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# Interactions of gulf cordgrass, *Spartina spartinae* (Trin.) Merr. ex Hitchc., habitat with ixodids on the South Texas coastal plain

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## Abstract

Many ixodid species on the South Texas coastal plain can transmit pathogens to their hosts. Substantial areas are dominated by gulf cordgrass, *Spartina spartinae* (Trin.) Merr. ex Hitch. The *S. spartinae* habitat was examined in terms of abiotic and biotic factors that likely impinge upon ixodids using the plant for questing. Natural enemies, temperature, humidity, and plant structure were investigated as possible mortality factors and improving ixodid survival. *Spartina spartinae* (soil and foliage) harbored few natural enemies of ixodids, and soil salinity was nonlethal. Conditions were cooler and more humid inside *S. spartinae* clumps than in the canopies; hence, questing ixodids can rehydrate inside the clump when threatened by desiccation. Leaves were mostly “V” shaped in cooler months and, during warm months, the tightly folded leaf slot predominated, into which larvae crawled. Immature ixodids were more abundant in the concave side of the “V”-shaped leaves than on the exposed convex side. Larvae sought refuge from potential lethal ambient air conditions by entering tight warm season leaf folds. The leaf “V” and fold offer opportunities for rehydration on the leaf without moving to the clump’s base. In addition to five other species collected on the grass, a relatively heavy larval southern cattle fever tick, *Rhipicephalus (Boophilus) microplus* (Canestrini), population was detected, suggesting that abundances in the South Texas cattle fever tick eradication quarantine zone are increasing and might spread further into Texas.

**Keywords** Behavior, Cattle fever tick, Plants, Questing, Relative humidity, *Rhipicephalus microplus*, Tick, Vegetation

## Introduction

The subtropical South Texas, USA, coastal plain of Cameron and Willacy counties provides a corridor for wild animals that host multiple ixodid (Ixodida: Ixodidae) species, extending from the Rio Grande to large cattle ranches in Willacy County and farther northward. Some of the ixodids transmit important disease agents that infect humans, livestock, and wildlife (Showler and Pérez

de León 2020). Soil salinity caused by occasional shallow flooding with hypersaline Lower Laguna Madre bay water (due to wind tides and storm surges) has a crucial role in the region’s distribution of ixodids that involves the ovicidal action of hypersaline water and egg predation by halophilic mud flat fiddler crabs, *Uca rapax* Smith (Showler et al. 2019b). While dense stands of sea ox eye daisy, *Borrchia frutescens* (L.) DC, are indicative of saline habitat in the region and *U. rapax* populations (Showler et al. 2019b), direct interactions of ixodids with predominant plant species on the wildlife corridor have not been described.

The roles of plants appear to be important to ixodid ecology, with some plant types and plant species possibly

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being more influential than others. Areas of brush and low trees in Oklahoma, USA, for example, harbored  $\geq 3$ -fold more ixodid adults and 15-fold more nymphs than surrounding areas dominated by lower-growing grasses and other plants (Hair and Howell 1970). In Arkansas, USA, 69.6% of the lone star tick, *Amblyomma americanum* (L.) occurred in brushy habitat compared to 30.4% in grassland (Lancaster 1957), and other reports suggest that survival of the southern cattle fever tick, *Rhipicephalus (Boophilus) microplus* (Canestrini), and the cattle fever tick, *Rhipicephalus (Boophilus) annulatus* Say, was favored more by honey mesquite-, *Prosopis glandulosa* Torr., shaded and mixed brush vegetation than by open grass and by grass mixed with brush (Davey et al. 1994; Teel et al. 1997). Although ixodids use plants as elevated sites from which to acquire passing host animals, a behavior known as “questing”, interactions with plants have not been assessed sufficiently to elucidate complexities.

Aside from the relatively diverse mesquite-thorn scrub habitat and saline areas mainly occupied by *B. frutescens*, some parts of the South Texas coastal plain are dominated by gulf cordgrass, *Spartina spartinae* (Trin.) Merr. ex Hitchc. (Showler et al. 2019b). *Spartina spartinae* is a widely distributed perennial bunchgrass on coastal areas of the Western Hemisphere (Bertness 1991), often excluding other plant species (Oefinger and Scifres 1977). *Spartina spartinae* grows in clumps with a  $\approx 1$  m diam canopy of thin leaf blades that extend upward and outward, like a fountain, from a dense base where the leaves are mostly vertical. While highly productive (Garza et al. 1994), *S. spartinae* is coarse and relatively unpalatable to livestock (Angell et al. 1986). The purpose of this study was to identify interactions of ixodids with the South Texas *S. spartinae* habitat that likely affect the parasites’ survival, including prevalence of predatory arthropods, ambient abiotic conditions, and, in particular, plant structure and leaf shape. Data collected was used to describe relationships between potentially relevant ecological compartments that, together, inform on a habitat-based ixodid environmental system. Determination of ecological interactions enhances understanding of how medially and agriculturally important arthropods survive and proliferate in some environmental systems.

## Materials and methods

Field experiments were performed on the South Texas coastal plain in Cameron and Willacy counties, Texas, in *S. spartinae* and mesquite-thorn scrub habitats. That information was collected in order to characterize key abiotic and biotic factors that likely affect ixodid survival in the South Texas *S. spartinae* habitat. Field data was collected from Jan to Aug 2018, and one outdoor experiment in Aug 2019 was conducted at the U.S.

Department of Agriculture – Agricultural Research Service’s Knipling-Bushland United States Livestock Insects Research Laboratory (KBUSLIRL) in Kerrville, Kerr County, Texas, USA. Ixodid samples from *S. spartinae* plants were collected in 2022; the interval between those samples and earlier parts of the study was due to employer-mandated travel restrictions associated with COVID-19.

## Soil salinity

Soil samples were collected from the top 7.6 cm using a 20,502 Pro steel weeder, narrow-blade shovel (Radius Garden, Ann Arbor, Michigan, USA). At each of 12 sampling sites, six in *S. spartinae*-dominated habitat and six in mesquite-thorn scrub habitat (Table 1), soil was taken from five places 5–10 m apart from each other to obtain a total of  $\approx 3.8$  L of soil in a plastic bag; the bag was shaken vigorously for 30 s to mix the soil. Electrical conductivity, expressed as mmhos/cm and used as a measure of soil salinity, was determined by the Texas Plant and Soil Lab, Edinburg, Hidalgo County, Texas.

## Plant habitat composition

A 0.25 m<sup>2</sup> quadrat was tossed three times in random directions at each of six *S. spartinae*-dominated areas and at each of six mesquite-thorn scrub areas (two of the samples from each habitat were taken at Port Mansfield and four at Holly Beach) (Showler et al. 2019b) (Table 1). Numbers of plants of each species were counted and percentage ground cover was visually estimated within the quadrats 11–14 Jun 2018.

## Temperature and relative humidity of *S. spartinae* clumps

Temperature and relative humidity were measured using an MS6508 digital temperature-humidity meter (Peakmeter, Shenzhen, Guangdong, China) within the basal clump of 10 randomly-selected *S. spartinae* plants ( $\approx 5$  cm above the soil surface) and in the open canopies ( $\approx 20$  cm below the top of the plant) within 500 m of N 26° 08.20’ W 97° 17.41’ in Cameron County. Wind speed was taken once 30 cm above each of the *S. spartinae* canopies. These measurements and the *S. spartinae* leaf shape observations were recorded at 1100 to 1400 h on 15 Feb, 24 Apr, and 12 Jun 2018.

## Leaf shape

Six *S. spartinae* leaves from each of 10 different randomly selected plants in Cameron and Willacy counties were excised with scissors at their bases and visually examined to determine whether the leaf was open or folded, 29 Jan, 25 Apr, 12 Jun, and 25 Oct 2018. The breadths of the “V” in 60 randomly selected “open” leaves, and of the slot in 60 randomly selected “folded” leaves at the midpoint of each, were measured using a digital caliper (resolution

**Table 1** Sampling locations for tick flag sampling (both habitats), and for pitfall traps for *U. rapax* and other arthropods (cordgrass habitats only), and for sweep net sampling (cordgrass habitats only), in Cameron and Willacy counties, Texas, 12–15 Feb, 23–25 Apr, and 11–13 Jun 2018

Habitat	County	GPS coordinates <sup>a</sup>	No. transects			
			Feb	Apr	Jun	
Cordgrass	Cameron	N 26° 08.20' W 97° 17.41'	5	3	3	
		N 26° 08.15' W 97° 17.47'	5	3	3	
		N 26° 08.19' W 97° 17.59'	4	3	3	
		N 26° 08.04' W 97° 18.10'	5	3	3	
		N 26° 32.40' W 97° 25.22'	5	2	2	
	Willacy	N 26° 32.48' W 97° 25.38'	4	3	3	
		Cameron	N 26° 08.01' W 97° 18.27'	5	3	3
			N 26° 08.06' W 97° 18.38'	5	3	3
			N 26° 08.04' W 97° 18.51'	4	3	3
			N 26° 07.57' W 97° 18.26'	5	3	3
Willacy	N 26° 32.41' W 97° 25.25'		5	2	2	
	N 26° 32.52' W 97° 25.37'	4	3	3		

<sup>a</sup>Transects occurred within 500 m of the GPS coordinate and transects for each GPS coordinate were ≥ 100 m apart

0.01 mm, model 61,585, Pittsburgh Pro, Camarillo, California, USA). Leaves for determining the breadth of leaf “V”s and slots were obtained from five *S. spartinae* locations (two samples per location) in Cameron and Willacy counties.

**Larval and nymphal questing site preferences on individual *S. spartinae* leaves**

We released 50 larval and 50 nymphal *A. americanum* on ten adjacent *S. spartinae* plants in Cameron County. The ixodids were reared on *Bos taurus* L. calves in a closed colony of wild-caught (Aug 2006) *A. americanum* maintained at the USDA-ARS Knipling-Bushland United States Livestock Insects Research laboratory in Kerrville, Texas (USDA-ARS 2012), for ≥20 generations. Larvae and nymphs used in this study were 6–12 d old after hatching and molting, respectively. At the end of the field observations described below, the ten *S. spartinae* plants were treated with silica gel-based desiccant dust (CimeXa, Rockwell Labs, Kansas City, Missouri, USA) using a hand-held manual duster (Dustin-Mizer, Earthduster, Fayetteville, Arkansas, USA), which has been shown to be effective for controlling gulf coast ticks, *Amblyomma maculatum* Koch, on *S. spartinae* in the same area and during relatively high wind conditions (Showler et al. 2018). After 1 d, visual inspection of the

plants, followed by flag sampling, indicated that the ixodids had been eliminated.

The *S. spartinae* plants were growing in an area that local hunters indicated was frequented by wild ungulates, particularly white-tailed deer. *Odocoileus virginianus* Zimmerman, and feral nilgai antelope (originally from South Asia), *Bosephalus tragocamelus* (Pallas). Ten individual living and 10 dead *S. spartinae* leaves were examined from each of 10 selected infested plants and visually examined. Each leaf was characterized as either being “open”, with a cross-sectional “V” shape, or as being “folded” with a narrow slot. Dead leaves were all “closed” (tightly furled, lumen diam < 0.25 mm) excluding tattered distal tips. Ixodid larvae and nymphs on each leaf were counted and their positions in terms of distance from the distal end of the leaf, and whether the ixodid was inside the “V” or on the opposite convex side, were recorded. To determine relative positions on the leaves, we sampled leaves until 10 larval and 10 nymphal ixodids were found on each of the 10 selected plants. Ad hoc observations of *A. americanum* behavior on folded leaves were also recorded. Fifty dead leaves were cut in half lengthwise with a razor and the interiors were visually inspected for ixodids.

In a second experiment conducted on 6 Aug 2019, thirty 50 cm lengths of *S. spartinae* leaves with the slot

shape were excised from whole plants growing at lat. N 26° 08.359'; long. W 97° 17.709'; Cameron County, Texas, alongside the mainland shore of Lower Laguna Madre. The basal, cut ends of the leaves were inserted into a 15 cm deep plastic bag containing water, and the mouth of the bag was cinched around the protruding stalks using a rubber band. The bag, kept upright, was transported to KBUSLIRL. On 8 Aug at 1200 h, 36.7 °C, 80% relative humidity, under a cloudless sky, the leaves (still green) were removed from the water in the plastic bag and the base of each of 10 leaves was embedded 1 cm deep in plastilina modeling clay (Sargent Art, Hazleton, Pennsylvania, USA); the clay had been stuck to a 1 m × 5 cm × 10 cm length of wood for support. The wood, with the clay and leaves attached, was placed outdoors at KBUSLIRL in direct sunlight. The long and supple leaves arched from bases at ≈45° angles, the slot sides ventral, all conforming to the growth habit of *S. spartinae* under natural conditions. Five larval *A. americanum* were transferred, using a #5 1.6 cm camel hair paint brush (Charles Leonard, Glendale, New York, USA), to the approximate middle of each leaf. Larvae were observed during the next hour. At the end of the hour, numbers of larvae on the external surface of each leaf were recorded and removed with the paint brush. The interiors of the leaf slots were then examined using a 10× magnification hand lens and larvae within were counted.

#### Flag sampling natural ixodid populations

Ixodids were collected from vegetation using a 48 cm × 100 cm (w × l) flag comprised of white 100% cotton flannel (Fabric, Kennesaw, Georgia, USA) attached to a 1.4-m-long wooden handle. The flag was manually dragged at walking speed across low-growing vegetation in 50-m-long transects 12–15 Feb, 23–25 Apr, and 11–13 Jun 2018. The flag was examined for ixodids every 10 m (hence, five subsamples per transect) and larvae, nymphs, and adults were counted. Six locations dominated by *S. spartinae* and six locations dominated by mixed mesquite-thorn scrub (Table 1) were sampled using 28 transects in each habitat (at least four transects per location) in February, and 17 transects in each habitat (at least two transects per location) in April and in June.

Ixodids were also flag-collected from *S. spartinae* in a 300 m<sup>2</sup> area where *S. spartinae* was prevalent, around 26° 08' 09" N, 97° 10' 42" W, Laguna Atascosa Wildlife Refuge, Cameron County, Texas, 23–25 May and 20–23 Jun, 2022. Sampling was conducted until ≥100 ixodids were collected on each day and stored in 70% alcohol-filled glass vials. The vials of ixodids were sent to the United States Department of Agriculture – Animal and Plant Health Inspection Service's National Veterinary Services Laboratory in Ames, Iowa, USA, for species identification of larvae, nymphs, and adults, and the sex of each

adult. The samples were collected to determine which ixodid genera and species were questing on *S. spartinae*.

#### Natural enemies of ixodids

***Uca rapax* populations and egg predation** At each of six locations in Cameron and Willacy counties (Table 1), five 10-m-long walking transects were conducted during which numbers of *U. rapax* holes were counted within 1.5 m on both sides of each transect. In *S. spartinae* habitats the person sampling had to walk between *S. spartinae* clumps instead of in a straight line.

At each of 12 locations in the same two counties (Table 1), a 470 ml plastic cup (10.5 cm × 9.9 cm × 7 cm, h × top diam × bottom diam) (Ball, Fishers, Indiana, USA) was buried flush to the lip 10–30 m apart at 1000 h to serve as a pitfall trap. Numbers of *U. rapax*, ants, and other arthropods collected in each were recorded 48 h after the traps were deployed.

Six marker flags were deployed >10 m apart from one another in *S. spartinae* habitats at each of six locations (Table 1) 12–15 Feb, 23–25 Apr, and 11–13 Jun 2018. At 1800 h a living 1 cm<sup>3</sup> *A. americanum* egg mass was placed at the base of each flag. At 0830 h on the following morning, the base of each flag was inspected for the presence of eggs. The eggs were deployed overnight because *U. rapax* mostly forages between dusk and dawn (Showler et al. 2019b).

**Other soil-associated natural enemies** Three pitfall traps were deployed at each of two *S. spartinae* habitats in Willacy County and four in Cameron County (Table 1); each sampling site was separated by ≥0.5 km. The pitfall traps were comprised of a 946.4 ml plastic drinking cup (17.8 cm × 10.9 cm × 9.8 cm, h × top diam × bottom diam) (Dart Solo, Dallas, Texas, USA) buried flush to its lip in the soil and filled halfway with ethylene glycol. A 22.9 cm diam paper plate (Harvest Pack, St. Paul, Minnesota, USA) was pierced 5 cm apart on each of two opposite sides and a 3.2 cm × 30.4 cm Ohuhu galvanized iron ground staple (Union City, California, USA) was fitted through each pair of holes. The legs of the staple were inserted in the soil on each side of the pitfall forming a shelter ≈4 cm overhead to slow evaporation and to protect the trap from being filled with debris. The traps were deployed on 2 May 2018 and collected 2 wk later on 16 May. The contents were poured onto a hand-held metal sieve (50 mesh/cm<sup>2</sup>) (TCP Global, San Diego, California, USA) and arthropods were counted and identified to family.

**Foliage-associated arthropods** Three sets of five 180° sweeps of a sweep net (38.1 cm diam, 1-m-long handle; 7600 Standard Series insect net with standard aerial bag, Bio Quip, Rancho Dominguez, California, USA) through the canopies of *S. spartinae* plants were conducted at each

of two *S. spartinae* habitats in Willacy County and four in Cameron County (Table 1) 23–25 Apr 2018. Collected arthropods were counted and identified to family.

### Statistical analyses

The two-sample t test (Analytical Software 2008) was used on data for temperature, relative humidity, soil salinity, numbers of *U. rapax* holes and *U. rapax* captured in pitfalls, and tick positions on *S. spartinae* leaves. One-way ANOVA was used for seasonal leaf shape data, means separated using Tukey's HSD (Analytical Software 2008). Percentage data was arcsin-square root-transformed before analysis (Analytical Software 2008). Because normality and homogeneity of variance assumptions were not violated, data were not log(x+1)-transformed.

## Results

### Soil salinity

Soils collected from *S. spartinae* habitat did not differ in terms of salinity from soils collected in mesquite-thorn scrub habitat (Showler and Osbrink 2020). Soil salinity in *S. spartinae* habitat was  $0.86 \pm 0.15$  mmhos/cm, and  $0.79 \pm 0.17$  mmhos/cm in mesquite-thorn scrub habitat.

### Plant habitat composition

In *S. spartinae*-dominated habitat, *S. spartinae* comprised 80–100% of the vegetational cover and in some places *S. spartinae* completely covered the soil surface (Table 2). Other plant species were less abundant (<5% ground cover) (Table 2). Most *S. spartinae* grew fully exposed to the sun interspersed by scattered *P. glandulosa* trees and small (<20 m<sup>2</sup>) patches of thorn scrub (Table 2 for broad-leaf species). Grasses in mesquite-thorn scrub habitat were mostly Vasey's grass, *Paspalum urvillei* Steud.; dallis grass, *Paspalum dilatatum* Poir., and little bluestem, *Schizachyrium scoparium* (Michx.) Nash (Table 2).

### Temperature and relative humidity of *S. spartinae* clumps

The temperature inside *S. spartinae* clumps in the winter was 4.5 °C lower than in the canopy ( $t=5.01$ ,  $df=1$ , 18,  $P=0.0001$ ) (Fig. 1). Relative humidity was 32.4% greater in the interiors of *S. spartinae* clumps than in the canopy ( $t=7.71$ ,  $df=1$ , 18,  $P<0.0001$ ) (Fig. 2). During spring, the temperature inside *S. spartinae* clumps was 3.5 °C lower than in the canopy ( $t=3.30$ ,  $df=1$ , 18,  $P=0.0040$ ) (Fig. 1). Relative humidity was 14.8% greater in the interiors of *S. spartinae* clumps than in the canopy periphery ( $t=3.24$ ,  $df=1$ , 18,  $P=0.0045$ ) (Fig. 2). In summer the temperature inside *S. spartinae* clumps was 3.1 °C lower than in the canopy ( $t=3.56$ ,  $df=1$ , 18,  $P=0.0022$ ) (Fig. 1) and relative humidity was 32.1% greater in the interiors of *S. spartinae* clumps than in the canopy ( $t=9.51$ ,  $df=1$ , 18,  $P<0.0001$ ) (Fig. 2).

### Leaf shape

Living *S. spartinae* leaves were  $64.7 \pm 4.9$  cm long. More than 98% of them were open or folded along  $\geq 80\%$  of their lengths. Excluding the wind-tattered distal 2–3 cm, dead dry leaves were all closed. In late January 2018,  $2.8\% \pm 2.8$  of the *S. spartinae* leaves were “folded”, forming a  $1.01 \pm 0.01$ -mm-wide groove or slot in the leaf instead of the  $3.94 \pm 0.08$ -mm-wide “V”. By late April, mid-June, and late October,  $86.1\% \pm 5.1$ ,  $63.9\% \pm 5.1$ , and  $57.5\% \pm 3.7$ , respectively, leaves were folded. Seasonal differences in numbers of folded leaves were detected, with 30.8-, 22.8- and 20.5-fold more in October, April, and June, respectively, than in January ( $F=50.27$ ,  $df=3$ , 23,  $P<0.0001$ ).

### Larvae and nymphs on individual *S. spartinae* leaves

*Amblyomma americanum* larvae and nymphs on living *S. spartinae* leaves were observed  $20.8 \pm 1.8$  cm and  $21.7 \pm 1.6$  cm from the distal end, respectively. Approximately  $44\% \pm 5.4$  and  $43\% \pm 4.2$  of larvae and nymphs, respectively, were within 10 cm of the leaf tips. Larval *A. americanum* were 1.7-fold more abundant ( $t=3.67$ ,  $df=1$ , 18,  $P=0.0018$ ) within the “V” of open leaves than nymphs (Fig. 3). Percentages of larvae within 10 cm of the distal end were  $\approx 1.8$ -fold more likely to be within the “V” than on the opposite side of the leaf ( $t=2.93$ ,  $df=1$ , 18,  $P=0.0089$ ) (Fig. 4). Percentages of nymphs were  $\approx 1.4$ -fold more abundant than larvae ( $t=2.73$ ,  $df=1$ , 18,  $P=0.0139$ ) on the opposite side of the “V” (Fig. 5). Larvae and nymphs were, on (pooled) average,  $16.0 \pm 3.3$  cm from the leaf tip on dead (closed) leaves, and 2.5- ( $t=2.45$ ,  $df=1$ , 18,  $P=0.0250$ ) and 2.2-fold ( $t=2.13$ ,  $df=1$ , 18,  $P=0.0472$ ), respectively, more numerous on living leaves than on dead leaves (Fig. 6). No ixodids were observed inside the lumens of dry, dead *S. spartinae* leaves.

In the second experiment, four of the *A. americanum* larvae were observed entering *S. spartinae* leaf slots. While  $3.5 \pm 0.3$  (70%) larvae were found on the external leaf surface 1 h after the larvae were released on the leaves,  $1.2 \pm 0.3$  larvae (24%) had taken refuge within the leaf slots. Most larvae, whether on the external leaf surface or in the leaf slot, were at the part of the leaf arc that was higher than the free-hanging distal end and the basal part of the leaf (due to negative geotactic ixodid behavior). A total of three larvae had fallen from the leaves during the experiment. The mean number of larvae on the external leaf surface was 2.9-fold greater than the number that was inside the leaf slot ( $t=4.87$ ,  $df=1$ , 18,  $P=0.0001$ ).

### Flag sampling natural ixodid populations

In mid-February and in late April 2018, questing flag-sampled larval, nymphal, and total ixodids were relatively common (Table 3). Whether absolute numbers of larvae, or clustered larval populations from an egg mass hatch were counted as one larva (to avoid introducing

**Table 2** Vegetation and estimated ground cover by each in cordgrass habitat and mixed low-salinity mesquite-thorn scrub habitat sampling habitats, Cameron and Willacy counties, Lower Rio Grande Valley, Texas, 26 Feb – 1 Mar 2018

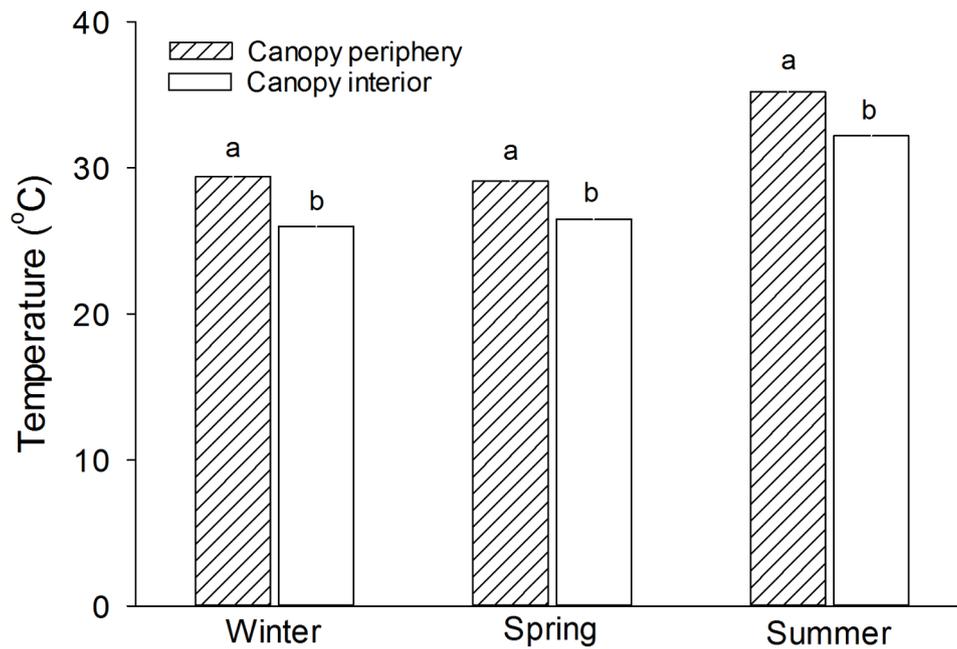
Habitat	Plants <sup>a</sup>	Percentage species <sup>b</sup>						
		Port Mansfield area sites		Holly Beach area sites				
		1	2	1	2	3	4	
<u>Cordgrass</u>	<i>Spartina spartinae</i> (Trin.) Merr. ex Hitchc. Gulf cordgrass	85	90	99	100	100	80	
	<i>Prosopis glandulosa</i> Torr. Honey mesquite	5	5				5	
	<i>Borrchia frutescens</i> (L.) DC Sea ox eye	5					5	
	<i>Mimosa pigra</i> L. Zarza		5	1			5	
	<i>Ziziphus obtusifolia</i> (W. Hooker ex J. Torrey & A. Gray) A. Gray Lote bush	5					5	
	Percentage ground cover <sup>b</sup>	80	90	100	100	100	90	
	<u>Mixed vegetation<sup>c</sup></u>	Grasses <sup>d</sup>	75	55	60	70	70	90
		<i>Mimosa pigra</i> L. Zarza	5	10	5		5	
		<i>Baccharis texana</i> (Torrey and A. Gray) A. Gray False prairie willow	15	10	10	20	10	5
		<i>Ziziphus obtusifolia</i> (W. Hooker ex J. Torrey & A. Gray) A. Gray Lote bush	5	5				
<i>Opuntia engelmannii</i> Salm- Dyck ex Engelm. Texas prickly pear						5	5	
<i>Solanum elaeagnifolium</i> Cav. Silverleaf nightshade			5					
<i>Salix</i> sp. Willow				15	10			
<i>Leucophyllum frutescens</i> (J. Berlandier) I.M. Johnston Purple sage			5	5		5		
<i>Larrea tridentate</i> (M. Sessé y Lacasta & J. Mociño ex A.P. de Candolle) F. Coville Creosote			5			10		
<i>Karwinskia humboldtiana</i> (J.A. Schultes) J. Zuccarini Coyotillo			5					
Percentage ground cover <sup>b</sup>	90	80	85	85	80	85		

<sup>a</sup>Other plant species occurred but in negligible (<0.5%) abundances

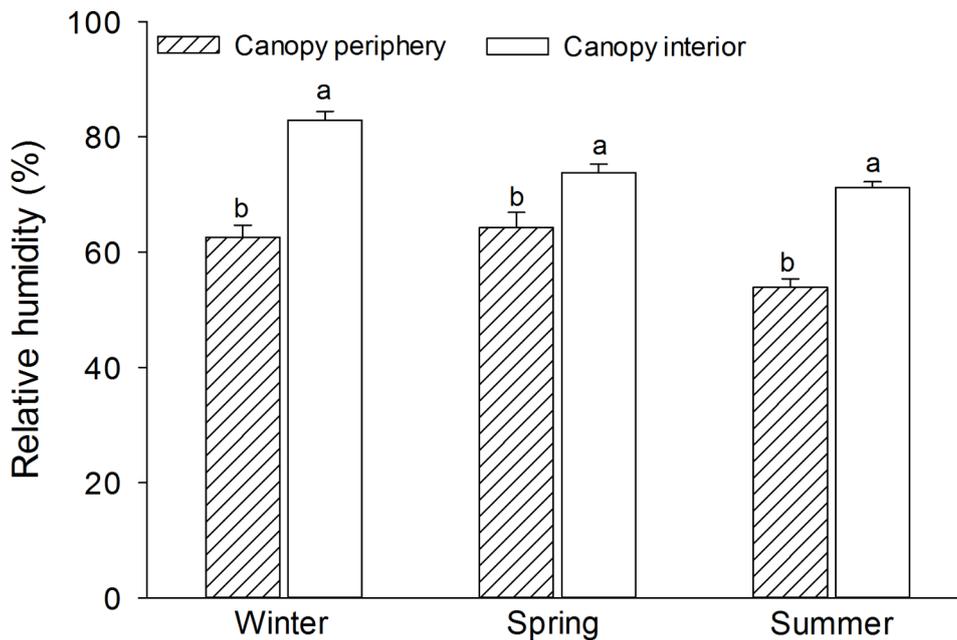
<sup>b</sup>Percentage of total plant ground cover

<sup>c</sup>Typical of low salinity soil

<sup>d</sup>Mostly hairy crabgrass, *Digitaria sanguinalis*; Vasey's grass, *Paspalum urvillei* Steud.; dallis grass, *P. dilatatum* Poir.; and little bluestem, *Schizachyrium scoparium* (Michx.) Nash



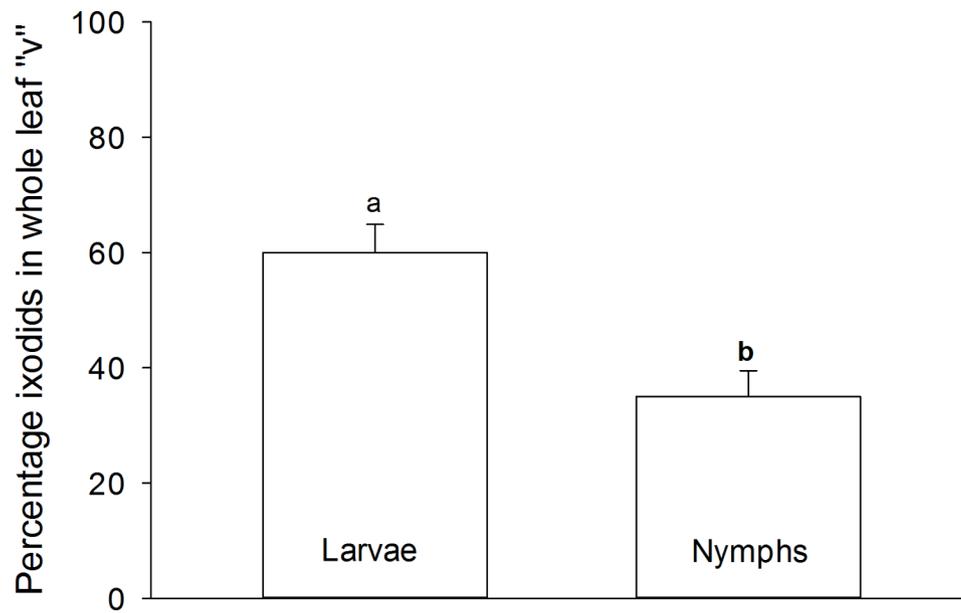
**Fig. 1** Temperatures in the interior and on the exterior of *Spartina spartinae* clumps, 14 Feb, 24 Apr, 12 Jun 2018, Cameron County, Texas, two-sample t test, 10 replicates, different letters over the bars within each cluster indicate a significant ( $P < 0.05$ ) difference ( $\pm$ SEs do not show on the bars because each was  $< \pm 0.7$ )



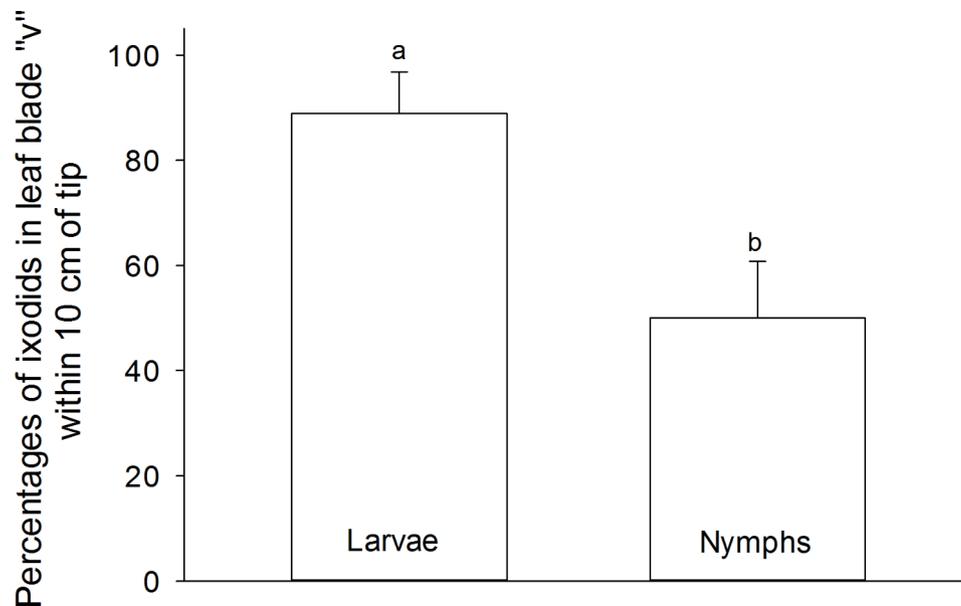
**Fig. 2** Relative humidity in the interior and on the exterior of *Spartina spartinae* clumps, 14 Feb, 24 Apr, 12 Jun 2018, Cameron County, Texas, two-sample t test, 10 replicates, different letters over the bars within each cluster indicate a significant ( $P < 0.05$ ) difference

substantial variation), differences between questing larval abundances on *S. spartinae* and mesquite-thorn scrub were not detected. In mid-June, differences were also not detected for questing larval, adult, and total ixodids, but nymphs were 5.8-fold more abundant in mesquite-thorn scrub than on *S. spartinae* ( $t=2.10$ ,  $df=1$ ,  $18$ ,  $P=0.0439$ ) (Table 3).

Ixodid samples collected from *S. spartinae* 20–23 Jun 2022 contained individuals, including larvae (91%), nymphs (5.5%), and adults (3.5%) of six species: *A. maculatum* (0.1%); the northern cayenne tick, *Amblyomma mixtum* Koch (0.1%); the false cayenne tick, *Amblyomma tenellum* Koch (8.5%); the tropical horse tick, *Anocentor nitens* (Neumann) (1.9%); the American dog tick,



**Fig. 3** Mean percentages of larval and nymphal *A. americanum* located within the upper "V"-shaped surface of living *S. spartinae* leaves, 14 Feb 2018, Cameron County, Texas, two-sample t test, 10 replicates (each replicate comprised of 10 subsamples), different letters over the bars indicate a significant ( $P < 0.05$ ) difference

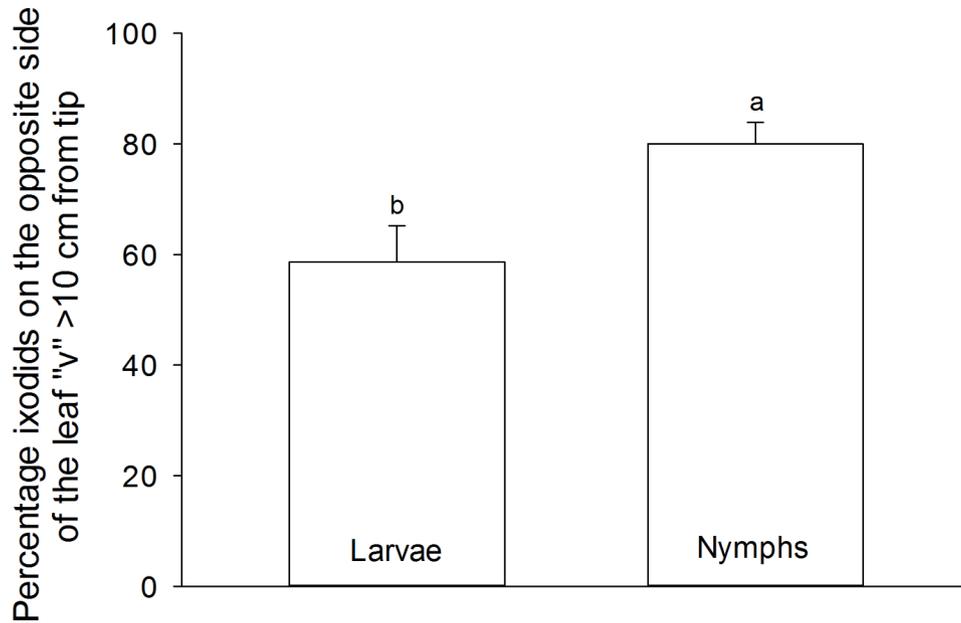


**Fig. 4** Mean percentages ( $\pm$ SE) of larval and nymphal *A. americanum* located within 10 cm of the leaf blade tip were found inside the living *S. spartinae* leaf "V", 14 Feb 2018, Cameron County, Texas, two-sample t test, 10 replicates (each replicate comprised of 10 subsamples), different letters over the bars indicate a significant ( $P < 0.05$ ) difference

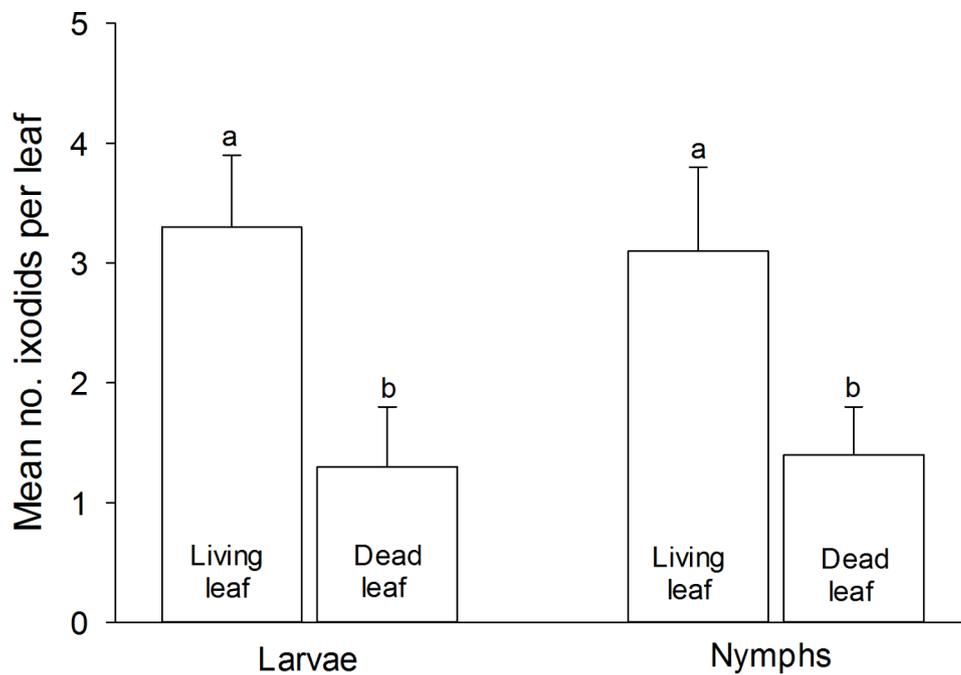
*Dermacentor variabilis* (Say) (0.3%); and *R. (B.) microplus* (89.1%) (Table 4). *Anocentor nitens* and *R. (B.) microplus* are one-host ixodids, hence, only larvae were detected on the vegetation (Table 4). *Rhipicephalus (B.) microplus* larvae constituted 97.9% of the total number of larvae (Table 4).

**Natural enemies of ixodids**

***Uca rapax* populations and egg predation** Numbers of *U. rapax* holes were not different between the *S. spartinae* and mesquite-thorn scrub habitats, with a pooled average of  $0.34 \pm 0.17$  holes/m<sup>2</sup>. Numbers of pitfall-collected *U. rapax* were also not different, with a pooled mean of  $0.20 \pm 0.13$ /trap.



**Fig. 5** Mean percentages ( $\pm$ SE) of larval and nymphal *A. americanum* located on the opposite (outer) part leaf blade "V" on living *S. spartinae* leaves, 14 Feb 2018, Cameron County, Texas, two-sample *t* test, 10 replicates (each replicate comprised of 10 subsamples), different letters over the bars indicate a significant ( $P < 0.05$ ) difference



**Fig. 6** Mean ( $\pm$ SE) numbers of larval and nymphal *A. americanum* on living and dead *S. spartinae* leaves, 14 Feb 2018, Cameron County, Texas, two-sample *t* test, 10 replicates (each replicate comprised of 10 subsamples), different letters over the bars within each cluster indicate a significant ( $P < 0.05$ ) difference

Negligible numbers ( $\leq 1$ ) of *A. americanum* egg masses were removed in *S. spartinae*-dominated habitats during the night regardless of the season. The egg masses were all intact and had not been disturbed.

**Other soil-associated natural enemies** Ground-associated arthropods were sparse in *S. spartinae* habitats with

$\leq 1.2$  individuals of each taxa (Table 4) collected over a 2-wk period. Only blattellids (wood cockroaches) were more abundant at  $5.5 \pm 3.4$ /trap. Predators included *U. rapax*, scorpions, spiders, formicids, elaterids, and reduviids (Table 5).

**Table 3** Mean ( $\pm$ SE) numbers of ticks collected in winter, spring, and summer seasons of 2018 per 50 m flag transect sample in *S. spartinae*-dominated areas and in habitats comprised of mixed vegetation typical of low-salinity soils, Cameron and Willacy counties, Texas

Season 2018 <sup>a</sup>	Habitat <sup>b</sup>	Tick life stage <sup>b</sup>			Total ticks <sup>c</sup>
		Larvae	Nymphs	Adults	
Winter	Gulf cordgrass	0.54 $\pm$ 0.17	0.61 $\pm$ 0.17	0.04 $\pm$ 0.04	1.18 $\pm$ 0.28
	Mixed low-salinity Vegetation	0.96 $\pm$ 0.24	0.89 $\pm$ 0.19	0.04 $\pm$ 0.04	1.89 $\pm$ 0.38
Spring	Gulf cordgrass	4.2 $\pm$ 2.5	2.9 $\pm$ 0.8	0.06 $\pm$ 0.06	7.2 $\pm$ 2.8
	Mixed low-salinity vegetation	15.5 $\pm$ 13.5	3.6 $\pm$ 1.9	0.06 $\pm$ 0.06	19.2 $\pm$ 13.3
Summer	Gulf cordgrass	12.2 $\pm$ 8.1	0.7 $\pm$ 0.3b	0.2 $\pm$ 0.1	13.2 $\pm$ 8.1
	Mixed low-salinity vegetation	6.4 $\pm$ 3.6	4.1 $\pm$ 1.6a	0.4 $\pm$ 0.2	10.8 $\pm$ 3.9

Means followed by different letters within each season and tick life stage are significantly different ( $P < 0.05$ )

<sup>a</sup>Winter, 26 Feb – 1 Mar; spring, 23–26 Apr; summer, 11–13 Jun 2018

<sup>b</sup>The gulf cordgrass habitat was comprised of  $\geq 80\%$  *S. spartinae*, mixed low-salinity vegetation habitat typically included grasses (mostly hairy crabgrass, *Digitaria sanguinalis*; buffelgrass, *Pennisetum ciliare* (L.) Link; Vasey’s grass, *Paspalum urvillei* Steud.; and dallis grass, *P. dilatatum* Poir.) and broadleaf species (e.g., zarza, *Mimosa pigra* L.; false prairie willow, *Baccharis texana* (Torrey and A. Gray) A. Gray; and lote bush, *Ziziphus obtusifolia* (W. Hooker ex J. Torrey & A. Gray) A. Gray)

<sup>c</sup>Tick species were not identified

**Table 4** Larval, nymphal, and adult ixodid species, collected from *Spartina spartinae*, Laguna Atascosa Wildlife Refuge, Cameron County, Texas, 20–22 June, 2022

Ixodid species	Larvae	Nymphs	Adults	
			♀	♂
<i>Amblyomma maculatum</i>	0	0	0	1
<i>Amblyomma mixtum</i>	0	1	0	0
<i>Amblyomma tenellum</i>	0	42	8	16
<i>Anocentor nitens</i>	15	0	0	0
<i>Dermacentor variabilis</i>	0	0	1	1
<i>Rhipicephalus (Boophilus) microplus</i>	694	0	0	0

Total ixodids: 779

**Foliage-associated arthropods** Sweep net collected arthropods were sparse, usually  $\leq 4$  per sample, and mostly small ( $\leq 1$  mm long) (Table 6). The most common arthropods were cicadellids and dipterans. Predators were limited to negligible numbers ( $< 3$ /trap) of linyphiid and salticid spiders, and one reduviid.

**Discussion**

Terrestrial plant communities on the South Texas coastal plain generally conform to one of three vegetational habitats. One habitat is characterized by *B. frutescens* that grows in dense stands on saline (6.8–91.0 mmhos/cm) soils created by occasional wind tides and infrequent storm surges from the hypersaline Lower Laguna Madre (Showler et al. 2019b; Showler and Pérez de León 2020). Hypersaline bay water is lethal to ixodid eggs but saline

**Table 5** Arthropod orders and families collected in pitfall traps from *Spartina spartinae* habitats, Cameron and Willacy counties, Texas, 2–16 May 2018

Order	Family
Decapoda	Ocypodidae
Isopoda	Oniscidae
Scorpiones	Buthidae
Opiliones	Phalangiidae
Aranaea	Linyphiidae
	Lycosidae
Isoptera	Termitidae
Coleoptera	Cerambycidae
	Elateridae
	Scarabaeidae
	Tenebrionidae
	Trogidae
Homoptera	Reduviidae
Hymenoptera	Formicidae
Orthoptera	Blattellidae

soil is not particularly ovicidal (Showler et al. 2019b). On the other hand, saline soil is associated with large, dense populations of *U. rapax*, an efficient ixodid egg predator (Showler et al. 2019b). Relative to mesquite-thorn scrub, ixodid numbers in dense stands of *B. frutescens* are negligible (Showler et al. 2019b). The second major vegetational habitat is comprised of mesquite-thorn scrub typical of low salinity soil on the coastal plain and the third is dominated by *S. spartinae* (Showler et al. 2019b), also on low salinity soil. Other habitats (e.g., sand dunes, marsh, hardwood forest) are spatially limited relative to

**Table 6** Arthropod orders and families collected in sweep net samples from *Spartina spartinae*, Cameron and Willacy counties, Texas, 23–25 Apr 2018

Order	Family
Aranaea	Linyphiidae
	Salticidae
Diptera	Chironomidae
	Muscidae
	Phoridae
	Tephritidae
Coleoptera	Cantharidae
	Chrysomelidae
Homoptera	Cicadellidae
	Reduviidae
Hymenoptera	Formicidae
	Parasitic wasp spp.
Orthoptera	Phasmatidae

areas of mesquite-thorn scrub (grasses are a component) and *S. spartinae*-dominated areas.

The relatively low soil salinity in the *S. spartinae* habitat indicates that salinity is not an ixodid mortality factor (Showler et al. 2019b). *Uca rapax* is an effective ixodid egg predator in typically saline, *B. frutescens*-dominated habitats (Showler et al. 2019b), but because soil salinity was low in *S. spartinae* habitats, so, too, were *U. rapax* populations. Hence, *U. rapax* predation on ixodid eggs in mesquite-thorn scrub habitats and in *S. spartinae*-dominated habitats was negligible. Sweep net and pitfall arthropod sampling yielded few predators and did not suggest the existence of predatory species and populations that might appreciably suppress ixodid abundances. Predatory ants have been implicated with the suppression of ixodid populations (Fleetwood et al. 1984; Sutherst et al. 2000), but recent research demonstrated that ants, including *S. invicta*, of the South Texas coastal plain wildlife corridor, West Texas (Brewster County), and the Texas Hill Country (Kerr County), do not attack *A. americanum* eggs, larvae, nymphs, unfed adults, and blood-engorged adults (Showler et al. 2019a, b). Some ixodid genera (i.e., *Amblyomma*, *Dermacentor*, and *Rhipicephalus*) emit an allomone that masks them from being recognized by ants as food (Yoder et al. 1992, 2009; Yoder and Domingus 2003; Showler et al. 2019a). Pressure from natural enemies in *S. spartinae* habitat does not appear to strongly affect ixodid survival.

Ixodid populations tend to increase during and after rainy periods and to decrease in dry times (McCulloch and Lewis 1968; Rawlins 1979; Daynes and Gutierrez 1980; Cardozo et al. 1984). As a group, ixodids can survive longer than many other arthropods without drinking water because they can also absorb moisture from the air (Needham and Teel 1991; Perret et al. 2003). While ambient temperature and humidity are important to ixodid (especially the larval stage) survival (Davey et al. 1991,

1994; Estrada-Peña 2001; Corson et al. 2004; Estrada-Peña and Vanzal 2006), localized factors can affect it by modifying temperature and humidity (Wilkinson and Wilson 1959; Cherny and de la Cruz 1971; Branagan 1978; Sutherst 1983; Sutherst et al. 1983; Utech et al. 1983; Sutherst and Maywald 1985; Perret et al. 2003). Ixodids interact with plants in a variety of ways, particularly by climbing vegetation to quest for passing hosts (Garris and Popham 1990; Schulze et al. 2001a; Perret et al. 2003; Randolph 2004). Anomalies related to ixodid populations and levels of activity suggest that microclimatic factors related to vegetation influence ixodid survival (Hoogstraal 1956; Branagan 1978; Perret et al. 2003); at the drier margins of ixodid habitats, for example, relative humidity within plant transpirational microclimates can be important to survival (Branagan 1978; Perret et al. 2003). The brown ear tick, *Rhipicephalus appendiculatus* Neumann, for instance, is usually confined to areas that offer particularly favorable conditions, such as dense grass cover (Yeoman and Walker 1967), and Yeoman (1967) correlated reduced grass cover with declining ixodid abundances because sparse grass cover exposes ixodids to lethal desiccating climatic factors. Phillips et al. (2014) suggested that *R. microplus* and *R. annulatus* were more likely to be found at the edges of thorn thicket and *P. glandulosa* patches than in adjacent open grassy areas because the former habitats are more favorable and because hosts often take refuge in dense vegetative cover to avoid desiccation. Survival of *R. microplus* was 61.5–76.9% lower in open habitats dominated by buffelgrass, *Pennisetum ciliaris* (L.) Link, than in *P. ciliaris* under *P. glandulosa* canopy (Davey et al. 1994). Questing *A. americanum* are also particularly abundant along shady woodland cattle and deer trails and in shady places in pastures (Harris and Burns 1972; Goddard 1992; Schulze et al. 2001b). Further, plant morphology and plant surface moisture can affect larval ixodid clustering (Sutherst 1983) and longevity (Garris and Popham 1990; Perret et al. 2003).

Areas dominated by *S. spartinae* tend to have little or no tree overstory shade that would provide reduced temperatures and increased relative humidity levels favoring ixodids more than conditions of direct sunlight (Perret et al. 2003). *Spartina spartinae* plants, however, themselves provision lower temperatures and greater relative humidities within the dense basal clump relative to the canopy where questing occurs. The lower numbers of questing nymphs collected from *S. spartinae* compared to mesquite-thorn scrub in the summer suggest that ambient daytime conditions on the sun-exposed *S. spartinae* canopy (not necessarily inside the clump) can be lethal. Ixodids likely find refuge in the clump's interior during unfavorably hot and dry conditions. Using an automated video tracking system that continuously recorded

movements of immature sheep ticks, *Ixodes ricinus* L., Perret et al. (2003) found that the parasites ascended plants to quest and intermittently descended to microhabitats on the same plant and on the soil where standing and airborne moisture (humidity) allow for rehydration before they ascended again to continue questing.

Ixodid questing involves expenditure of energy and water loss in search of nourishment from hosts (Perret et al. 2003). Larvae, however, can survive off-host for 8–9 mo in hot semi-arid environments before they expire from starvation (Hitchcock 1955; Utech et al. 1983; Needham and Teel 1991; Perret et al. 2003). Individual *S. spartinae* clumps provided substrates for questing and for intermittent (quiescent) periods of rehydration in protected microenvironments. While temperature and relative humidity conditions in the basal parts of the *S. spartinae* clumps were significantly different from the more exposed canopy, and potentially able to protect ixodids from desiccation, the shapes of living *S. spartinae* leaf blades also might affect ixodid survival. During cool months, *S. spartinae* leaf blades present a long concave surface that likely conserves humidity on the concave side, and morning dew was retained longer in the relatively open “V” and in the slot-shaped “folded” leaves than on the more exposed, convex side of the leaves. Conservation of humidity and moisture in the concave side is suggested by the larger percentage of *A. americanum* larvae observed in the “V” than on the convex side, even though the concave side of the leaves usually faced up. The body surface area:volume ratio is smaller in nymphs than in larvae and less conducive to integumentary water loss, hence, nymphs might rely less than larvae on being in the convex side of the leaf blade “V” or in the slot-like fold for survival. Questing larval *A. americanum* were most abundant in the distal 10 cm of the open leaf “V” where it is possible that relative humidity was greater than on the convex side. The greater numbers of *A. americanum* larvae and nymphs on living than on dead *S. spartinae* leaves were likely because of the humidity- and dew-conserving “V” shape of many living leaves in contrast with the exposed outer surface of the dead, dry, and completely furled leaves. Living leaves were also more erect (>45° angle relative to the soil surface) than dead leaves (most <45° relative to the soil surface) which were likely less preferred by negatively geotaxic ixodids (Kroeger et al. 2013; Romaschenko et al. 2013). Dead leaves, being dry, were also unlikely to conserve as much moisture as living leaves that contain water.

During most of the year, when the weather is warm, *S. spartinae* leaf shape changes from the “V” to a narrow slot. While field sampling, two instances occurred where larval ixodids (species not determined), sometimes >10 individuals, within a leaf slot dropped from the slot onto an exposed human forearm that was inadvertently

brushed against the leaves. The experiment conducted at KBUSLIRL demonstrated that larval ixodids actively enter *S. spartinae* leaf slots under conditions of direct sunlight and warm temperatures. Although more *A. americanum* larvae in the experiment were observed on the exterior surfaces of *S. spartinae* leaves than inside the leaf slots, it is nevertheless important that a substantial percentage of the larvae entered the leaf slots. The narrow leaf slots likely provide favorable conditions for ixodid larvae at their questing sites, particularly during desiccating ambient conditions. It was expected that a proportion of the larvae would be questing while a minority moved into the protected leaf slot to rehydrate.

*Spartina spartinae*-dominated habitats on the wildlife corridor generally have two spatial configurations. In many areas *S. spartinae* clumps are not densely packed together, with bare and lightly vegetated areas surrounding each clump or small group of clumps. The “loose” configuration of clumps affords ungulate hosts numerous choices of paths to traverse and a herd can disperse among the clumps while retaining cohesion. Alternatively, in areas where *S. spartinae* clumps are dense, tightly abutting one another, the soil surface is often >90% obscured by matted leaves; ungulate trails are fewer and more clearly defined than in the “loose” configuration. Hence, in dense *S. spartinae* stands, movement of ungulates is largely confined to established trails beyond which some ixodid species populations might be lower. Because ixodid abundance is substantially influenced by host frequency (Branagan 1978), distribution of ixodids that are restricted to ungulate hosts, such as *R. microplus* (a one-host parasite) larvae, in relatively widely spaced *S. spartinae* habitat might be more uniform than where *S. spartinae* clumps are sufficiently dense to confine ungulates to well-defined trails. Ixodid species parasitizing small hosts that can easily move through dense *S. spartinae* habitat, however, likely have less restricted distributions.

*Spartina spartinae* occupies substantial areas of the South Texas coastal plain wildlife corridor. Ixodid populations are not appreciably different between *S. spartinae* and mesquite-thorn scrub habitats likely because neither habitat involves high soil salinity that favors *U. rapax* egg predation, and the mostly nonshaded *S. spartinae* offers refuges from desiccation for reabsorbing water within the leaves and in the interiors of plant bases between periods of questing. Our study demonstrated that multiple ixodid species, including larvae, nymphs, and adults, occur on *S. spartinae*. It is likely that any ixodid species in that habitat will quest on *S. spartinae*, as well as other plant species. Surveillance for ixodids should include *S. spartinae* habitats while recognizing that quiescent ixodids are not detected; only actively questing individuals collected using flags and other methods that select for questing

ixodids, are detected. Basing ixodid population estimates on flag sampling (and other means of exclusively sampling for questing individuals) is likely to skew data by not including quiescent cohorts. Our findings indicate that ixodids, on *S. spartinae* and possibly other plant species, can reabsorb water in more than one place on the plant where they are not questing and available to be sampled using flagging (Perret et al. 2003).

Located in the Cattle Fever Tick Quarantine Zone in South Texas, this study indicated that *R. (B.) microplus* larvae occurred as a relatively heavy infestation on vegetation in contrast to single specimens collected on vegetation at two locations in the same quarantine zone in 2018 (Osbrink et al. 2020). The large numbers of *R. (B.) microplus* larvae on vegetation is the result of substantial reproduction in the Texas quarantine zone. Vigilance outside of the quarantine zone warrants intensification (Showler and Pérez de León 2020, Showler et al. 2021). For surveillance involving populations on vegetation, *S. spartinae* habitat should be given as much attention as other habitats.

This study demonstrates that *S. spartinae* habitats on the South Texas coastal plain do not harbor soil-borne and foliar predatory arthropods in sufficient abundances to govern ixodid population levels. Soil and water salinity, both of which are lethal particularly to ixodid eggs (Showler et al. 2019b), are also not substantial mortality factors in the *S. spartinae* habitat. High ambient temperature and low relative humidity can each, and in combination, induce lethal desiccation to off-host ixodids. The *S. spartinae* plant offers two possible refuges in which ixodids can undergo rehydration quiescence: in the basal clamp and within concave parts of leaf blades.

Relating pertinent ecological compartments has provided clarity in terms of how a medically and agriculturally important arthropod can survive in environmental systems, using the cordgrass habitat as an example, that would otherwise be lethal. Understanding of environmental systems by determining abiotic and biotic ecological compartments can contribute to new opportunities to manage such pests.

#### Acknowledgements

Thanks to Wayne Ryan for rearing *A. americanum* and to William Brady for assistance in the field, and James Mertins for identification of ixodids collected from gulf cordgrass.

#### Author contributions

ATS had lead role in all matters pertaining to this study.

#### Funding

No funding was obtained for this study.

#### Data availability

All data generated or analyzed during this study are included in this published article.

## Declarations

### Ethics approval and consent to participate

This article does not contain any studies involving humans and animals other than their arthropod pests.

### Consent for publication

Consent given.

### Competing interest

The author declares that there was no conflict of interest.

Received: 24 May 2023 / Accepted: 1 July 2023

Published online: 11 August 2023

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