of most other species spend their entire larval development at this site (Knisley and Pearson, 1984; Pear-

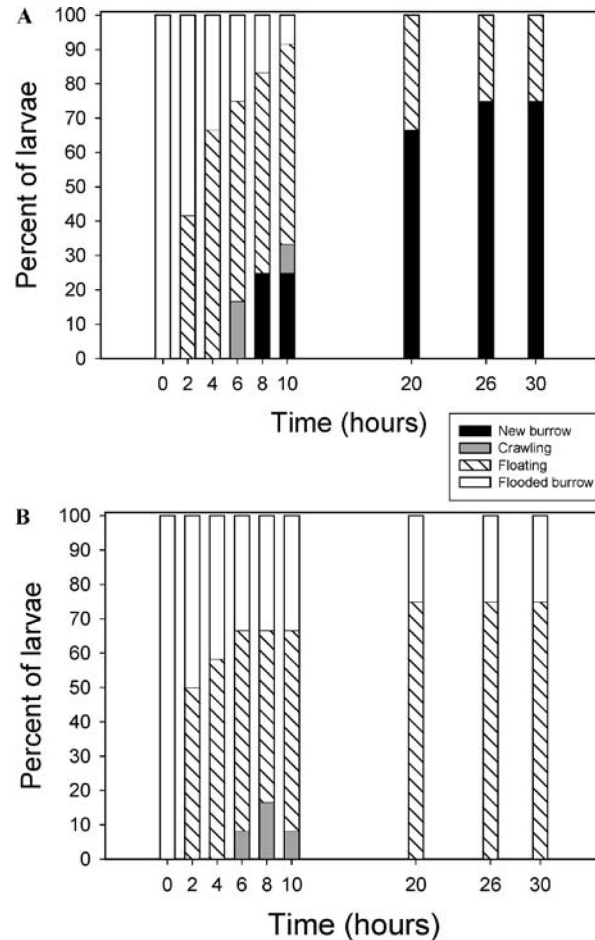


Figure 3. Response of larvae to flooding in light (A) and dark (B) conditions. Bars represent percent of total larvae ($N=12$ per condition; 2 replicates).

son and Vogler, 2001). While the adult female *C. hirticollis* selects the initial larval habitat by her selection of an oviposition site, the larvae move in response to drying (Shelford, 1980), immersion, or other factors. This study suggests that third instar *C. hirticollis* can also select burrow location based on soil moisture. Larvae did not establish new burrows in the dark; however, we observed larvae crawling on the moist sand in the dark during the experiment, which indicated that they initially escaped immersion (Figure 3). These

results suggest that the larvae cannot determine their location in relation to surface water under dark conditions. As this experiment was conducted in small containers, the larvae were unable to crawl in a single direction for any significant distance, whereas under natural conditions it might be possible for larvae to move in one direction, perhaps using a surface gradient to select a burrow location and avoid standing water. It is likely that populations of *C. hirticollis* vary in movement depending on the stability of the local environment. For example, field observations of *Cicindela hirticollis* grava during a 36-h period at Limantour Point in Point Reyes National Seashore, Marin County, California, found no larval movement among 83 marked larval burrows (Brust, 2004). However, the larvae at this site occur in a protected area and despite unusually high tides during the observation period, larvae were not flooded. Moreover, the depths to the water table remained fairly constant (Brust, 2004) and were nearly identical to those found by Wilson (1967) for burrows along Lake Michigan ranging between 20 and 30 cm below the soil surface. The specificity in selecting these locations suggests that larvae require a narrow range of soil moisture.

Presumably, the population of *C. hirticollis* at Point Reyes is likely to relocate burrows only during stormy spring conditions which produce local flooding. Larvae from other populations, in sites where water levels fluctuate, are frequently seen changing burrow locations. At shoreline sites along the Chesapeake Bay, which have less protected habitat than at Point Reyes, *C. hirticollis* larvae are frequently seen crawling on the sand surface, often moving toward the back beach (Knisley and Schultz, 1997). Brust (pers. obs.) has also collected *C. hirticollis* larvae while pitfall trapping in the general vicinity of larval burrows along the Platte River in Nebraska.

Our studies suggest that larvae select burrow locations that have at least 30% soil moisture (7% surface moisture [Figure 1]). The reason larvae select wetter surface soils is unknown but it may be to avoid difficulties associated with digging in loose, dry sand. To form a burrow slightly larger than the pronotal diameter, some soil moisture is necessary for cohesion of soil particles and to prevent collapse of the burrow walls. Moreover, dry sand may abrade soft-bodied larvae, which could lead to desiccation.

During the trials in which water was added to top of the soil, all burrows collapsed when flooded and most larvae wriggled through the sand and floated to the water surface. In trials where non-flooded substrate was available, larvae managed to reach drier sand by bending and flipping their bodies until they reached the edge of the flooded sand. In natural riverine situations, larvae that leave burrows would be carried to a new location downstream. Thus, under natural conditions, flooding may serve as a dispersal mecha-

nism for larvae of *C. hirticollis* by transporting them downstream in rivers or downwind in lake settings. This mode of dispersal has not been previously proposed for tiger beetle larvae, and it has long been assumed that tiger beetle dispersal occurred only during the adult stage (Pearson and Vogler, 2001).

In unaltered river systems in which sandbars move and new suitable habitat becomes exposed on a regular basis, such a mode of larval dispersal might be beneficial. If flooding moves larvae downstream, then adult *C. hirticollis* may fly upstream during dispersal flights. Such upstream dispersal of aquatic macroinvertebrates has long been known (Roos, 1957; Hershey *et al.*, 1993; Williams and Williams, 1993).

Most large rivers have been altered by dams and flooding regimes have changed, often leading to prolonged periods of high and low water in downstream areas. This results in the encroachment and succession of vegetation to the high water mark (Baxter, 1977; Knisley, 2003) and reduces the amount of suitable habitat available to water-edge tiger beetle species. Dispersal during flooding events may cause larval mortality where anthropogenic changes to rivers have eliminated appropriate habitat. In such a situation, most larvae that wriggle free of the burrow and wash downstream probably die as a result of predation or desiccation while searching for suitable habitat. As a result, populations in such areas would likely decline with each flooding episode.

Thus, dispersal behavior may have contributed to the decline of *C. hirticollis abrupta* in the Sacramento River system in California. This subspecies once occurred in five limited areas within approximately 8,000 km² on the Sacramento and Feather Rivers in central California (Knisley and Schultz, 1997), and its recent dramatic decline in distribution and abundance is believed to be the result of habitat changes associated with the Oroville and Shasta Dams (Knisley, 2003). This subspecies has not been found since 1984 (Knisley, pers. obs.). Dams are also believed to have caused the decline of *Cicindela columbica* Hatch in the Pacific Northwest (Beer, 1971; Shook, 1981), although the behavioral responses to flooding in this species are unknown.

The simulated flooded beach conditions yielded similar results to the soil moisture experiment. Both experiments resulted in some larval death after prolonged exposure to immersion. This suggests that larvae respond to flooding by escaping flooded areas, perhaps to compensate for low immersion survival (Brust *et al.*, 2005). Other species which inhabit salt flats exposed to static water (Hoback *et al.*, 1998) survive immersion in hypoxic water by switching to anaerobic metabolism (Hoback *et al.*, 2000a). Tropical species which inhabit the Amazon River basin exhibit alternative adaptations to survive long periods of immersion including aquatic respiration, extreme tolerance of anoxia, and rapid development to the adult stage (Zerm

and Adis, 2002; Zerm and Adis, 2004; Zerm *et al.*, 2004). It is likely that the Amazonian species cannot use similar behavioral strategies as *C. hirticollis* because of the magnitude of water level changes associated with the Amazon River, the length of the rainy season, and the duration of flooding (exceeding 6 months in some areas).

Other tiger beetle species, such as *C. repanda*, occur in similar habitats in North America but have not experienced the severe population declines recorded for *C. hirticollis*. Its unusually frequent larval movement in response to desiccation and immersion may make *C. hirticollis* particularly vulnerable to habitat changes. Such behavior seems to risk predation and desiccation, particularly during daylight hours, and our behavioral studies indicate that larvae require light for burrow re-establishment (Figure 3). While nocturnal movement might result in long-term exposure to nocturnal predators, daytime movement could expose *C. hirticollis* to greater risk of trampling on beaches used by humans, as recreational activities are more likely to occur during daylight hours. Thus, this species could be especially susceptible to human impacts through flooding on altered rivers and recreational use of shoreline beaches.

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