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# Divergent oviposition behaviors in a desert vs a marsh grasshopper

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## Abstract

Comparing closely related species from disparate habitats can uncover habitat-specific adaptations. We compared 32 environment and oviposition characteristics in two closely related grasshoppers from opposite environments: *Romalea microptera* from the Florida Everglades wetlands vs *Taeniopoda eques* from the Chihuahuan Desert. These closely related species can interbreed, but differ in oviposition characteristics. Desert *T. eques* deposited long, straight, deep pods containing more eggs, and tended to lay within vegetation where they were shaded and hidden from predators. They did not oviposit in the early morning, late afternoon or evening, and males did not mate-guard. In contrast, wetlands-inhabiting *R. microptera* laid smaller pods closer to the soil surface, and often laid exposed to full sunlight on elevated ground away from water and nearby vegetation, in the morning or even after dark, and were usually mate-guarded. Oviposition phenology also differed, with *R. microptera* ovipositing in the summer and *T. eques* in the fall, possibly as a consequence of life-history shifts driven by local seasonal rainfall patterns. Our results suggest rapid trait divergence in these sister species. These divergent behaviors appear to be adaptive, given the divergent (desert vs wetland) environments of these species.

## Key words

Romaleidea, Acrididae, Chihuahuan desert, Everglades, oviposition, egg, egg pod, grasshopper, lubber, *Taeniopoda*, *Romalea*, mate-guarding, clutch size, thermoregulation

## Introduction

Some of the best evidence for the adaptive significance of traits comes from comparing closely related species living in disparate environments (Endler 1986). This is because similar species should normally possess similar traits. Therefore, the discovery of dissimilar traits in closely related species, especially when the divergent traits clearly aid survival in their respective habitats, suggests the action of environment-specific selective forces and rapid trait-specific evolution (Futuyma 1998). Searching for divergent traits among closely related allopatric species can uncover the specific mechanisms that allow survival in divergent environments.

Examples among the Orthoptera of divergent adaptive trait evolution among related taxa include natatorial (spatulate) hind tibiae in marsh-inhabiting grasshoppers, but not in related terrestrial grasshoppers (de Zolessi 1956, Carbonell 1959, Uvarov 1977); serrated ovipositor valves in plant-ovipositing grasshoppers, but not in related soil-ovipositing species (Braker 1989, Stauffer & Whitman 1997); raptorial (spinose) legs in carnivorous, but not herbivorous tettigoniids (Whitman *et al.* 1994, Rentz 1996); expanded tarsi in sand-inhabiting crickets, but not rock-inhabiting

crickets (Irish 1986); elongate bodies in grass-feeding grasshoppers (Uvarov 1977); and higher metabolism in Orthoptera from cold or short-season habitats (Hadley & Massion 1985, Dingle *et al.* 1990, Fielding 2004).

In this paper, we compare the oviposition behavior and ecology of two closely related species of grasshopper that live in divergent habitats, and ask if the divergent behaviors could be adaptive. The Western Lubber Grasshopper, *Taeniopoda eques* (Burmeister), survives in the dry Chihuahuan Desert of northern Mexico and southwest USA (Rehn & Grant 1961, Whitman & Orsak 1985), whereas its close relative, the Eastern Lubber Grasshopper, *Romalea microptera* (Beauvois), inhabits the southeastern USA (Hebard 1925a). Some populations of *R. microptera* reside in or adjacent to seasonally flooded freshwater marshes of the Everglades area of south Florida (Rehn & Grant 1961, Capinera *et al.* 2004).

Rehn and Grant (1961) hypothesized that the *Taeniopoda* group evolved in Central America, where most of the 11 species of *Taeniopoda* reside (Hebard 1925b). They posited that in pre-Pleistocene times, an ancestor of both *T. eques* and *R. microptera* dispersed into northern Mexico and eastward across the southern USA as far as Florida. Subsequent Pleistocene glaciations isolated the Florida and Mexico populations, facilitating the speciation of monotypic *R. microptera* in the Florida peninsula. Postglacial warming then allowed the two species to migrate to their present allopatric ranges (Rehn & Grant 1961). Dispersal was undoubtedly a long process, because females of neither species fly, and must disperse via walking. In addition, *R. microptera* are good swimmers and it is possible that some translocation occurred via water or hurricanes.

Although *T. eques* and *R. microptera* are currently placed in different genera, this is probably an error that does not represent their true systematic relationship (Whitman unpub.). The two species are strikingly similar, and quite dissimilar to all other American grasshoppers. The nymphs are nearly indistinguishable, with similar orange, yellow, or red stripes on a black background (Hebard 1925a). Both species aggregate as early nymphs, roost at night, and are flightless and polyphagous, but favor liliaceous food plants (Whitman & Orsak 1985; Whitman 1988, 1990). Both species are aposematically colored and chemically defended with a metathoracic tracheal defense gland, and are the only grasshoppers known to possess this unique structure (Whitman *et al.* 1985, 1991). The most convincing evidence for their close relatedness is that the two species can mate and produce viable hybrids in the laboratory (Whitman unpub.).

In contrast to their similarities, these two species live in dissimilar environments. The Chihuahuan Desert of northern Mexico and

southwestern USA, is characterized by low annual precipitation ( $\sim 31$  cm/y), and low soil moisture (Brown 1982, NOAA). The sparse rains come in winter and fall, with a hot summer drought. Chihuahuan Desert vegetation consists of sparse, drought-resistant shrubs, grasses, and desert annuals (Fig. 1a, Pl. VI), and soils are exposed to intense solar heating that fosters soil desiccation (Brown 1982). Southern New Mexico and Arizona, the northern-most extension of *T. eques*, shows great seasonal temperature variation. During the summer, soil surfaces can reach  $69^{\circ}\text{C}$  and 0.02% moisture, which is lethal to grasshopper eggs (Chladny & Whitman 1998, Thoma *et al.* 2006, S. Moran, pers. com.), and winter soil surfaces fall below freezing (Whitman 1987, NOAA).

In contrast, *R. microptera* ranges across the humid southeastern USA, from the southern tip of Florida, north to South Carolina, and west to east-central Texas (Hebard 1925a, Rehn & Grant 1961). In south Florida, *R. microptera* is found in and adjacent to the Everglades, a humid, subtropical environment that is the antithesis of the Chihuahuan Desert. The Everglades area experiences high precipitation ( $\sim 135$  cm/y), as well as high and fluctuating water tables and soil surface moisture levels (Chen & Gerber 1990, Lodge, 2005). Much of the Everglades area floods during the summer rainy season, and in some locations *R. microptera* are semi-aquatic, existing in seasonally flooded marshes on emergent vegetation. South Florida contains numerous plant communities (Myers & Ewel 1990, Lodge 2005), but vegetation (Fig. 1b, Pl. VI) tends to be more lush than in the Chihuahuan Desert, and the soil often remains wet and shaded from solar radiation. Annual temperature variation is relatively narrow, and the soil never freezes (Chen & Gerber 1990, NOAA).

In southern New Mexico, *T. eques* oviposits in the fall (September and October). The eggs hibernate through the cold winter, and aestivate through the hot and dry spring and early summer. They

hatch in July, in conjunction with the beginning of the late-summer rainy season (Whitman & Orsak 1985). In contrast, the eggs of *R. microptera* from the Everglades Nation Park of south FL, are laid in the summer (June-August), hibernate through the mild Florida winter, and hatch between early February and late March, just before the beginning of the Florida rainy season. Unlike *T. eques*, the eggs of *R. microptera* are not subjected to extreme drought or freezing temperatures, but can experience prolonged flooding.

The two species also face different predator loads. The Chihuahuan Desert contains substantially more predatory ants (Johnson 1996, Deyrup 2003), grasshopper egg predators (Rees 1973), and crepuscular and nocturnal grasshopper predators, including insectivorous mammals, desert toads, giant centipedes, tarantulas, *etc.* (Hoffmeister 1986, Lowe 1980, Lodge 2005). Adult lubbers are generally immune from diurnal predators, because potent toxins deter birds and reptiles, and large size (up to 16 g) deters most invertebrate predators (Whitman & Orsak 1985; Whitman 1987, 1988, 1990; Yosef & Whitman 1992). Some nocturnal predators will take them, but lubbers escape crepuscular and nocturnal predators by roosting at night at the tops of bushes (Whitman 1987).

Finally, the two species exhibit different sexual behaviors. Male *T. eques* copulate  $\sim 14$  h in the field and up to 5 d in the lab, and then dismount (Whitman & Orsak 1985), whereas *R. microptera* copulate for shorter periods (3 to 10 h), and then the male mate-guards for up to 5 d, or until the female oviposits (Huizenga *et al.* in process). During mate-guarding, the male rides on the female's back and drives away competing males.

In this paper, we compare a desert population and a wetlands population of two closely related grasshopper species. We demonstrate differences in oviposition behavior and ecology, and then ask if these differences provide fitness benefits in their respective habitats, in which case they may represent adaptations. We hypothesize that

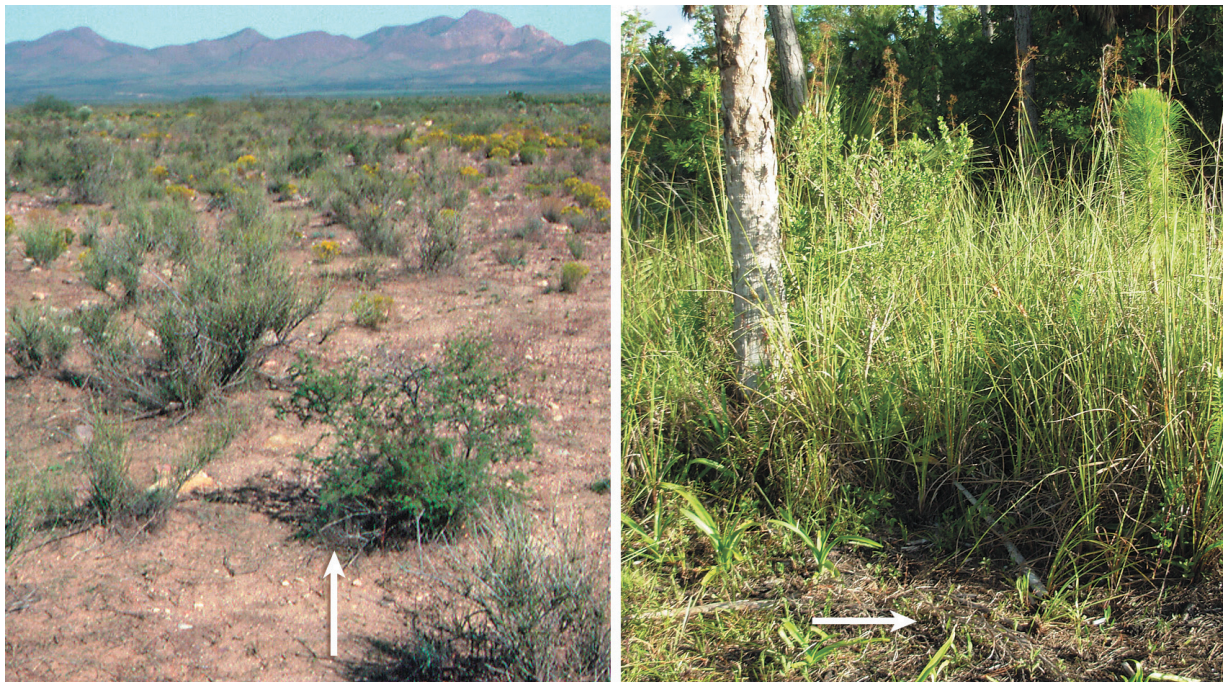


Fig. 1. a) Chihuahuan Desert brushland, showing bare ground interspersed with isolated bushes. *Taeniopoda eques* tends to oviposit among low grasses and annuals that grow near the base of bushes (see arrow), where they are visually hidden and shaded. b) *Romalea microptera* from the Florida Everglades prefers to oviposit in sunlight, away from thick vegetation (see arrow), and where they are visually exposed (Photos by Kevin Kocot). See also PLATE VI.

each species will exhibit a distinct set of ovipositional characteristics that matches their particular habitat. Comparative studies of this type can illuminate possible adaptive traits and help us understand the specific mechanisms that allow organisms to survive in different environments (Thornhill & Alcock 1983, Endler 1986).

## Methods

Lubbers are ideal for this type of study because adult females are large (2 to 16 g, 4 to 8 cm) and conspicuous (yellow, orange, and black), and thus easy to locate (Rehn & Grant 1961, Whitman 1990). Also, they are flightless, sluggish, occur in high densities, and are relatively unresponsive to human presence, traits common to insects expressing a chemical defense syndrome (Whitman *et al.* 1985, 1990; Whitman 1990; Lamb *et al.* 1999).

*Taeniopoda eques* was studied from before sunrise to after sunset near Rodeo NM, on September 21-24, 2001, in a sparse desert brushland (Fig. 1, Pl. VI) containing scattered *Acacia*, *Mimosa*, *Gutierrezia*, *Ephedra*, and *Prosopis* bushes of various sizes (Whitman & Orsak 1985). The highly permeable inorganic soils were dry and consisted of silt loose to compacted, sand, gravel, and/or rock. The site was flat (< 2° slope), although soils tended to mound up at the bases of bushes and as a few kangaroo-rat mounds. Rocks and occasional dead branches covered the ground. Population density at this site was ~11 lubbers/100 m<sup>2</sup>.

*Romalea microptera* was studied twice in 2005. In each case, we surveyed from sunrise until after sunset. Both sites were chosen, in part, because of the diversity of microhabitats, which included open bare ground, dense shady grasses and weeds, dense shady bushes and low trees, flooded marsh, flooded swamp, moist soil transitions between flooded and nonflooded areas, and elevated drier soils. We undertook the first study June 11, 2005, at Trail Lakes Campground, 3 km east-southeast of Ochopee, FL. This site consisted of ~12 ha of inorganic, permeable limestone gravel, sand, and small amounts of sandy loam, elevated ~0.75 m above the surrounding wetlands. However, we restricted our survey to just three of the 30 acres. Vegetation consisted of various ornamental trees, shrubs, herbs, and lawns, surrounded by and interspersed with natural vegetation. The site included gravel roads, small ponds, and mobile homes. This area was surrounded on three sides by relatively undisturbed seasonally flooded marsh, with scattered willow swamp, cypress, wax myrtle, and elevated pine woods. Lubber density was ~18/100 m<sup>2</sup>.

The second study, on July 31, 2005 was 20 km north of Cope land, FL, and consisted of 0.08 ha of irregular ground, averaging 1.5 m elevation above the surrounding seasonally flooded wetland, which contained dense, rank vegetation, including sawgrass, *Ludwigia*, *Phragmites*, cattail, scattered willow, and other wetland species. Soils consisted primarily of crushed limestone gravel, with patches of shallow inorganic, permeable sand or sandy loam. Grasshopper density was 33/100 m<sup>2</sup>.

For all three studies, we walked through the site every 10 to 35 min from dawn until a few hours after sunset, in order to locate ovipositing females. Transit times through the site depended on the number of females ovipositing, and were shorter when few females were laying. We specifically attempted to survey each area of our plots equally, so as not to bias our sampling (*e.g.*, not to over-sample open areas *vs* dense vegetation, or sandy *vs* gravelly substrates, *etc.*). When a female began exhibiting oviposition behavior or was discovered already laying, we marked the site with a flag and recorded time of day, habitat type, percent of female body in sunlight, shaded air temperature at 1 m, soil-surface temperature

next to the female (under identical sun/shade conditions as the female), the most recent rain, and the percentage of the sky covered by clouds. Temperatures were recorded using a Sensortec™ BAT-12 thermometer equipped with a needle-probe thermocouple. During temperature measurements the thermocouple was shaded.

Once a female was confirmed to be laying, as opposed to simply probing (based on persistence and depth of abdomen in the soil), we noted the time to complete laying, the type, height, density, and distance of surrounding vegetation, whether or not the female was under a bush or tree (*i.e.*, within the drip line), and recorded site topography (slope, smooth *vs* rough ground), if the female laid against a stem, branch, rock, fence, *etc.*, and any conspecific (mate guarding, group oviposition, or cannibalism) or allospecific (predator) interactions. For possible group oviposition, we recorded the number of females that chose to lay within 1 m of another ovipositing female. We also measured exposure (open to view or hidden amongst vegetation). This was determined as the percent of time that the insect could be observed from five locations: 1 m N, E, S, W, and directly overhead). For example, a female ovipositing in the middle of a bare lawn would have 100% visual exposure, whereas a female laying within a dense, ground-hugging bush might have 0.0% exposure.

Once a female finished ovipositing, we collected additional site-environmental data, and dug up the pod to record pod depth, length, width, shape, orientation, and clutch size. We then collected adjacent soil into a sealed plastic bag, weighed it, and dried it in an oven to determine soil moisture as percent mass attributable to water. We also determined the maximum amount of water that could occur in our soils by determining water content in flooded soils (when the water table is at or above the soil surface), and in saturated soil (the percent mass of the soil consisting of water after flooded soil was allowed to drain for 1 min from a porous container). Note that, using this method, 100% flooded soils contain only 10 to 38% water, by mass.

In addition to these three "day-long" studies, we included information from ovipositions encountered during the last 25 y, while conducting various other field studies. For many of these observations, we collected only partial data (for example, we seldom dug up pods or measured soil moistures). Hence, in our results, N varies for each variable. For time of day comparisons in Figure 2, we used only data from the three "day-long" studies (above), because these studies had uniform temporal sampling. Finally, we compared lab-laid egg pods *vs* field-laid egg pods to examine environmental influences on pod form. To obtain laboratory pods, we allowed 50 lab-reared females (Matuszek & Whitman 2001) of each species to oviposit into 15-cm tall transparent plastic cups containing moist (~2% water) fine silica sand (Chladny & Whitman 1997). We analyzed sun exposure, cloud cover, vegetation type, spatial relation to bushes and trees, visual exposure, propensity to lay near objects, group laying, and mate guarding using Chi-square; for other variables we used Student's t-test.

## Results

*Oviposition Behavior of Taeniopoda eques from the Chihuahuan Desert.*—During this 4-d study, days 1 and 2 had 30-70% cloud cover. Cloud cover on day 3 was ~5% from 9 am until 2 pm, but reached 100% by 4 pm. Day 4 was cloudless. Precipitation was virtually nil, except for a heavy rain on day 3 from 4 to 4:30 pm. Mean dawn, 1 pm, and dusk temperatures of shaded air at 1 m, were 14, 36, and 26°C, and of sun-exposed soil surface, 15, 54, and 29°C

**Table 1.** Comparison of oviposition characteristics of *Taeniopoda eques* vs *Romalea microptera* females in the field. Data given as mean  $\pm$  SD, (range), N (total individuals observed), or as percentage of N. Classification data analyzed by Chi-square test, continuous variables analyzed by t-test. See Methods section for explanation of terms and how data were collected.

Time, habitat, and weather	<i>T. eques</i>	<i>R. microptera</i>	Test statistic	p
Habitat type	Chihuahuan Desert brushland/grassland	Florida Everglades disturbed habitat, marsh, and swamp		
General time of laying	Morning to early afternoon, N = 22	Morning and late afternoon, N = 174		
Earliest start of oviposition	8:28 am, N = 22	6:58 am, N = 131		
Latest oviposition completion	5:01 pm, N = 22	9:38 pm, N = 131		
Time to complete laying (min)	96.3 $\pm$ 26.0, N = 18	80.2 $\pm$ 21.9, N = 61	t = 2.65	<0.05
Temperature when oviposition discovered ( $^{\circ}$ C):	$\bar{x}$ $\pm$ SD (Range), N	$\bar{x}$ $\pm$ SD (Range), N		
Air (1 m in shade)	33.6 $\pm$ 3.8 (26-39), 20	29.7 $\pm$ 3.09 (24.5-32.5), 32	t = 3.04	<0.01
Soil surface	36.0 $\pm$ 6.0 (27-44), 18	29.3 $\pm$ 2.21 (25-33), 33	t = 4.73	<0.001
Temperature when oviposition terminated ( $^{\circ}$ C):	$\bar{x}$ $\pm$ SD (Range), N	$\bar{x}$ $\pm$ SD (Range), N		
Air (1 m in shade)	33.2 $\pm$ 6.1 (20-41), 18	29.4 $\pm$ 3.4 (24.5-34), 30	t = 2.44	<0.05
Soil surface (within 1 cm)	38.7 $\pm$ 6.0 (29-51), 18	29.7 $\pm$ 3.1 (26-37), 30	t = 5.91	<0.001
Percent cloud cover at:	$\bar{x}$ (Range), N	$\bar{x}$ (Range), N		
Start of oviposition	14.4 % (0-40%), 18	43.8% (5-100%), 33		
End of oviposition	23.3% (0-100%), 18	44.5% (5-100%), 29		
Slope of land	All < 10 $^{\circ}$ , most had 0 $^{\circ}$ slope, N = 18	7.9 $^{\circ}$ $\pm$ 6.6 $^{\circ}$ (0-65 $^{\circ}$ ), N = 24		
Female: shade vs sun exposure	33.4% in shade, 28.6% in mix, 38.1% in sun, N = 21	36.4% in shade, 9.1% in mix, 54.5% in sun, N = 110	$\chi^2$ = 6.44	<0.05
Percentage that lay against object (stem, rock, etc.)	50.0% (16 of 32)	2.9% (5 of 174)	$\chi^2$ = 65.6	<0.001
Horizontal distance to water (m)	N/A	4.15 $\pm$ 2.8 m (0.2-15 m), N = 87		
Elevation above water (m)	N/A	1.08 $\pm$ 0.3 m (0.01-2 m), N = 87		
Soil type	Variable: dry loose sand, silt, gravel or rocks	Variable: moist or wet sand, sandy loam, gravel, rock or leaf litter		
Soil moisture (% H <sub>2</sub> O)	0.24% (0.03 - 0.57%), N = 18	18.90% (9.3 - 38%), N = 13	t = 8.14	<0.001
<b>Interaction with other individuals</b>				
Percent with males	4.5% (1 of 22)	74.1% (129 of 174)	$\chi^2$ = 42.32	<0.001
Percent with ovipositing females within 1 m	22.2% (4 of 18)	2.9% (5 of 174)	$\chi^2$ = 13.75	<0.001
Successful predation	8.6% (2 of 23)	0% (0 of 174)		

respectively. Before 8:00 am ground temperatures were similar to or cooler than air temperatures, but after this time ground temperatures were warmer than air temperatures. Soil moisture averaged 0.24% and never exceeded 0.6% during oviposition (Table 1). There was never standing water in the habitat. Sunrise was at 6:05 am and sunset at 6:15 pm.

We recorded data from 18 female *T. eques* during our 4-d survey, plus an additional 14 ovipositions from other times. Females initiated oviposition from 2.4 h after sunrise (8:28 am) to 3:12 pm (3 h before sunset), with a peak in midmorning  $\sim$  4 h after sunrise (Fig. 2). The last female completed laying at 5:01 pm, 74 min prior to sunset. Hence, no females were still laying at sunset (Table 1). Females required 96  $\pm$  26.0 min to complete oviposition (Table 1).

The majority of *T. eques* females laid at the base of desert shrubs (41%) or > 10 cm from the base of shrubs, but amongst grass and

herbs (22%) (Figs 1, 3, Pl. VI; Table 2). Only 38% laid in the open (*i.e.*, both beyond the drip line of bushes and with little surrounding vegetation). As a result, 59% were fully or mostly hidden during oviposition, and only 38% laid in full sun (Fig. 4; Tables 1, 2). Thirty-six percent of laying females were fully visually exposed and 33% were shaded (Fig. 3; Tables 1, 2). Soil surface temperatures for females beginning oviposition ranged from 27 to 44 $^{\circ}$ C, and air temperatures 1 m above the laying females ranged from 26 to 39 $^{\circ}$ C. Females that laid before noon, tended to avoid full shade (only 1 of 14 laid in full shade), whereas only 1 of 5 females that laid in the hotter afternoon laid in full sun. During our study, cloud cover at the start of oviposition ranged from 0-40% (Table 1). Half of 32 (50%) ovipositing females laid against an object such as a rock, dead branch, or trunk of a bush (Table 1). Females that laid under bushes or in clumps of grass tended to lay into slightly elevated

soils, because additional soil tended to collect around the bases of such plants. However, no females laid in the elevated hillocks of kangaroo-rat mounds. One female attempted to oviposit (probe) into an asphalt road. During our 4-d study, soil moisture near fresh-laid egg pods ranged from 0.03 to 0.57% (Table 1). No females oviposited during or in the afternoon of the single rain shower that occurred on day 3. At our site, 100%-flooded silty, sandy, and rocky soils contained 26%, 16%, and 14% water respectively.

In the laboratory, *T. eques* egg pods tended to be long, straight, vertical, cylindrical, and deep ( $\bar{x}$  maximum depth = 9.4 cm), with  $\bar{x}$  = 69 eggs/pod (Fig. 5, Table 3). However, in the field, the pods varied in shape and depth ( $\bar{x}$  maximum depth = 9.3 cm), due to the presence or absence of subsurface rocks, which sometimes forced digging females to angle or shorten their holes (Table 3). Some pods were bent by as much as 24° from vertical. However, in rock-free soils, field pods were similar to lab pods. Mean clutch size in the field was 54 eggs/pod, and was significantly smaller than in the laboratory ( $p < 0.001$ ,  $t$ -test) (Table 3).

We observed no "hole filling" after females completed oviposition; instead, females simply walked away from holes after depositing their foam. During our study 4 of 18 (22%) ovipositing females laid within 1 m of another ovipositing female (Table 1). Three of those females were found within 30 min of each other ovipositing within a 1-m<sup>2</sup> area. One of 22 (4.5%) ovipositing females was associated with a male (Table 1). We observed predation on two ovipositing females (9% of 23 ovipositions) (Table 1). One female was attacked by a giant desert centipede, *Scolopendra heros*. The other female was cannibalized by a conspecific female.

*Oviposition Behavior of Romalea microptera from the Everglades area.*—Weather during our first study was influenced by a nearby hurricane. The previous four days had seen moderate to large amounts of rain, soils were damp to saturated with patches of standing water, and there was 40 to 75% cloud cover for much of the day of the study. It sprinkled lightly and briefly at 10 am and 7 pm, with an additional ~ 2 cm rainfall between 2 and 4 pm. Dawn, 1 pm, and dusk temperatures were: air at 1 m: 23, 30, and 28°C, and sun-exposed soil surface: 23, 31, and 28°C respectively. Sunrise and sunset were at 6:34 am and 8:17 pm respectively.

Weather conditions during our second study were typical for south Florida: warm and relatively clear until 2 pm, intense thundershowers from 2 to 3:30 pm, followed by overcast skies and cooler temperatures into the evening. Dawn, 1 pm, and dusk air temperatures were 25, 35, and 26°C and sun-exposed soil-surface temperatures 25, 40, and 28°C respectively. Sunrise and sunset were at 6:51 am and 8:11 pm respectively.

We observed seven *R. microptera* females lay during the first study, 26 during the second study, and an additional 141 at other times. During the first and second studies, females initiated oviposition from 6:58 am (~ 8 min after sunrise) until 7:45 pm (~ 32 min prior to sunset), with peaks in midmorning and late afternoon (Fig. 2, Table 1). Eight of 33 (24%) females were still laying after sunset, the last female finishing at 9:38 pm (~ 1.5 h after sunset). Most *R. microptera* laid in the open, or away from dense or medium vegetation (Figs 1, 3, Pl. VI). Hence, most were visually exposed to predators, and over half laid in full sun (defined as > 66% of the body in sunlight) (Fig. 4; Tables 1, 2). Because our sites contained trees and some structures, which cast shadows, many visually exposed females were partially or fully shaded. Air temperatures 1 m above females initiating oviposition ranged from 25 to 33°C, and soil-surface temperatures adjacent to such females ranged from 25

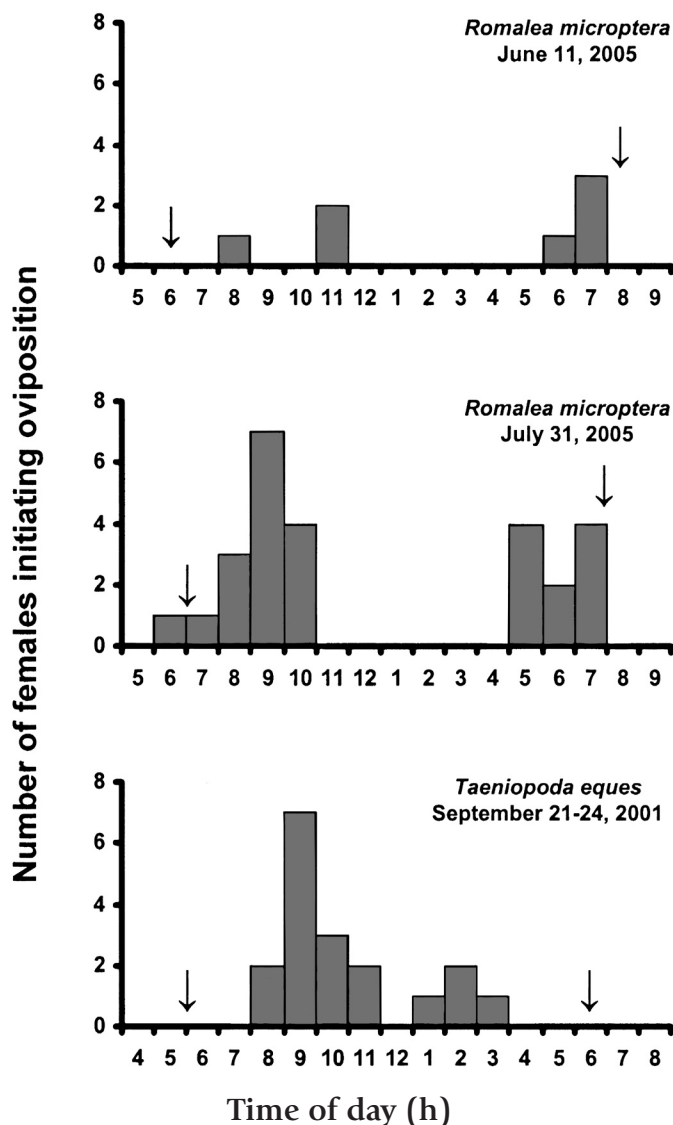


Fig. 2. Number of females initiating oviposition throughout the day during two field studies on *R. microptera* in Florida (2005) and one study on *T. eques* in Arizona (2001). Sunrise and sunset times for each locality are depicted by arrows.

to 33°C (Table 1). Cloud cover at the start of oviposition ranged from 5 to 100% (Fig. 4, Table 1). Females laid into sand, sandy loam, gravel, crushed rock, and into a hard, packed gravel and dirt road. Females avoided moist leaf litter in depressions under thick, shaded bushes and trees. In contrast, numerous females laid into 0.5- to 2.0-cm thick dry leaf litter and sticks, over sandy loam, at a sunny, open site, whose leaf litter had been created by mowing rank vegetation. We also observed females attempting to probe into asphalt and large rocks, and 4 of 132 appeared to be ovipositing into fire ant mounds. Only 5 of 174 (2.9%) laid against objects (Table 1).

When uneven topography was available and females had a choice, nearly all laid away from water at elevated locations (mean horizontal distance from standing water = 4.2 m, range 0.2 to 15 m, mean vertical distance = 1.1 m, range 0.01 to 2 m) (Table 1). Females did not avoid slopes: mean slope = 7.9° ± 6.6°, range 0 to 65° (Table 1). One female laid into the side of a 70-cm high pile

of packed sandy loam devoid of vegetation. She laid at a spot that was 50 cm high with a slope ~65°. Another laid in a humus-filled crack of a large rock that was ~40 cm above the surrounding soil. Another laid 30 cm above the surrounding soil into the top of a root ball of a downed tree. In contrast, where the topography was flat and low and females had no choice, many laid within a few cm elevation of standing water. For example, in a flat area after a rain, some females laid within 20 horizontal cm, and 1 vertical cm of shallow, temporary puddles.

We also observed several *R. microptera* lay in a lawn next to a swamp. The next morning this site was under 5-6 cm of water because the water level of the swamp had risen due to a 5-cm rain-fall. We presume that those eggs remained submerged for weeks, because it was the beginning of the rainy season. At another time, we observed a female lay in a slight depression. A severe rainstorm then flooded her under 5 mm of water; only her head and anterior prothorax remained above the water. Eventually the storm abated and the water drained through the sandy soil. The female then completed her pod and eventually moved away. Many females laid during or immediately after rains, when the ground was saturated. Soil moisture adjacent to fresh-laid egg pods ranged from 9% to 38% (Table 1). At our first and second sites, 100%-flooded soil contained 28% and 30% water, respectively.

In the laboratory, *R. microptera* tended to lay shallow ( $\bar{x}$  maximum depth = 5.8 cm) cylindrical, vertical, slightly curved egg pods containing on average 46 eggs/pod (Figs 5, 6, Pl. VII; Table 3). Pods laid in the field tended to be more shallow ( $\bar{x}$  maximum depth = 3.9 cm), cylindrical to teardrop-shaped, and more curved, with significantly fewer eggs per pod ( $23 \pm 6.5$  eggs/pod, range = 14-36) ( $p < 0.001$ , *t*-test) than in the field (Table 3). We observed no "hole filling": females walked away from holes after depositing their foam. In the field, a majority of females, 129 of 174 (74%), were contact mate-guarded, but only 5 of 174 (2.9%) of females oviposited within 1 m of a previously ovipositing female (Table 1).

We observed no successful predation on ovipositing *R. microptera*, although fire ants (*Solenopsis wagneri*) were common at our sites. However, on two occasions, females probed near fire ant mounds, then withdrew their abdomens and moved away, when ants contacted and possibly stung them. As previously mentioned, four

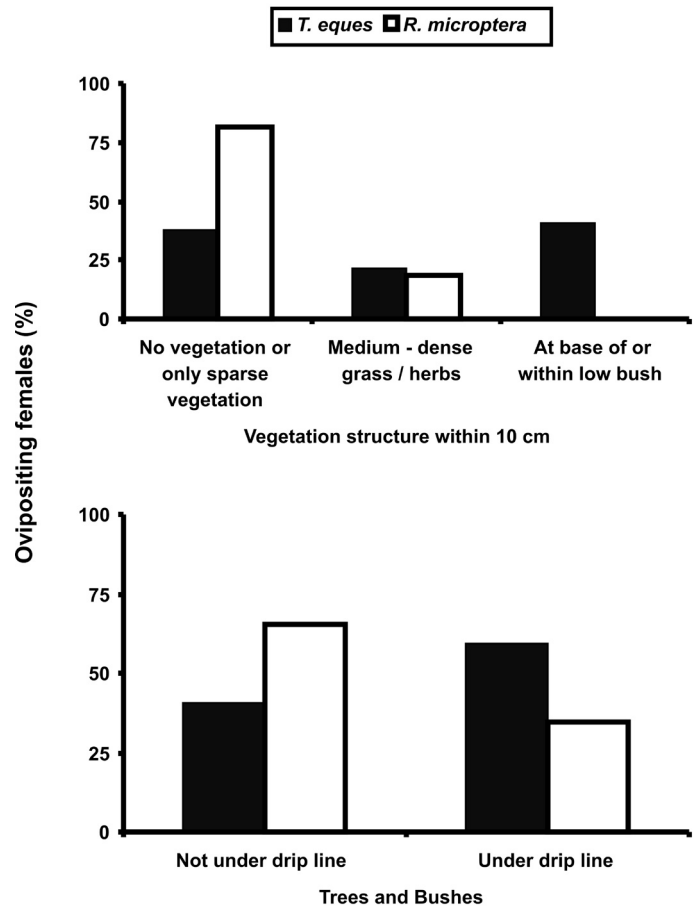


Fig. 3. Vegetation characteristics for ovipositing *T. eques* (N = 32) and *R. microptera* (N = 150) grasshoppers in the field. Ovipositing females of the two species were distributed significantly differently in regards to type of vegetation within 10 cm ( $p < 0.001$ , Chi-square) and whether or not they laid under trees/bushes vs in the open ( $p < 0.001$ , Chi-square). See Methods section for explanation of terms and how data were collected.

Table 2. Comparison of vegetation characteristics and degree of visual exposure of ovipositing lubber grasshoppers in the field. See methods section for explanation of terms and how data were collected.

Vegetation structure within 10 cm of laying female	<i>T. eques</i>	<i>R. microptera</i>
No vegetation or only sparse vegetation	37.5% (12 of 32)	81.3% (126 of 155)
Medium to dense grass/herbs	21.9% (7 of 32)	18.7% (29 of 155)
At base of, or within low bush	40.6% (13 of 32)	0% (0 of 155)
<b>Relation of female to trees and bushes</b>		
Beyond drip line of tree or bush	40.6% (13 of 32)	65.3% (98 of 150)
Within drip line of tree or bush	59.4% (19 of 32)	34.7% (52 of 150)
<b>Exposure to visual predators</b>		
> 75% exposure	36.4% (8 of 22)	77.2% (122 of 158)
50 to 75% exposure	4.5% (1 of 22)	15.8% (25 of 158)
25 to 49% exposure	27.3% (6 of 22)	5.7% (9 of 158)
< 25% exposure	31.8% (7 of 22)	1.3% (2 of 158)

other females appeared to be ovipositing into fire ant mounds, and, at the time, were not being attacked by ants above ground. We do not know if they were attacked underground. We also encountered a dead, dry *R. microptera* female, whose abdomen was buried in the ground implying oviposition. The internal contents of this female had been removed, suggesting ant predation during oviposition.

## Discussion

*T. eques* and *R. microptera* are closely related and can even interbreed in the laboratory (Stauffer pers. obs.), yet they differ greatly in oviposition biology. Included are differences in phenology, time of day, location, degree of visual exposure, temperature, sun exposure, cloud cover, soil moisture, clutch size, pod shape, size and depth, and degree of clumping, mate-guarding, and predation during oviposition. The large number of trait differences exhibited by these two closely related species suggests rapid divergent evolution, and perhaps adaptation to local conditions. Below we discuss each of these differences in turn. We ask if the differences in trait values are innate or environmentally induced, and if they might be adaptive, given the disparate habitats (desert *vs* wetland) of these two species.

**Phenology.**—*T. eques* oviposits in September and October, whereas *R. microptera* oviposits June to August. This divergence may have resulted from selection to hatch and develop under appropriate local climatic conditions. Grasshoppers require heat and rainfall for growth and survival (Joern & Gaines 1990), conditions that are available in spring in south Florida, but are not available until July in SE Arizona because of the summer drought. Thus, *T. eques* hatching is restricted to a narrow seasonal window. They cannot hatch before July, because there is no food (summer annuals), and cannot hatch after August, because they could not mature before the onset of freezing weather (Whitman 1988). The fact that each population hatches near the beginning of its respective rainy season dictates that desert *T. eques* generally mature and lay into dry soils, at the end of their 3-mo rainy season, whereas *R. microptera* lay during the peak of the 6-mo Florida rainy season. The consequence is that the two populations lay into dramatically different soil moistures, which may have selected for disparate oviposition behaviors.

**Time of day.**—*T. eques* and *R. microptera* laid at different times of the day (Fig. 2). These differences probably relate to disparate temperatures and predator loads in the two habitats. Both species roost at night in vegetation, but descend to the ground in the morning (Whitman 1987). Morning descent is much later for *T. eques*, because of cold dawn desert temperatures (Whitman 1987, 1988), which explains why *T. eques* lay later in the morning. However, acute temperatures cannot explain why *T. eques* did not, but *R. microptera* did, oviposit in the late afternoon; this is because afternoon desert temperatures are actually warmer than in the Everglades. Also, some *T. eques* oviposited at cooler temperatures in the morning than existed in the afternoon, suggesting that afternoon temperatures by themselves, were not inhibitory for *T. eques*. We offer two (not mutually exclusive) hypotheses to explain why *T. eques* fails to oviposit near dusk.

A *temperature hypothesis* suggests that *T. eques* has evolved to avoid becoming trapped on the ground by rapidly decreasing nocturnal desert temperatures. Female *T. eques* require ~96 min to complete oviposition at warm temperatures, but take much longer when cold. Temperatures can drop dramatically in the Chihuahuan Desert after

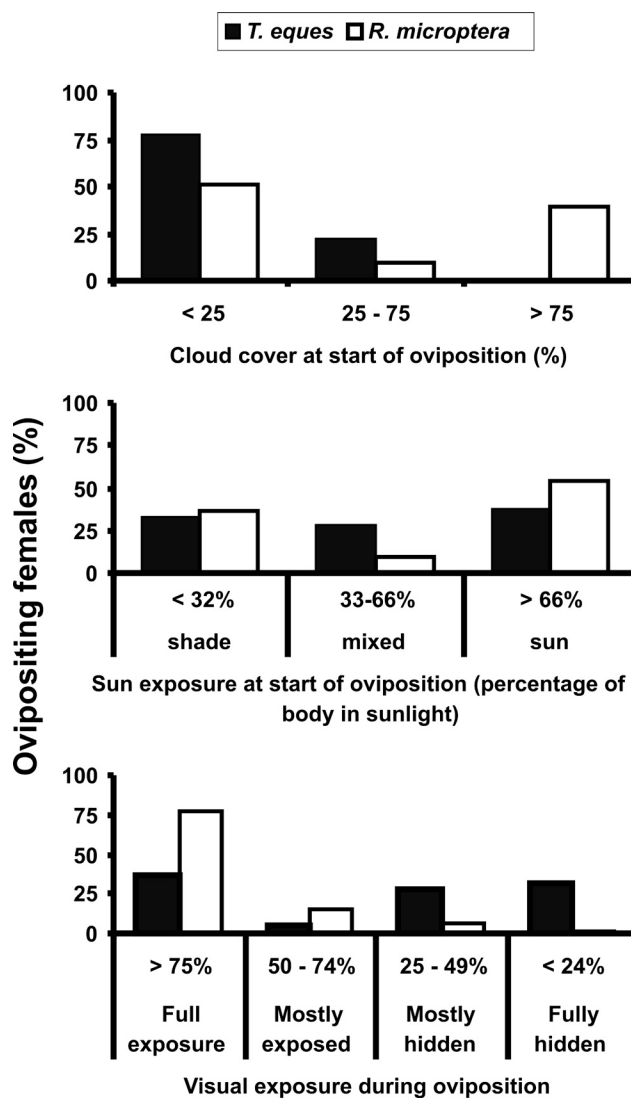


Fig. 4. Environmental conditions and degree of exposure for ovipositing *R. microptera* and *T. eques* in the field. Cloud cover refers to percentage of sky covered by clouds. Sun exposure refers to percentage of grasshopper body in direct sunlight. Visual exposure refers to percent of time the insect could be observed from 5 locations: 1 m N, E, S, W, and directly overhead. The two species differed significantly in all three traits: For clouds,  $p < 0.01$ ; sun exposure,  $p < 0.001$ ; and visual exposure,  $p < 0.05$ . Chi-square Test used for all three factors.

sunset because of its 1250-m elevation, low humidity, lack of insulating clouds, and distance from temperature-mediating bodies of water. As desert temperatures fall at dusk, females on the ground may become chilled, unable to complete oviposition or ascend nocturnal roosts, and as a result, fail to complete pods or suffer greater predation. We have recorded night air temperatures as low as 8°C at our site in September. Such temperatures immobilize *T. eques* (Whitman 1988, Chappell & Whitman 1990). In contrast, there may be no thermal disadvantage for *R. microptera* to oviposit at dusk, because of the warm (20 to 26°C) night temperatures in subtropical south Florida in June and July (NOAA).

A *predator hypothesis* suggests that predatory pressures alone have selected against dusk-oviposition in *T. eques*. Crepuscular and nocturnal ground-predator loads are higher in the desert than



**Table 3.** Characteristics of egg pods of *T. eques* and *R. microptera* grasshoppers laid in the lab vs the field. Clutch size and linear data analyzed by t-test. See Methods section for explanation of terms and how data were collected.

Egg Pod Characteristics	<i>T. eques</i>	<i>R. microptera</i>	Test statistic	p
<b>In the field</b>				
Pod shape/orientation	Elongate/straight to bent	Teardrop/curved/diagonal		
Clutch size	53.7 ± 12.0 (37-79) N = 20	22.8 ± 6.5 (14-36) N = 12	t = 32.25	<0.001
Depth to top of eggs (cm)	4.3 ± 0.7 (3-5) N = 20	2.0 ± 0.9 (0.9-3.5) N = 12	t = 82.14	<0.001
Depth to bottom of eggs (cm)	9.3 ± 1.2 (7-12) N = 20	3.9 ± 0.8 (2.9-5.6) N = 12	t = 13.85	<0.001
Width of egg pod (cm)	1.0 ± 0.1 (1-1.3) N = 18	1.1 ± 0.4 (1-1.5) N = 12	t = 0.83	n.s.
<b>In the Laboratory</b>				
Pod shape/orientation	Elongate/straight/vertical	Elongate/slight curve		
Clutch size	69.0 ± 9.6 (28-87) N = 50	46.1 ± 10.3 (20-67) N = 50	t = 11.49	<0.001
Depth to top of eggs (cm)	4.5 ± 1.02 (2-6.5) N = 50	3.2 ± 0.9 (1.5-5) N = 50	t = 6.77	<0.05
Depth to bottom of eggs (cm)	9.4 ± 0.9 (8 - 11.5) N = 50	5.8 ± 1.6 (3-9.5) N = 50	t = 14.02	<0.001
Width of egg pod (cm)	1.0 ± 0.7 (1 - 1.4) N = 50	1.2 ± 0.5 (1-1.7) N = 50	t = 1.67	n.s.

in the Everglades (Lowe 1980, Whitman *et al.* 1985, Lodge 2005).

Both *T. eques* and *R. microptera* shelter in vegetation at midday (Whitman 1987), but differ: some *T. eques* remain midday at the base of desert shrubs where they stay in contact with soil and are shaded from radiative heating (Whitman 1987). In contrast, *R. microptera* tend to roost high on stems at midday, which takes them away from their oviposition substrate. This difference in preferred microhabitat at midday may explain why *T. eques* did, and *R. microptera* did not, lay at this time of day (Fig. 2).

*Place of laying: vegetation, visual exposure, and sunlight.*—In our study, most *T. eques* laid under bushes or within low vegetation, whereas *R. microptera* preferred to lay in the open. Laying under bushes reduces visual and solar exposure. Fifty-nine percent of oviposition acts by *T. eques*, but only 8% by *R. microptera*, were fully or mostly hidden. This difference is made more significant by the fact that it is difficult to hide under Chihuahuan Desert bushes, because of their small leaves and open-stem architecture. Differences in place of laying cannot be explained by vegetative patterns: the Chihuahuan Desert is primarily open habitat with sparse vegetation (Fig. 1, Pl. VI), yet most *T. eques* laid within vegetation. The Everglades is mostly vegetated, yet most *R. microptera* laid in the open.

However, thermal relationships might explain these differences. High midday desert temperatures cause desert grasshoppers to seek shade (Uvarov 1977), an interaction even more severe for *T. eques*, which are black and rapidly heat when exposed to solar radiation (Whitman 1987). Black color benefits *T. eques* on cold desert mornings and on cold October days; but on hot days, it prevents prolonged sun exposure, forcing them into shading vegetation (Whitman 1987, 1988). Laying under shady bushes keeps *T. eques* eggs cool and moist through the hot summer. Also, lubbers hatch as soft vermiform (worm-like) nymphs, which wiggle up through the soil, immediately molt to become first instars, then immediately ascend vegetation. Laying under bushes obviates the need to emerge, molt, and traverse lethal, sun-baked soil surfaces. Finally, laying under perennial bushes allows hatchlings to immediately ascend vegetation to escape the ubiquitous desert ants, which take a high percentage of hatchlings on the ground, but not on vegetation (Whitman & Orsak 1985). We once observed ants kill half of ~25 hatchlings as they emerged over 25 min from a single egg pod.

In contrast, there may be little thermal disadvantage for *R.*

*microptera* to oviposit in full sunlight. The pale-yellow and orange adult *R. microptera* presumably do not heat as rapidly or reach as hot a temperature as the black *T. eques*, and thus probably suffer less from long-term solar exposure (Chappell & Whitman 1990). Furthermore, maximum summer air and soil-surface temperatures in the Everglades area tend to remain much cooler than they do in the Chihuahuan Desert (NOAA), because of greater cloud cover, frequent rains, moist soils, and evaporative cooling from abundant surface water. Finally, the Everglades area has greater cloud cover during the summer, which could further reduce harm from exposure.

*Place of laying: elevation and soil moisture.*—Our desert site was relatively flat; thus, we could not determine if oviposition in *T. eques* was influenced by local elevation or slope. However, *T. eques* tended to lay under bushes, and soil tended to mound up around the bases of such shrubs. Hence, pods laid under bushes were elevated a few cm above those laid away from bushes.

In contrast, our Everglades sites contained uneven ground. When *R. microptera* had a choice (when there was nearby elevated ground), most females laid at higher elevations, away from standing water. Some climbed to oviposit in cracks on the tops of emergent boulders or root balls of downed trees. Although our Everglades sites were surrounded and interspersed with flooded areas containing gravid females, no females laid immediately adjacent to such bodies of water. Alternatively, where the topography was flat, and small puddles were common (for example after rains), some *R. microptera* females laid within 20 horizontal and 1 vertical cm of such puddles. Many *R. microptera* females laid immediately after heavy thundershowers, when soils were saturated, and a few females who had been laying prior to storms, continued to lay through the rain, as up to 0.5 cm-deep water surrounded them.

Our study suggests that *R. microptera* prefer to lay at elevated sites, and away from water when it is possible to do so, but can lay into 100% saturated soil during or following rains. Laying in elevated locations may be adaptive for this marsh-inhabiting grasshopper, because it reduces the risks associated with attempts to develop, hatch, respire, and molt under water. Flooding and moisture can encourage fungal growth or suffocate grasshopper eggs and, because of capillary action, make it impossible for the soft vermiform nymphs to move through the soil (Hunter-Jones 1972, Ewer 1977, Stauffer

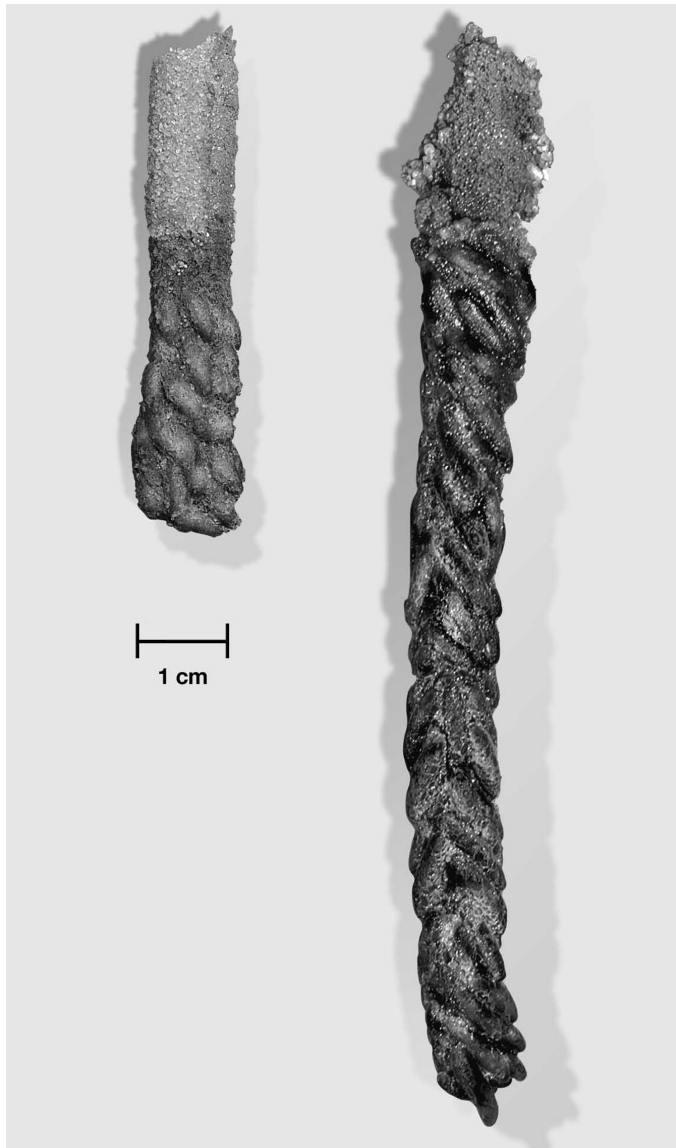


Fig. 5. Egg pod morphology of *R. microptera* (left) and *T. eques* (right).

& Whitman 1997). Flooding is a real possibility for *R. microptera*, because as much as 30 cm of rain can fall in 48 h in the Everglades, and over the course of the summer rainy season, the water table can rise 1 m in some locations. Because of the flat topography of the Everglades area, pods that are laid into dry soil can become submerged for months, as large areas flood during the summer. In contrast, *T. eques* oviposits into dry soils (0.03 to 0.57% water content), and desert soils generally remain dry.

*Place of oviposition: soil type.*—Both *T. eques* and *R. microptera* accepted a wide range of soil types including loose to compacted silt, sand, sandy loam, gravel, and rocky soils. *R. microptera* even laid into fire ant mounds and into jagged, crushed-limestone gravel averaging  $2 \times 2 \times 1$  cm in size, with little sand or smaller particles between the individual gravel pieces. Hence, soil grain size does not appear to be a dominant factor in oviposition-site choice. Soil hardness and compactness also may be of little importance for initial probing, since both species attempted to probe into hard asphalt. One *R. microptera* laid into a packed-gravel/dirt road, others into humus-



Fig. 6. Ovipositing *T. eques* in the laboratory. See also PLATE VII.

filled cracks in boulders. *R. microptera* laid into leaf litter at open, sun-exposed sites, suggesting that vegetation structure and sunlight are more important than soil type for oviposition site choice.

*Place of oviposition: laying against objects.*—In the laboratory, both *T. eques* and *R. microptera* generally lay against the sides of their containers, because they back up when they initially start to probe (Stauffer & Whitman 1997). In laboratory choice tests, *R. microptera* laid significantly more pods against sticks than in bare sand, and ovipositing females were even attracted to two-dimensional vertical images drawn on paper (Stauffer *et al.* 1998). In the field, similar behaviors would bring lubbers to lay against rocks, sticks, and emergent plant stems. Placing pods against such objects might increase moisture level or erosion resistance (Stauffer & Whitman 1997). For example, egg pods of grasshoppers inhabiting xeric areas can benefit from being laid against large flat rocks, because runoff from such rocks produces zones of higher soil moisture, preventing pod desiccation (Andrewartha & Birch 1954). In the field, *T. eques* and *R. microptera* differed in propensity to oviposit against objects. Half

of *T. eques* oviposited against a rock, stick, or stem, but only 2% of *R. microptera* did, despite the tendency for this species to oviposit against objects in the lab (Stauffer *et al.* 1998).

*Attraction to conspecifics.*—In some species, ovipositing grasshoppers aggregate in large groups or are sequentially attracted to oviposition sites, producing highly concentrated egg pods (Stauffer & Whitman 1997). For example, Popov (1954) recorded 1,620 pods/m<sup>2</sup> for *Schistocerca gregaria*. In the laboratory, *R. microptera* tend to clump when ovipositing: up to 16 females will oviposit together in a tight, touching aggregation (Stauffer *et al.* 1998). Females also oviposited near tethered live conspecifics, into sand containing previously laid egg pods, and near grasshopper frass (Stauffer *et al.* 1998). Group oviposition may or may not benefit grasshopper eggs in terms of predators, pathogens, and desiccation resistance (Stauffer & Whitman 1997, Stauffer *et al.* 1998).

The above observations made us eager to examine the possibility of group oviposition in the field, especially because of previous reports of strong migratory aggregation by *R. microptera* (Watson 1941). However, we observed little ovipositional clumping in *R. microptera* during this field study, suggesting that our previous observations (Stauffer *et al.* 1998) were laboratory artifacts. In contrast, *T. eques* did exhibit mild clumping during oviposition, but it was not the tight (touching) aggregations observed in the laboratory with *R. microptera* (Stauffer *et al.* 1998). We believe that the field oviposition clumping that we observed with *T. eques* was not due to conspecific attraction, but resulted from independent attraction to bushes. All ages and sexes of *T. eques* are attracted to large bushes where they roost, shade, feed, and oviposit (Whitman & Orsak 1985). Because large bushes are scattered, multiple grasshoppers tend to collect around these resources. Bushes that contain numerous females may occasionally have two females oviposit simultaneously.

*Mate guarding.*—At our two Everglades sites, 74% of ovipositing females were mate guarded. In contrast, only 1 of 22 ovipositing *T. eques* females had an accompanying male. Because *T. eques* males generally separate from females soon after copulation, we suggest that this one instance represents a male who was attempting to copulate, and not a male who had previously copulated and was now mate guarding. We believe that *R. microptera* does, and *T. eques* does not, mate guard.

*Clutch size.*—Maximum clutch size in grasshoppers depends on the number of ovarioles possessed by the female (Stauffer & Whitman 1997). *T. eques* from Rodeo, NM, average 86, *R. microptera* from Copeland, FL, 67, ovarioles (Whitman unpub.); hence, *T. eques* can theoretically lay larger clutches. However, clutch size in large grasshopper species seldom matches ovariole number, because grasshoppers resorb some developing oocytes when stressed (Stauffer & Whitman 1997, Sundberg *et al.* 2001). In the lab, under “ideal” conditions, clutch size was 69 eggs/pod for *T. eques* and 46 eggs/pod for *R. microptera*. Both species laid smaller clutches in the field, and *T. eques* laid significantly larger clutches (54 eggs/pod) than *R. microptera* (23 eggs/pod). [The large pods laid by *T. eques* should be more resistant to drying (Stauffer & Whitman 1997).]

Our *R. microptera* populations were heavily parasitized by dipteran and gregarine parasites. At the time of our studies, ~46% of *R. microptera* at our first site and 29% at our second site contained living maggots of either *Anisia serotina* (Tachinidae) (Lamb *et al.* 1999), or a second unknown species of maggot (Whitman unpub.). Likewise, ~46% of *R. microptera* at the first site and 100% at the second site

contained *Boliviana floridensis* (Protozoa: Eugregarinida) parasites in their guts (Johny & Whitman 2005). Parasitization probably induced oocyte resorption in females, leading to low clutch sizes in *R. microptera*. In contrast, we have never observed dipteran or gregarine parasites at our New Mexico site, although these parasites exist in other *T. eques* populations (Whitman unpub.).

*Pod shape.*—When given moist sand in the laboratory, *T. eques* lays vertical, straight, cylindrical, and deep pods, whereas *R. microptera* tends to lay shorter, slightly curved pods. These differences were exaggerated in the field, where *R. microptera* tended to lay curved, tear-drop shaped, shallow pods, and where maximum pod depth was significantly greater for *T. eques* (9.3 cm) than *R. microptera* (3.9 cm).

Deep pods are probably adaptive for desert-dwelling *T. eques*, because deeper pods would experience higher moisture, milder temperatures, and perhaps fewer predators and parasites. Temperatures above 32 °C can kill lubber eggs (Chladny & Whitman 1998) and, as previously mentioned, soil surface temperature in the Chihuahuan Desert can exceed 69 °C in summer, and fall below freezing in the winter. Likewise, grasshopper diversity and abundance in southern Arizona and New Mexico are among the highest in North America (Ball *et al.* 1942, Capinera *et al.* 2004). As a result, this habitat contains a high diversity and abundance of grasshopper egg-pod predators and parasites (Rees 1973). Deep pods may reduce egg mortality from natural enemies. Finally, deep pods reduce mortality from wind- or flash-flood erosion.

In contrast, shallow pods are probably adaptive for *R. microptera*, in the Everglades, with its higher moisture levels and milder soil-surface temperatures. As mentioned previously, prolonged flooding can kill developing grasshopper embryos (Stauffer & Whitman 1997). Also, it is difficult for the tiny hatchlings to wiggle upwards through saturated soils, because of surface tension. Likewise, even the most shallow *R. microptera* egg pods are far too deep to be harmed by the occasional Everglades surface fire (Branson & Vermeir 2007). Finally, the Everglades area has few grasshopper egg parasites. In such an environment, shallow egg pods might be advantageous. Hence, for *R. microptera*, there may be little advantage, and perhaps great disadvantage, for deep egg pods.

*Oviposition behavior: innate or environmentally influenced.*—Our results suggest that both inherent and environmental factors influence oviposition in lubber grasshoppers. When reared in the laboratory under identical conditions, each species exhibits distinct oviposition tendencies. However, in the field, the expression of these characteristics is shaped by current environmental conditions. Some features, such as egg-pod depth, maximum clutch size, and presence or absence of mate guarding, have a strong genetic component, because these differences are maintained when these species are reared in the laboratory under identical conditions. Other features clearly vary with the environment. For example, time of laying is probably controlled in nature by current temperature and radiant heating, with both high and low thermal thresholds. In October 1983, we observed two days of cold weather, during which *T. eques* never descended from their roosts, and therefore laid no eggs. Environment also influences clutch size and egg-pod shape, because stress induces oocyte resorption and subsurface rocks cause short or bent egg pods.

Environmental conditions vary greatly over the course of the oviposition season, and from site to site. Oviposition behaviors undoubtedly vary accordingly, as well as with female age, population

density, parasite load, *etc.* Hence, our study is a snapshot of possible oviposition responses. Under different conditions, we would expect different results. For example, we do not know if *T. eques* would lay into saturated soils after a severe rain, or if *R. microptera* would lay into dry soils during a drought.

*Are these disparate oviposition behaviors adaptive?*—Many of the oviposition differences we observed appear to be adaptive. Among these is a tendency for *T. eques* to lay large, deep pods, under vegetation in the shade, but not in the late afternoon. Such behavior would be advantageous given the climate and predator conditions of the Chihuahuan Desert. In contrast, we suggest that for *R. microptera*, laying shallow pods in elevated locations, and away from standing water is adaptive in its seasonally flooded Everglades environment. Laboratory experiments further suggest that these two species have adapted to their respective environments. For example, when offered a choice between sands of 4% vs 85% of saturation, the Everglades species chose the latter and the desert species chose the former (Stauffer & Whitman 1997). In addition, *T. eques* eggs can survive severe desiccation and *R. microptera* eggs can survive prolonged submersion (Stauffer unpub.).

*Comparison with other grasshoppers.*—About 85% of the ~ 12,800 known species of grasshopper oviposit into soil, but among these, oviposition characteristics vary widely (Uvarov 1966, 1977; Stauffer & Whitman 1997). Most species lay in the day, but some lay in early evening or at night. Temperature and radiative heating are extremely important to grasshoppers (Chappell & Whitman 1990, Ji *et al.* 2006), and many temperate, alpine, and high-latitude species oviposit in full sunshine; other species seek shade. Some oviposit in bare, open ground, others in dense vegetation. Some lay into the bases of grasses, into leaf-litter/detritus, or adjacent to specific plant species (Pfadt 1994, Bashir *et al.* 2000). Some species prefer moist, others prefer dry soils. Desert species tend to lay deep pods, whereas those from hydric habitats tend to lay shallow pods, or even above ground. A few marsh species lay underwater on submerged vegetation.

Although lubbers express preferences, they have fairly wide tolerances for soil moisture and type, vegetation and visual exposure. However, *R. microptera*, apparently avoids thick vegetation. Most grasshoppers will accept a variety of soil particle sizes; however, our observation of *R. microptera* ovipositing into piles of jagged 1 × 2 cm-size crushed rock is unique. As far as we know, *R. microptera* is the only grasshopper that prefers to oviposit in elevated locations, although some species lay into the sunny sides of ant or gopher mounds, or even piles of grain, probably because these sun-exposed sites have elevated temperatures (Stauffer & Whitman 1997). Only a few grasshopper species aggregate when ovipositing; but for those that do, density can be quite high (Popov *et al.* 1994, Launois-Luong & Lecoq 1996). We believe that the minimal “clumping” that we observed in *T. eques* does not represent a true oviposition aggregation, but instead attraction to bushes. Lubbers are among the largest of grasshoppers, and therefore tend to lay larger, deeper pods with more eggs than other species. Many species lay curved, diagonal pods, or spherical pods, and a few species even lay horizontal pods. In the lab, *T. eques* pods are almost always straight and vertical and *R. microptera* pods tend to be very slightly curved and off-vertical. Some other species cover the oviposition hole with dirt after laying; lubbers do not.

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