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Assemblage Organization of Surface-Active
Arthropods in Sonora Desert
Dune Ecosystems

Clifford S. Crawford

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Horizontal Moisture Gradients in a Coastal Sonoran
Desert Ecosystem

Clifford S. Crawford
Mariel L. Campbell
William H. Schaedla
Sarah Wood

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**ASSEMBLAGE ORGANIZATION OF SURFACE-ACTIVE
ARTHROPODS IN SONORAN DESERT
DUNE ECOSYSTEMS**

Clifford S. Crawford

Department of Biology
University of New Mexico
Albuquerque, NM 87131, USA

ABSTRACT

I tested the hypothesis, in northwestern Sonora, that temporal patterns of organization among surface-active arthropods resemble each other in dune and interdune habitats from coastal (Puerto Peñasco) and inland (Gran Desierto) dune ecosystems. Seasonal (October and May) counts of arthropods at 12-h intervals were made from pitfall-trap grids at both sites. Although the coastal interdune had the greatest plant cover (32%), rarefaction analysis showed its expected species richness of arthropods, $E(S_n)$, to be similar to richness in the inland interdune. In both interdune habitats, $E(S_n)$ was significantly greater in spring than fall, and generally much greater than in dune habitats. Both $E(S_n)$ and trap-capture frequencies averaged higher at night than during the day in all habitats.

Values of Hill's N_2 diversity and Hill's modified E_5 evenness in coastal and inland interdune assemblages were similar at night in spring. Otherwise, few correlations involving habitat, season, and diel time were evident, except that evenness was usually greatest at night. Neither plant cover nor recent precipitation at the coast were correlated with species richness. Species turnover (Sørensen's Index) was greater between inland habitats than between interdune habitats when sites were compared. Overall, evidence for consistent resemblance in assemblage organization between similar habitats -- especially dunes -- over seasonal and diel time was not strong.

RESUMEN

En el noroeste de Sonora probé la hipótesis de la similitud de los patrones de organización temporal de artrópodos en hábitats de dunas e interdunas de los ecosistemas de la costa (Puerto Peñasco) y continental (Gran Desierto). Censos de artrópodos con intervalos de 12-h fueron efectuados temporalmente (Octubre y Mayo) usando transectos de trampas de agujero (pitfall trap) en ambos sitios. Aunque el área de interduna en la costa tenía la mayor cobertura vegetal (32%), el análisis de "rarefaction" mostró que la riqueza calculada de especies de artrópodos, $E(S_n)$, es similar a la del área de interduna continental. En ambos hábitats de interduna, $E(S_n)$ fue significativamente mayor en primavera que en otoño, y generalmente mayor que en los hábitats de dunas. Ambos valores, $E(S_n)$ y la frecuencia de captura por trampa, promediaron valores más altos durante la noche que durante el día en todos los hábitats.

Los valores de diversidad de Hill N_2 y el modificado E_5 de similitud de Hill, en las congregaciones de interduna de la costa y continental fueron similares durante la noche en primavera. Por otro lado, hubo muy poca correlación entre hábitats, temporada y hora del día, excepto en que la similitud fue mayor durante la noche. Ni la cobertura vegetal ni la reciente

precipitación pluvial en la costa tuvieron correlación con la riqueza de especies cuando fueron comparadas. El índice de incorporación de especies (índice de Sørensen) fue mayor entre hábitats continentales que el de interdunas. En general, la evidencia de similitudes en la organización de las congregaciones, entre hábitats semejantes, especialmente en dunas, durante temporadas y hora del día no fue evidente.

INTRODUCTION

Arthropod assemblages in desert dune ecosystems consist of unexpectedly large numbers of species (e.g. Pierre 1958, Holm and Scholtz 1979) that vary considerably in space and time wherever their populations have been studied (e.g. Ghabbour et al. 1977, Crawford and Seely 1987, Crawford 1988). Climatic and topographic instability clearly account for some of this variation (Seely and Louw 1980), as should the age and degree of isolation of a given dune field.

Little attention, however, has been paid to patterns of species richness and diversity that underly assemblage organization in different desert dune ecosystems. In this paper I examine such patterns, as they relate to diel and seasonal time, in coastal and inland dune ecosystems of northwestern Sonora. In doing so I test the null hypothesis that there are no important differences in the temporal organization of assemblages from similar coastal and inland dune ecosystem habitats.

STUDY AREA

Study sites with dune and interdune habitats (Fig. 1) were located approximately 1) 5 km east of the Centro de Estudio Desierto y Oceaneo (CEDO) on the coastal outskirts of Puerto Peñasco, Sonora, and 2) 10 km northeast of Gustavo Sotelo, a small railroad stop about 35 km northwest of Puerto Peñasco and 6 km inland from Adair Bay on the upper Gulf of California. The coastal site consisted of low dunes within 50-200 m of the intertidal zone, together with more level "interdune" plains beyond. Separated from the coastal site by 40 km, the inland site was situated roughly 2 km into the Gran Desierto dune field. A faint vehicular track connects Gustavo Sotelo with the dune field.

Rainfall at Puerto Peñasco is sparse and variable (Ezcurra and Rodriguez 1986); it averaged 122 mm between 1960 - 1977 (Durrenberger and Xicotencatl Murrieta 1978), with most arriving between September and December. Monthly temperatures averaged about 30°C in July and August and 11°C in December and January (Durrenberger and Xicotencatl Murrieta 1978). Climatic data do not exist



Fig. 1. Dune-interdune study sites. Top: coastal site with large *Atriplex canescens* on dune, and *Ambrosia dumosa* (light) as well as *Frankenia palmeri* (dark) shrubs in interdune. Bottom: inland site showing dune with *Croton wigginsii* (foreground, right) and possibly *Asclepias subulata* (foreground, center) and *Ephedra trifurca* part way down slope, also mainly *E. trifurca* and *Helianthus niveus* in broad interdune; Sierra Pinacate in distance above the dunefield.

for the inland region, but should be generally similar, except that dewpoint is occasionally reached at night on the coast (CEDO weather records).

Colorado Valley type vegetation, i.e. pure stands of widely spaced shrubs, characterizes the region as a whole (Johnson 1982). Study site descriptions are given below. Habitats studied had sandy substrates that were more consolidated in interdunes than dunes. Sand grain texture was coarser at the coast than inland.

MATERIALS AND METHODS

Surface activity of arthropods was measured using pitfall traps, usually in single grids of 25, each trap being 5 m apart. Except for one inland interdune grid, each was used for at least two seasons. Traps were constructed of plastic cups, 9 cm in diameter at the opening and 11.5 cm deep. Two cups, one inside the other, were positioned with their openings at the ground surface. The inner trap was removed for specimen counts; arthropods not retained as vouchers were released, after counting, on the surface at least 1 m from a given trap. Diurnal and nocturnal specimen counting occurred as close as possible to sunset and sunrise, respectively.

Sampling at the coast took place in October 1983 (nine successive 12-h grid counts per habitat) and in May 1984, October 1984, and May 1985 (each of these periods with four successive grid counts per habitat). Sampling at the inland site took place only in May 1984 (two interdune grids and one dune grid, each with four successive counts) and October 1984 (four successive grid counts per habitat).

Specimens were identified to species when possible; alternatively they were described as morphospecies. Functional categories included 1) "carnivores," i.e. species with at least mainly predaceous immature stages; 2) "detritivores," i.e. mainly saprophagous species, at least as juveniles; 3) "herbivores," and 4) ants, which I considered to be mostly omnivores or granivores. Surface-active mites and collembolans were not counted, while tiny *Anthicus* sp. coleopterans (*Anthididae*) were counted but not included in analyses because of their size.

Indices of richness (i.e. rarefaction), diversity (Hill's N_2), and evenness (modified Hill's E_5 ratio) were calculated using licensed software programs available in Ludwig and Reynolds (1988). Sørensen's similarity index (Magurran 1988) was used to calculate species turnover (beta-diversity). Importance value of vegetation was calculated as relative density + relative dominance + relative frequency (Cox 1985).

RESULTS

Habitat-specific vegetation

Vegetation at the coastal and inland sites differed markedly; however, shrubs were visually dominant relative to forbs and grasses in both places. There was no overlap of obvious plant species between coastal and inland interdune habitats (Tables 1 and 2). In the latter, low-lying hummocks of the borage, *Tiquilia palmeri*, accounted for over half of the total plant cover. Total cover at the coastal interdune was 3 - 4 times that of the inland interdune, which was in turn about twice that of each dune habitat.

Vegetation characteristics within circles 1 metre in diameter around each pitfall trap are summarized in Table 3. In dune habitats, distances from traps to nearest plants averaged 4 - 5 times those of interdune habitats. Plant species richness and cover in interdune habitat circles at both sites greatly exceeded richness and cover in dune habitat circles.

Trap capture frequencies

The habitat-specific capture frequencies of surface-active arthropods averaged between 0% and 77% (Table 4). Average frequencies were nearly always greater in spring than in fall, especially at night. Average frequencies from interdune habitats were always greater than those recorded simultaneously from dune habitats. The average \pm SE percentage of captures with ants was $50.7 \pm 3.4\%$ ($n = 60$), compared to $42.9 \pm 3.3\%$ ($n = 59$) without ants.

Arthropod species richness, diversity, and evenness

Arthropod species and morphospecies collected in pitfall traps during study periods are listed, in Table 5, as a function of presumed trophic level, and relative to habitat, season, and diel intervals when trapping occurred. The list is conservative because I lumped species (e.g., of lycosid spiders) when unsure of their identities. The list includes a total of 61 "species." Of these, I considered 23 to be carnivores, 23 to be detritivores, and seven to be herbivores, while eight are ants. A breakdown of these categories, by site and habitat, is given in Table 6, which shows that while detritivore species were more abundant than those of carnivores in dune habitats, both trophic groups were about equally represented in interdune habitats.

Rarefaction analysis of all species except anthicid beetles and ants was used to compare habitat-specific species richness at the smallest sample size in any

Table 1

Importance values (and percentage cover) at the coastal site of dune and interdune vegetation. Measured 3 November 1983.

Habitat	<i>Atriplex canescens</i>	<i>Atriplex</i> sp.	<i>Ambrosia dumosa</i>	<i>Frankenia palmeri</i>	<i>Aristida</i> sp.	Total cover (%)
Dune	113 (3.5)			187 (0.1)		(3.6)
Interdune	34 (0.7)	8 (2.2)	66 (11.0)	128 (17.4)	126 (0.7)	(32.0)

Table 2

Importance values (and percentage cover) at the inland site of dune and interdune vegetation. Measured 15 May 1984.

Habitat	<i>Tiquilia palmeri</i>	<i>Dalea</i> sp.	<i>Helianthus niveus</i>	<i>Larrea tridentata</i>	<i>Ephedra trifurca</i>	<i>Croton wigginsii</i>	Total cover (%)
Dune						3 (4.4)	(4.4)
Interdune	210 (4.8)	51 (1.8)	11 (0.5)	16 (1.1)	13 (0.6)		(8.8)

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Table 3.

Pitfall trap distances to nearest plant, and vegetation characteristics within 1-m diameter circles surrounding pitfall traps in coastal and inland dune and interdune habitats.*

Site/habitat	Distance (m) to nearest plant $\bar{x} \pm SE$	No. of plant species in circles $\bar{x} \pm SE$	Estimated plant cover in circles $\bar{x} \pm SE$
Coastal dune	2.22 \pm 0.90	0.24 \pm 0.10	7.20 \pm 3.20
Coastal interdune	0.45 \pm 0.09	1.76 \pm 0.91	19.40 \pm 4.52
Inland dune	2.75 \pm 0.52	0.08 \pm 0.06	1.20 \pm 0.90
Inland interdune	0.48 \pm 0.12	1.20 \pm 0.25	10.00 \pm 2.27

* All measurements made between 12-15 May 1984.

Table 4

Mean seasonal and diel trap capture frequencies (%) relative to site and habitat and to presence and absence of ants.
(n = number of 12-h sampling periods)

Habitat/traps with or without ants	Diurnal		Nocturnal		Diurnal		Nocturnal	
	$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$	(n)	$\bar{x} \pm SE$	(n)
Costal dune/with	3.0 \pm 1.9	(4)	70.0 \pm 13.5	(4)	31.4 \pm 6.1	(7)	49.0 \pm 4.7	(6)
Coastal dune/without	0	(4)	70.0 \pm 13.5	(4)	29.7 \pm 6.3	(7)	49.3 \pm 4.7	(6)
Coastal interdune/with	77.0 \pm 3.4	(4)	74.0 \pm 3.8	(4)	64.0 \pm 7.2	(7)	58.7 \pm 10.4	(6)
Coastal interdune/without	35.0 \pm 7.7	(4)	73.0 \pm 4.7	(4)	52.6 \pm 8.4	(7)	50.0 \pm 8.9	(6)
Inland dune/with	0	(2)	24.0 \pm 12.0	(2)	50.0 \pm 10.0	(2)	34.0 \pm 10.0	(2)
Inland dune/without	0	(2)	24.0 \pm 12.0	(2)	36.0 \pm 2.0	(2)	34.0 \pm 10.0	(2)
Inland dune/with	52.0 \pm 2.3	(3)	73.0 \pm 9.1	(4)	40.0	(1)	59.0 \pm 27.0	(2)
Inland interdune/without	29.3 \pm 4.8	(3)	69.0 \pm 8.7	(4)	40.0	(1)	42.0 \pm 14.0	(2)

Table 5

Species richness and relative abundance+of surface-active arthropods from pitfall traps relative to habitat, season, and diurnal (D) or nocturnal (N) activity.

Trophic category	Coastal dune		Coastal interdune		Inland dune		Inland interdune	
Order: family	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Genus/species	D N	D N	D N	D N	D N	D N	D N	D N
Carnivores								
Araneae: Agelinidae								
<i>Gen. sp. #1</i>				*				
Araneae: Caponiidae								
<i>Gen. Sp. #1</i>				*				
Araneae: Gnaphosidae								
<i>Gen. sp. #1</i>		*						
Araneae: Lycosidae								
<i>Geolycosa sp.</i>				*				
<i>Gen. sp. #1</i>			*	*			*	*
Araneae: Pholcidae								
<i>Modismus sp.</i>	*							*
Araneae: Sparassidae								
<i>Heteropoda sp.</i>	*	*	*				*	*
<i>Olios sp.</i>								

+ * = presence; ** => an average of one individual/trap; *** = => an average of 10 individuals/trap.

Table 5 (continued)

Trophic category Order = family Genus/species	Coastal dune		Coastal interdune		Inland dune		Inland interdune	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
	D N	D N	D N	D N	D N	D N	D N	D N
Araneae: Theridiidae								
<i>Gen. sp. #1</i>		*	*					
Araneae: Thomisidae								
<i>Gen. sp.</i>				*			*	
Pseudoscorpiones								
<i>Gen. sp. #1</i>				*				
Scorpiones: Buthidae								
<i>Centruroides sp.</i>				*				
Scorpiones: Vaejovidae								
<i>Gen. sp. #1</i>				*				
<i>Gen. sp. #2</i>				*				
Hemiptera: Reduviidae								
<i>Gen. sp. #1</i>				*				
Neuroptera: Myrmeleonidae								
<i>Gen. sp. #1</i>		*					*	*
Coleoptera: Carabidae								
<i>Tetragonoderus sp.</i>								**

† * = presence; ** => an average of one individual/trap; *** => an average of 10 individuals/trap.

Table 5 (continued)

Trophic category	Coastal dune	Coastal interdune	Inland dune	Inland interdune
Order = family	Spring Fall	Spring Fall	Spring Fall	Spring Fall
Genus/species	D N D N	D N D N	D N D N	D N D N
Hymenoptera: Multilidae				
<i>Dasymutilla</i> sp.				* *
<i>Sphaerophalama</i> sp. #1		*	*	*
<i>Sphaerophalama</i> sp. #2				*
<i>Sphaerophalama</i> sp. #3				*
<i>Sphaerophalama</i> sp. #4		*		*
Hymenoptera: Tiphiidae				
<i>Gen. sp. #1</i>	*	*		* *
Detritivores				
Isopoda: Tylidae				
<i>Tylos punctatus</i> Holmes & Gay		*	**	*
Thysanura: Lepismatidae				
<i>Gen. sp. #1</i>		*		*
<i>Gen. sp. #2</i>				*
Orthoptera: Rhaphidophoridae				
<i>Ceuthophilus imperialis</i> Cohn	*	*		*
<i>Macrobaenetes sierrapintae</i> Tinkham			*	*
Blattodea: Polyphagidae				
<i>Arenivaga</i> sp.	*	*	*	* *
Dermoptera:				
<i>Gen. sp. #1</i>				*

† * = presence; ** => an average of one individual/trap; *** => an average of 10 individuals/trap.

Table 5 (continued)

Trophic category	Coastal dune		Coastal interdune		Inland dune		Inland interdune	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
	D N	D N	D N	D N	D N	D N	D N	D N
Coleoptera: Anthicidae								
<i>Anthicus</i> sp.	***	*	*	*				
Coleoptera: Ptinidae								
<i>Niptus ventriculus</i> LeConte	*		*				*	
Coleoptera: Tenebrionidae								
<i>Areoschizus</i> sp.	*		*		*		**	
<i>Agroporis</i> sp. A				*				
<i>Argoporis</i> sp. B			*					
<i>Asbolus laevis</i> LeConte	*		*	*			*	*
<i>Asbolus verrucosus</i> LeConte	*		**					*
<i>Cayptadius tarsalis</i> Blaisdell	*							
<i>Edrotes arens</i> La Rivers		*			*	*		
<i>Edrotes ventricosus</i> LeConte	*	*		*				
<i>Eleodes armatus</i> LeConte		** **		** *				*
<i>Eleodes blaiselli</i> Doyen			*	* *	*	* *	*	* **
<i>Eusattus dilatatus</i> LeConte				*				
<i>Notibius puberulus</i> Le Conte			** *	* *			*	*
Gen. sp. #1	*							
Gen. sp. #3								*
Herbivores								
Phasmida: Phasmatidae								
Gen. sp. #1				*				

+ * = presence; ** => an average of one individual/trap; *** => an average of 10 individuals/trap.

Table 5 (continued)

Trophic category	Coastal dune		Coastal interdune		Inland dune		Inland interdune	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
	D N	D N	D N	D N	D N	D N	D N	D N
Hemiptera: Miridae								
<i>Gen. sp. #1</i>						*		
Hemiptera: Cydnidae								
<i>Gen. sp. #1</i>	*		*	** *				*
Homoptera: Cicadellidae								
<i>Gen. sp. #1</i>						*		
Coleoptera: Crysomelidae								
<i>Gen. sp. #1</i>				*		*		
Coleoptera: Curculionidae								
<i>Gen. sp. #1</i>						*		
<i>Gen. sp. #2</i>						*		
Ants								
Hymenoptera: Formicidae								
<i>Crematogaster</i> sp.				*				
<i>Myrmecocystus</i> sp.				*				
<i>Pogonomyrmex</i> sp. A			** *	** *			** *	* *
<i>Pogonomyrmex</i> sp. B							* *	* *
<i>Gen. sp. #1</i>							*	
<i>Gen. sp. #2</i>							*	
<i>Gen. sp. #3</i>			**					
<i>Gen. sp. #4</i>			*					

+ * = presence; ** => an average of one individual/trap; *** => an average of 10 individuals/trap.

Table 6

Site and habitat species richness comparisons of trophic levels and ants.

Site/habitat	Carnivores	Detritivores	Herbivores	Ants
Coastal dune	5	12	1	0
Inland dune	1	5	5	0
Coastal interdune	12	14	1	4
Inland interdune	15	15	3	4

set of comparisons. Figures 2 and 3, for example, give expected levels of species richness, $E(S_n)$, in the coastal interdune habitat (four season/diel interval combinations) and the inland interdune habitat (two such combinations). $E(S_n)$ values for sample sizes of 80 individuals (coastal) and 30 individuals (inland) reveal close similarities between both interdune habitats during periods of greatest surface activity, e.g., spring nights (most) and fall nights (next most). This relationship, as well as the dominance of nocturnal over diurnal $E(S_n)$ levels in both coastal habitats (Fig. 3), is quantified in Table 7 for 10 site/habitat/season/diel period combinations in which at least 30 nonsocial arthropods were trapped. Interestingly, both the highest (13.4) and lowest (1.3) $E(S_n)$ values came from the same habitat (coastal dune) but at opposite seasons and diel periods (spring nights and fall days, respectively).

Indices of Hill's N_2 diversity and Hill's modified E_5 evenness, calculated relative to season, diel period, sampling effort, and individuals captured are given in Table 8 for all but two habitat combinations. Except for the remarkable similarity of all parameters relating to coastal and inland interdune spring nights, few other correlations are evident. However, when the remaining two habitat combinations (dune, spring, day) having either one and no captures (inland and coastal habitats, respectively) are added to the list, several distinctions can be made between combinations having evenness rankings higher or lower than eight.

First, in the top-ranked group, six combinations are nocturnal compared with two in the other group. Second, in the top-ranked group, the correlation between E_5 and N_2 values is very poor ($r = 0.17$), while in the group with low evenness (numbers 9 - 14) it is much better ($r = 0.50$), indicating a tendency for very abundant species to dominate in diurnal situations. Overall, the five most dominate species, ranked in order of abundance per sampling effort, were *Eleodes armatus* (tenebrionid detritivore: 10 combinations), *Tetragonoderus* sp. (carabid carnivore: one combination), *Tylos punctatus* (isopod detritivore: three combinations), *Areoschizus* sp. (tenebrionid detritivore: four combinations), and unidentified tenebrionid detritivore no. 2: six combinations.

The possible influence of habitat-specific plant cover on species richness was assessed by linear regression analysis. When estimated plant cover in 1-m diameter circles around each pitfall trap was compared with that trap's total individual spring or fall captures, the corresponding r -value was always low (<0.5).

Additionally, the possible influence of seasonal precipitation on species richness, and individual densities, was assessed at the coastal site (where weather

Table 7

Species richness rankings of site/habitat/season/diel period combinations at sample sizes of 30 pitfall-trapped arthropods (excluding ants, anthicid beetles and microarthropods). Expected number of species, $E(S_n)$, for all combinations are based on rarefaction curves. Rankings are based on non-overlapping 95% confidence intervals.

Rank	Site/habitat/season/diel period	$E(S_n)$
1	Coastal dune spring night	13.4
2	Coastal/inland interdune spring night	10.5 - 11.0
3	Coastal/inland interdune fall night	7.0
4	Inland dune fall night	5.5
5	Coastal dune fall night	3.7
6	Coastal interdune spring day	3.4
7	Coastal interdune fall day	3.2
8	Coastal dune fall day	1.3

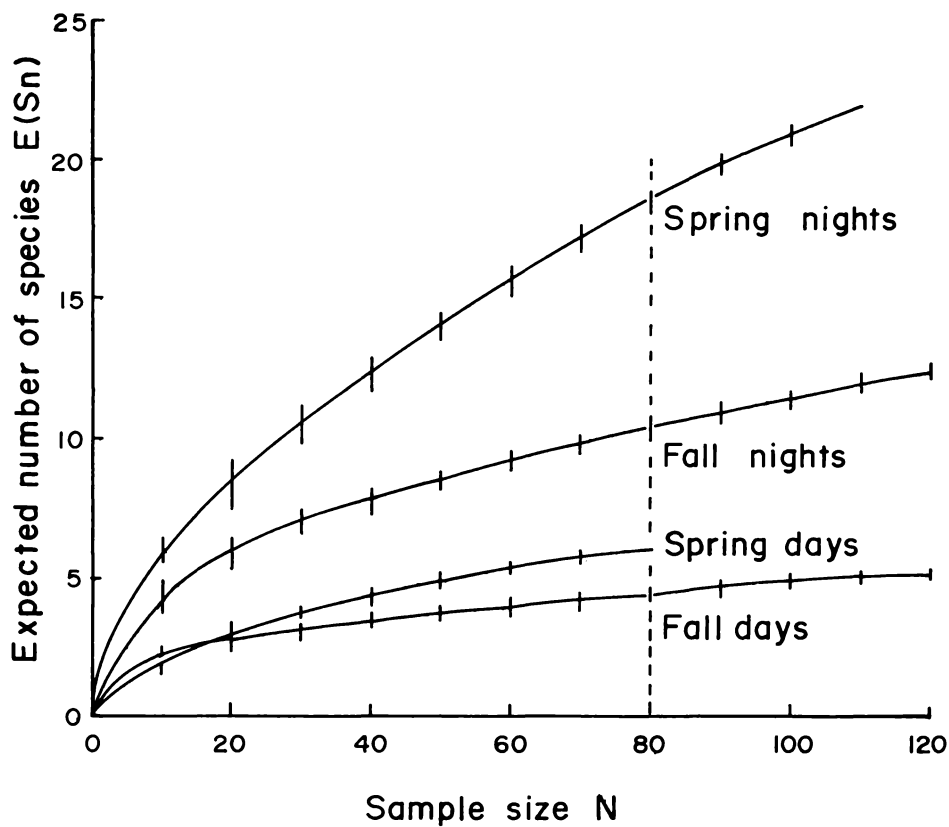


Fig. 2. Rarefaction curves for the expected number of surface-active arthropod species pitfall-trapped in the coastal interdune habitat. Vertical bars represented 95% confidence intervals. Dotted line shows $E(S_n)$ for samples of 80 individuals.

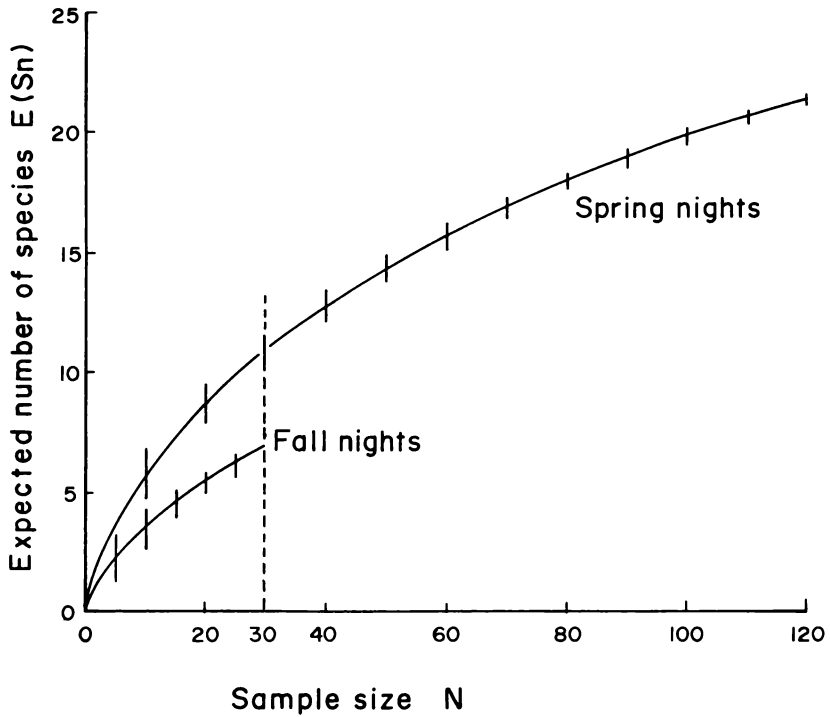


Fig 3. Rarefaction curves for the expected number of surface-active arthropod species pitfall-trapped in the inland interdune habitat. Vertical bars represent 95% confidence intervals. Dotted line shows $E(S_n)$ for samples of 30 individuals.

Table 8

Habitat-specific species evenness (Hill's E5, ranked) and species diversity (Hill's N2) relative to season, diel period, and number of 12-h sampling periods, and total numbers of species and individuals. Habitats with one or fewer species not included.

E5 rank	Site/habitat/season/diel period	E5	N2	Sampling periods	Numbers of spp.	Indiv.
1	Inland dune spring night	1.62	5.00	2	4	6
2	Coastal dune spring night	0.87	8.94	4	14	33
3	Inland dune fall night	0.75	2.84	2	6	36
4	Inland interdune spring day	0.72	2.59	2	5	18
5	Coastal interdune fall night	0.66	3.75	6	13	132
6	Inland dune fall day	0.63	1.83	2	4	12
7	Coastal interdune spring night	0.59	5.73	4	23	119
8	Inland interdune spring night	0.58	5.93	4	22	128
9	Coastal interdune fall day	0.56	1.56	7	7	165
10	Inland interdune fall day	0.54	1.14	2	2	16
11	Inland interdune fall night	0.50	1.98	2	7	31
12	Coastal interdune spring day	0.44	1.22	4	4	42
13	Coastal dune fall night	0.39	1.27	6	6	81
14	Coastal dune fall day	0.35	1.02	7	2	102

records applied) for interdune faunas (which were more consistently abundant than dune faunas). Regressions were made of total precipitation in the 30-day period preceding each fall and spring sampling versus seasonally corresponding $E(S_n)$ values at $n = 20$ (smallest sample size). The relationship, $r = -0.69$, was not significant at $P = 0.05$. When average numbers of individuals trapped per sampling period were substituted for $E(S_n)$ values the relationship was again non-significant ($r = -0.54$).

Patterns of beta-diversity

Species turnover between dune and interdune habitats at the inland site was twice that of the coastal site (Table 9). Turnover between interdune habitats at both sites was also twice that occurring between interdune habitats at both sites (Table 10).

When seasonal and diel patterns of beta-diversity are compared relative to location, season, and diel period, three patterns in particular become evident (Table 11). First, seasonal turnover in coastal dunes was distinctly greater than in inland dunes; seasonal turnover percentages in interdunes at both sites were similar and intermediate. Second, nocturnal-diel turnover percentages in dune habitats were twice those recorded from interdune habitats. Third, the usually species-rich habitats (interdunes) were more similar to each other in terms of diel time and seasonal time than were the usually species-poor dunes.

DISCUSSION

A diverse arthropod fauna populates soil surfaces of the warm coastal and inland dune ecosystems of northwestern Sonora. Especially well represented are spiders, mutillid wasps, tenebrionid beetles, and -- in the interdunes -- ants. Although these and other species comprise assemblages with often distinctive spatial and temporal patterns of species richness and diversity (Crawford et al. 1989), they collectively exhibit certain broad patterns as well. Therefore, before addressing the hypothesis of pattern similarity between similar habitats, I will compare some of this study's general findings with pitfall-trap results from 1) a much larger, cooler, and more arid coastal desert, the Namib (Crawford and Seeley 1987); and 2) a much smaller dunefield in the more mesic desert grasslands of central New Mexico (Crawford 1988).

Trap-capture efficiencies in the two larger deserts were similar, averaging about 51% ($\pm 4 - 7\%$), while the average efficiency in New Mexico was $66 \pm 8\%$.

Table 9

Habitat-specific species turnover between inland and coastal sites.

Site	Habitat-specific richness		Number of shared species	Community coefficient (%)
	Dune	Interdune		
Inland	11	30	5	24.5
Coastal	19	36	11	40.0

Table 10

Site-specific species turnover between inland and coastal sites.

Habitat	Site-specific richness		Number of shared species	Community coefficient (%)
	Coastal	Inland		
Dune	19	11	4	26.7
Interdune	36	30	17	51.5

Table 11

Seasonal and diel species turnover relative to sites and habitats.

Site/habitat	Comparative seasonal/diel richness		Number of shared species	Community coefficient (%)
	<i>Fall</i>	<i>vs Spring</i>		
Coastal dune	7	15	3	27.3
Inland dune	9	5	3	42.9
Coastal interdune	17	27	8	36.4
Inland interdune	10	26	6	33.3
	<i>Day</i>	<i>vs Night</i>		
Coastal dune	2	19	2	19.0
Inland dune	4	8	1	16.6
Coastal interdune	11	32	8	37.2
Inland interdune	9	29	8	42.1

Carnivore-detrivore species ratios in the Sonoran and Namib dune ecosystems were also similar, both approaching unity, while the ratio in New Mexico favored detritivores. It is possible that relative desert size may be associated with these findings, as may be desert location (within and between continents), regional climates, and biotic histories. Desert age, however, may be less relevant: the main Namib Sand Sea probably dates from the Pliocene (Ward et al. 1983), in contrast to the two North American ecosystems, which are probably no older than the late Pleistocene (Bowers 1982, S. Wells personal communication).

Similarly, geological time -- albeit less extensive in the present instance -- seems not to have been a major impediment to dispersal between the coastal and inland ecosystems considered in the present study, since about half of the coastal and inland interdune species were common to both of these sites. Fossils of the extant marine gastropod, *Muricanthus nigrilis*, occur at the western edge of the inland dunes (personal observation) and were probably laid down there before the end of the Pleistocene (J.J. Schreiber, personal communication). Therefore that site has probably not been part of a coastal ecosystem since that time.

Regardless of whether they occurred at the coast or inland, or at both places, surface-active species displayed some similar habitat- and time-specific patterns of assemblage organization. For example, estimated species richness in both the coastal and inland interdunes was seasonally similar at night, greater in spring than in fall, and greater at night than in daytime. (By contrast, in the Namib, Seely and Crawford (1987) trapped diurnally and nocturnally active species from many sites in approximately equal numbers.) Another similar pattern was that of interdune species richness, which greatly exceeded richness in the dunes, except on the coast, in spring, at night.

Otherwise, most combinations of site, habitat, and seasonal as well as diel period were relatively unique as regards species richness and diversity. The greatest variation in richness occurred in the coastal dunes. There, in the daytime a small number of species dominated surface assemblages; however, at night the proportional distribution of species was more even. Thus, in that habitat in particular, carnivory, detritivory, and herbivory may well vary extensively in seasonal and diel time, assuming surface activity is indicative of these processes.

Factors influencing assemblage organization were not obvious, suggesting that species' activities may be relatively independent of each other -- and therefore relatively non-interactive -- within assemblages. This observation is supported by the lack of any clear correlation between plant cover with species richness, or between recent precipitation with richness and numbers of individuals trapped.

These findings agree with most other studies of this kind to date (Crawford in press). However it is still probable that unusually heavy rainfall events occasionally enhance both richness and individual numbers in the upper Gulf of California region, as they do in other deserts (Seely and Louw 1980, Ghabbour and Shakir 1982, Crawford and Seely 1987).

Finally, resemblance of assemblages in similar habitats was not particularly good, especially in dunes, at the beta-diversity level. However, estimates of low species richness in the inland dunes may have to be revised (thereby decreasing estimated turnover) following greater long-term sampling effort, which is needed if we are to understand the ecology of surface-active assemblages in the Gran Desierto. Overall, the hypothesis of organizational pattern resemblance between 1) dune habitats and 2) interdune habitats from the coastal and inland dune fields of Sonora appears simplistic. While seasonal and diel patterns do show some similarity, in the interdunes, assemblages in dune habitats exhibit little consistent organization over time.

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**ASSEMBLAGE ORGANIZATION OF SURFACE-ACTIVE
ARTHROPODS ALONG HORIZONTAL
MOISTURE GRADIENTS IN A COASTAL
SONORAN DESERT ECOSYSTEM.**

**Clifford S. Crawford,
Mariel L. Campbell,
William H. Schaedla,
Sarah Wood.**

Department of Biology
University of New Mexico
Albuquerque, New Mexico 87131, USA

RESUMEN

Examinamos las diferencias a corto plazo en la organización de las comunidades de artrópodos activos en la superficie del suelo en una porción restringida del ecosistema de dunas cerca de Puerto Peñasco, Sonora, México. Para probar la hipótesis de que el gradiente de humedad del suelo influye en tal organización, se establecieron tres transectos de 32 m en dirección oeste hacia la costa 1) área de estero, 2) estanque de agua salada, y 3) área intermedia de desierto seco (control). El gradiente de humedad varió en el estero y estanque de 15% y 11% a <1% respectivamente, mientras que la humedad del suelo en la área control fue de <1% (valores promedio a 15 cm de profundidad). Cuatro lotes, proporcionalmente espaciados de 3 x 7 m a lo largo del transecto con trampas "pitfall" capturaron artrópodos continuamente por períodos de 12 horas, el número de trampas fue ocho en el estero, ocho en el estanque y seis en el control.

Se capturaron 558 artrópodos pertenecientes a 50 especies, se excluyeron las numerosas hormigas del género *Solenopsis*. El análisis de "rarefaction" con 80 como tamaño de muestra, mostró valores de 27 en el estero, 21.5 en el estanque y 18 para el sitio de control, cuando se eliminó el efecto de pantano de *Uca latimanus* (cangrejo que fue dominante en el estero y ausente en los otros dos sitios).

Los artrópodos, excluyendo cangrejos, fueron doblemente abundantes en el estero durante el día y cuatro veces más abundantes en la noche que en los otros dos sitios durante el día.

La proporción carnívoros-detrítivos en los tres sitios fue aproximadamente 2:1 (estero), 1:1 (estanque) y 1:2 (control). El valor de similitud (modificado de Hill E5) sin *Uca* fue similar en todos los sitios; sin embargo, grandes valores en diversidad (Hill N2) confirman la presencia de numerosas especies en el estero (escarabajos Carabidae y arañas Lycosidae). No se encontró relación significativa entre el porcentaje de cobertura vegetal y la densidad de artrópodos capturados. La medida del valor beta-diversidad (coeficiente de comunidad de Sørensen) reafirma la particularidad de la organización en el estero. Nuestra hipótesis inicial fue parcialmente apoyada porque la diferencia de especies, abundancia de individuos y proporción carnívoros-detrítivos tendió a incrementarse con el gradiente de humedad.

ABSTRACT

We examined short-term differences in assemblage organization of surface-active arthropods from a restricted portion of a coastal dune ecosystem near Puerto Peñasco, Sonora, Mexico. To test the hypothesis that soil moisture gradients influence organization, we established three, 32-m transects running westward from real or simulated shorelines, of 1) an estuary terminus ("estero"),

2) a salt-water pond ("seep"), and 3) an intermediate dry desert site ("control"). Transect moisture gradients ranged, at the estero and seep sites respectively, from 15% and 11% to <1%, while soil moisture at the control site was <1% (mean values to 15cm depths). Four evenly spaced plots, each 3 x 7m, along each transect contained pitfall traps that captured arthropods continuously for eight (estero, seep), or six (control), 12-h periods.

We trapped 558 arthropods comprising 50 species, excluding abundant ants of the genus *Solenopsis*. Rarefaction analysis for sample sizes of 80 gave expected species numbers, $E(S_n)$, of 27 (estero), 21.5 (seep), and 18 (control) when the swamping effect of *Uca latimanus* (crabs which were dominant at the estero, absent elsewhere) was removed. Arthropods other than crabs were twice as abundant at the estero and four times as abundant at night, respectively, as they were at the other two sites and during the day.

Carnivore:detritivore species ratios at the three sites were approximately 2:1 (estero), 1:1 (seep), and 1:2 (control). Evenness (modified Hill's E_5) values without *Uca* were similar at all sites; however, high diversity (Hill's N_2) values for the estero assemblage confirmed the presence of a small number of abundant species (carabid beetles, lycosid spiders) there. We found no significant correlation between percent plant cover and total densities or species richness of trapped arthropods. Measurements of beta-diversity (Sørensen's community coefficient) reinforced the uniqueness of the estero assemblage. Our initial hypothesis received support in that species differences, individual abundances, and carnivore:detritivore ratios all tended to increase along moisture gradients.

INTRODUCTION

The distribution and abundance of desert arthropods, including many species that are regularly active on the soil surface, is strongly influenced by the physical environment (Cloudsley-Thompson and Chadwick 1964, Crawford 1981, Wallwork 1982). Temperature and moisture extremes, in particular, can regulate the activities of individual species and species assemblages of these organisms (Cloudsley-Thompson and Idris 1964, Ghabbour et al. 1977, Holm and Scholtz 1980, Mispagel 1983). Use of suitable trapping methods, especially pitfall-trapping, enables one to assess the organizational patterns of such assemblages as patterns change between habitats and over time (Ghabbour and Shakir 1980, Pietruszka 1980, Crawford and Seely 1987, El-Shishiny and Ghabbour 1988, Pantis et al. 1988).

Differing patterns of assemblage organization can be attributed to soil conditions (Crawford 1988, in press) and local moisture regimes. Crawford and

Seely (1987) found that in relatively moist and recently wetted (by rain) soils, the species richness and population densities of carnivorous arthropods exceeded those of detritivorous arthropods. In deserts generally, species richness ratios of these two most common trophic groups are on average about even (Crawford in press).

In the present study we examined aspects of assemblage organization in two moist and one dry (control) desert habitats, all within < 1 km of each other. Since the latter typified local desert shrubland, we termed it the "control" habitat. Specifically, we use short-term pitfall-trap results to test the hypothesis that horizontal soil moisture gradients influence organizational patterns of surface-active arthropod assemblages in a restricted coastal desert ecosystem.

Study Sites

The study area (Fig. 1, 2) was located directly inland of the Centro de Estudios de Desiertos y Oceanos (CEDO), Puerto Peñasco, Mexico, in the Lower Colorado Valley subdivision of the Sonoran desert.

Initially we chose a water-filled swale, the "seep" site, located approximately 0.5 km northeast of CEDO, and an estuarine site (the "estero"), located approximately 1 km northeast of the seep site, for assemblage comparisons. A day later we established a "control" site in the desert between the seep and the estero. Vegetation in all three sites was dominated by the shrubs *Ambrosia dumosa* (Gray) Payne, *Atriplex canescens* (Pursh) Nutt., *Frankenia palmeri* S. Wats., *Lycium pallidum* Miers, and the grass *Hilaria rigida* (Thurb.) Benth. The grass, *Monanthocloe littoralis* Engelm., was prominent along the shoreline at both the seep and (especially) the estero.

The seep site was a small, irregularly shaped pond of saline water. A few clusters of the halophyte, *Salicornia* sp., were present at the water's edge. Parts of the western and southern shores were encompassed by steep banks of the coastal dunes, but most of the shore graded gradually into the surrounding desert. The estero site was a slightly larger lagoon connected by a narrow channel to the western end of Estero Morua, into which the normally dry Rio Sonyita flows only on rare occasions, about 10 km to the east (CEDO News, Vol. 2, 1989). Water at the estero site fluxes slightly with tidal flows entering Estero Morua from the Gulf of California, and has a salinity equivalent to that of the local sea water. Low banks were present on the north and south shores of the estero site; the western bank had a relatively gradual incline. Both the seep and estero sites were visited by an assortment of waterfowl.

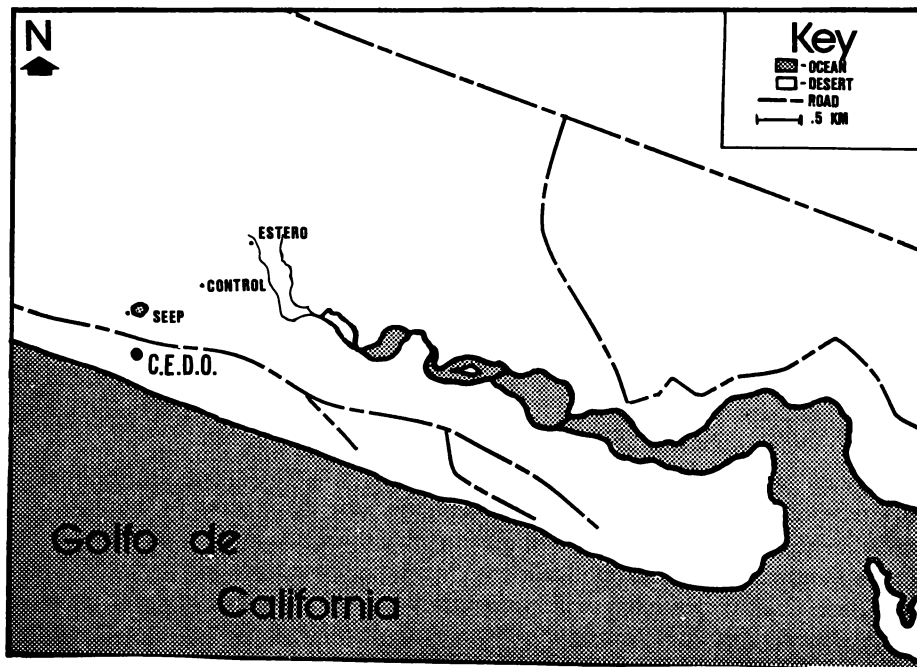


Fig. 1. Map of study sites and region near the study area.

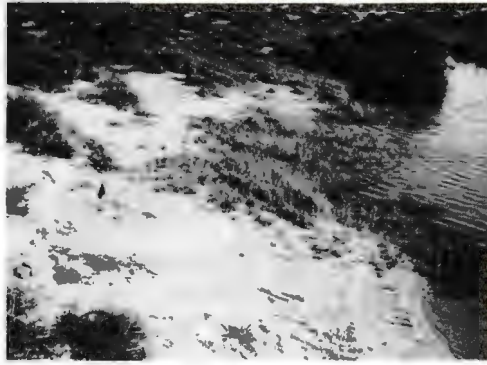


Fig. 2. Photographs, taken at time of sampling, of estero site (top), seep site (middle), and control site (bottom).

The control site was established on a relatively flat area of desert floor midway between the seep and the estero. We designated its eastern edge as simulated shoreline. Some *Opuntia bigelovii* was present on the western "bank".

MATERIALS AND METHODS

Three transects, oriented westward and perpendicular to the shoreline, were established on the west shore at each site. Transects were separated by 30-50 m, and reflected local differences in elevation and vegetation. Beginning at 2m from the actual or simulated shoreline, the transects were intersected at 10m intervals by rows of four pitfall traps, 2m apart and centrally located in a 3 x 7m plot. Pitfall traps were composed of doubled plastic 12-oz Solo^R cups, 9 cm wide at the opening and 12 cm deep.

Two maximum-minimum thermometers were buried 10 cm deep at the center of the two most central plots in the middle transect at the seep and estero sites. A weather station containing a recording hydrothermograph was placed adjacent to the control site.

Traps were checked and trap contents recorded each morning and evening. The study period ran from the morning of October 6 to the evening of October 9 at the seep and the estero; at the control site sampling did not begin until 24 hours later. Unknown specimens were preserved in alcohol for later identification. These and other voucher specimens were deposited in the University of New Mexico Insect Collection.

Indices of species richness (i.e., rare-faction), diversity (Hill's N2) and evenness (modified Hill's E5 ratio) were calculated using licensed software programs available in Ludwig and Reynolds (1988). Sørensen's similarity index (Magurran 1988) was used to calculate species turnover (beta-diversity).

Nonsocial arthropods other than crabs were classified according to trophic group following identification to species or morphospecies. Carnivores were defined as species having at least mainly predaceous immature stages, while detritivores were defined as mainly saprophagous species. The terms "omnivore," "algavore," and "ant" as used below are self-explanatory.

A vegetation survey was carried out in each plot. Height, width and length of each plant in the plot was recorded, and area of plant cover was determined by summing length x width measurements over the entire plot. Per cent cover was calculated as area of vegetation divided by the total area of the plot x 100.

Single samples from the upper 15 cm of soil were taken from each plot of the center transect at each site and placed in sealed plastic bags for soil moisture analyses. Soil moisture was determined from these samples by measuring mass loss after drying a small amount at 110° C for 24 h.

RESULTS

Climate

Twenty-four hour changes in air and soil temperatures and atmospheric relative humidity were recorded throughout the study. Diurnal high temperatures ranged between 30° C and 34° C (air), and between 33° C and 35° C (soil). Nocturnal lows ranged between 15° C and 22° C (air), and between 24° C and 27° C (soil). Atmospheric relative humidity ranged between 95% and 100% (nocturnal) and between 33% and 50% (diurnal).

Species Richness, Diversity and Evenness

The most prevalent arthropods collected during the study period at all three sites were ants of the genus *Solenopsis*, which due to their overwhelming numbers were excluded from calculations. With the exception of *Solenopsis*, a total of 558 arthropods comprising 50 species were collected at the estero, seep and control sites. Table 1 lists numbers of individuals in each species trapped at each site. The greatest species richness and individual abundance occurred at the estero, where, except for *Solenopsis* and 233 *Uca latimanus* (fiddler crabs), 145 individuals of 34 other species were trapped. This contrasts with only 77 individuals of 21 species (no crabs) at the seep site, and 76 individuals of 18 species at the control site (which received three-fourths of the sampling effort given the two "moist" sites).

Numbers of species other than *Uca latimanus* and *Solenopsis* trapped per site at all sites averaged (\pm SE) 3.6 \pm 0.7 (diurnal) and 10.2 \pm 0.9 (nocturnal), while numbers of individuals averaged 6.1 \pm 1.4 (diurnal) and 24.0 \pm 2.5 (nocturnal). The only apparent correlation between surface activity and climate was a nearly significant positive correlation between nocturnal (low) air temperatures (3 nights) and total numbers of individuals trapped ($r = 0.91$, $p < 0.1$).

Recognizing from species-area curves shown in Fig. 3 that this study did not sample the full number of species present, we used rarefaction analysis (Fig. 4) for all species except ants to obtain expected levels of species richness, $E(S_n)$, at a sample size of 80 individuals, which approximates sample sizes at the seep

and control sites. Results are consistent with actual trap data (above) when the swamping effect of *Uca* crabs is excluded. Thus, rarefaction curves at $n = 80$ indicate significant $E(S_n)$ differences (shown by 95% confidence intervals in Fig. 4) between the estero (27 species), the seep (21.5 species), and the control (18 species).

Diversity and evenness values at the estero were also affected by its high *Uca* density (Table 2). Without *Uca*, the low estero N_2 indicates that proportionally few very abundant species dominated that site, compared to the other sites. The greatest dominance of such species occurred at the control site, where *Tylos punctatus* (isopods) were relatively abundant. Similar E_5 values (when the contribution of *Uca* at the estero is excluded) at all sites indicate an overall similarity in their species' proportional distributions.

Numbers of individuals and species of arthropods in designated trophic levels varied at each site relative to distance from the shore or its artificial equivalent (Table 3). At the control site, detritivores outnumbered carnivores by two to one (species) and three to one (individuals). One crab, an omnivore, was identified. At the seep site, no crabs were present, and carnivores and detritivores were approximately equal in both numbers of species and individuals. At the estero, on the other hand, crabs were the dominant trophic group in terms of numbers of individuals. However, in terms of species richness, carnivores were dominant at the estero and outnumbered detritivores by two to one. At all three sites, the detritivore component consisted mainly of tenebrionid beetles and isopods (*Tylos*), whereas carnivores were largely spiders, scorpions and, at the estero, carabid beetles, which were found only within 14m of the shoreline.

Assuming that soil moisture measurements taken along the center transects at each site (Fig. 5) accurately reflected moisture in soil at similarly spaced points on the lateral transects, we obtained the following relationships between soil moisture and data shown in Table 3: (1) a highly significant direct correlation at the estero between soil moisture and density of *Uca latimanus* ($r = 0.99$, $p < 0.005$, Spearman rank correlation, 1-tailed test), (2) strong inverse trends between soil moisture and detritivore density at the estero ($r = -0.87$) and the seep ($r = -0.82$), and (3) a strong positive trend between soil moisture and total arthropod density at the control ($r = 0.85$). No other soil moisture relationships approached statistical significance.

Vegetative cover within plots ranged from <5% to 65%. No correlations approaching statistical significance were found between per cent cover and total

TABLE 1

Species richness and relative abundance of surface-active arthropods trapped at estero, seep, and control sites.

Trophic category:	Total numbers trapped			
	Order: Family	Estero	Seep	Control
Genus/species	(6 samples)	(6 samples)	(4 samples)	
Carnivores				
Araneae: Sparassidae				
<i>Heteropoda sp.</i>	7	9	9	
Araneae: Lycosidae				
<i>Pardosa sp.</i>	10			
<i>Lycosa sp.</i>		3		
Araneae: Pisauridae				
<i>Gen. sp. #1</i>	2			
Araneae: Clubionidae				
<i>Gen. sp. #1</i>	1	1		
Araneae: Linyphiidae				
<i>Gen. sp. #1</i>	1			
Araneae: Caponiidae				
<i>Gen. sp. #1</i>		2		
Araneae: Theridiidae				
<i>Gen. sp. #1</i>		1		
Araneae: Filistatidae				
<i>Gen. sp. #1</i>	1			
Araneae: Loxoscelidae				
<i>Loxosceles deserta</i>	1			

TABLE 1 (continued) p. 2

Araneae: Homalonychidae			
<i>Gen. sp. #1</i>			1
Araneae: unknown family			
<i>Gen. sp. #1</i>	1		
Scorpiones: Buthidae			
<i>Centruroides sp.</i>	1	1	
<i>Paruroctonus sp.</i>	1	6	6
Dictyoptera: Mantidae			
<i>Gen. sp. #1</i>	1	2	
Coleoptera: Histeridae			
<i>Gen. sp. #1</i>	5		
Coleoptera: Cicindellidae			
<i>Gen. sp. #1</i>	4		
Coleoptera: Carabidae			
<i>Dyschirius aratus</i> LeConte	30		
<i>Tachys sp. (?) #1</i>	17		
<i>Tachys sp. (?) #2</i>	7		
Coleoptera: Staphylinidae			
<i>Aleochara sp.</i>	1		
Hymenoptera: Bradynobaenidae			
<i>Gen. sp. #1</i>	1		
Hymenoptera: Mutillidae			
<i>Sphaerophthalma sp.</i>		1	1
<i>Dasymutilla sp.</i>	3	2	
 Detritivores			
Isopoda: (Tylidae)			
<i>Tylos punctatus</i> (Holmes and Gay)	16	24	33
Thysanura: Lepismatidae			
<i>Gen. sp. #1</i>	4	7	6
<i>Gen. sp. #2</i>			1
Thysanura: Nicoletiidae			
<i>Gen. sp. #1</i>	1		2

TABLE 1 (continued) p. 3

Dictyoptera: Polyphagidae			
<i>Arenivaga</i> sp.	2	1	
Dermaptera: Labiduridae			
Gen. sp. #1	1	1	
Coleoptera: Tenebrionidae			
<i>Areoschizus</i> sp.	1	1	
<i>Argoporis bicolor</i> LeConte	1	1	
<i>Asbolus verrucosus</i> LeConte		1	2
<i>Cayptaduis tarsalis</i> Blaisdell	3	8	8
<i>Edrotes ventricosus</i> LeConte	3		3
<i>Eleodes armatus</i> LeConte	5		
<i>Eleodes caudatus</i> (Horn)	3	2	
Gen. sp. #1		1	
Gen. sp. #2			1
Gen. sp. #3			1
Coleoptera: Staphylinidae			
<i>Carpelimus</i> sp	9		
Coleoptera: Ptinidae			
<i>Niptus ventriculus</i> LeConte	1	2	1
Algavores			
Coleoptera: Staphylinidae			
<i>Bledius</i> sp. #1	1		
<i>Bledius</i> sp. #2	1		
Omnivores			
Crustacea:			
<i>Uca latimanus</i>	223		
<i>Uca crenulata</i>			1

TABLA 1 (continued) p. 4

Ants

Hymenoptera: Formicidae

Dolichoderine sp. #1

3

Dolichoderine sp. #2

1

Gen. sp. #1

3

TOTAL NUMBER OF SPECIES

34

21

18

TOTAL INDIVIDUALS*

145

77

76

(*excluding ants and *Uca*)

TABLE 2

Species diversity (Hill's N2) and evenness (modified Hill's E5) values for the three study habitats.

Habitat	N2 diversity	E5 evenness
Control	5.95	0.58
Seep	9.04	0.67
Estero (with <i>Uca</i>)	2.81	0.31
Estero (without <i>Uca</i>)	14.03	0.68

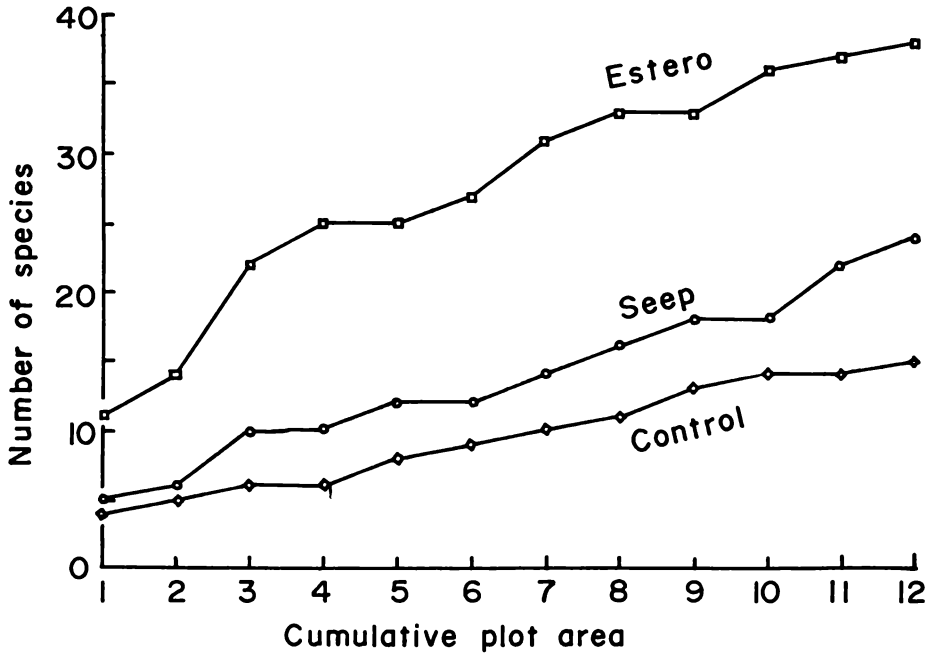


Fig. 3. Species-area curves for surface-active arthropod assemblages at the estero, seep, and control sites.

TABLE 3

Trophic group composition (carnivores, detritivores, *Uca* crabs) at control, seep, and estero sites.

Site position*	Number of species			Number of individuals		
	Car.	Det.	<i>Uca</i>	Car.	Det.	<i>Uca</i>
Control						
2 m	2	7	0	2	12	0
12 m	2	3	1	4	3	1
22 m	4	6	0	7	24	0
32 m	3	5	0	5	22	0
Total	5	11	1	18	61	1
Seep						
2 m	6	4	0	14	7	0
12 m	2	2	0	4	5	0
22 m	6	7	0	10	19	0
32 m	6	6	0	9	20	0
Total	12	11	0	37	52	0
Estero						
2 m	9	2	1	48	2	143
12 m	12	4	1	40	2	73
22 m	5	7	1	10	14	4
32 m	5	6	1	5	25	3
Total	22	12	1	103	48	223

*Values refer to distance westward along transect from actual or simulated shoreline.

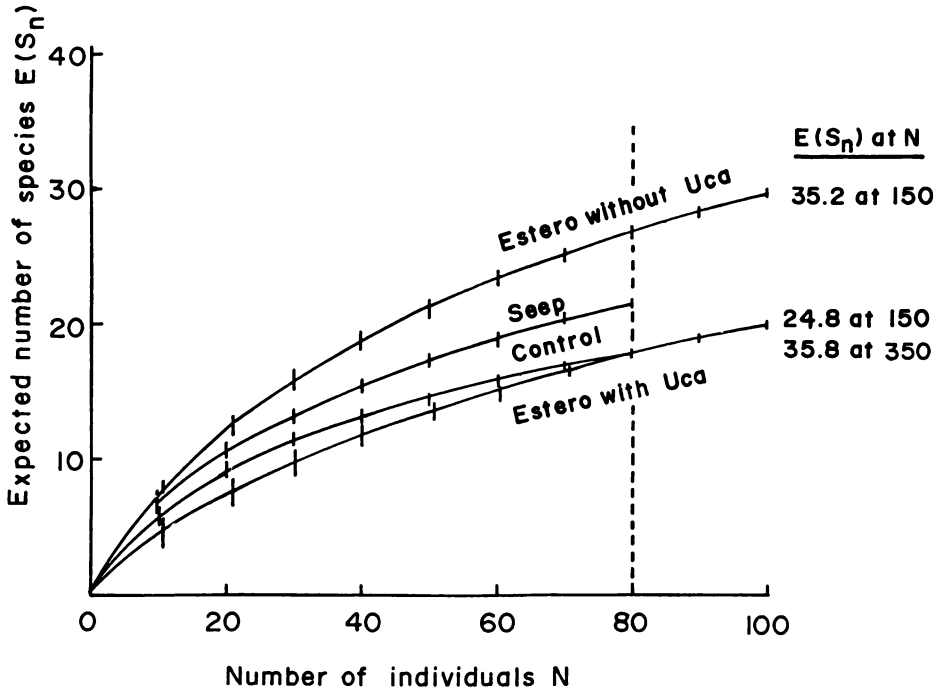


Fig. 4. Rarefaction curves for species trapped at estero, seep, and control sites. Vertical bars are 95% confidence intervals.

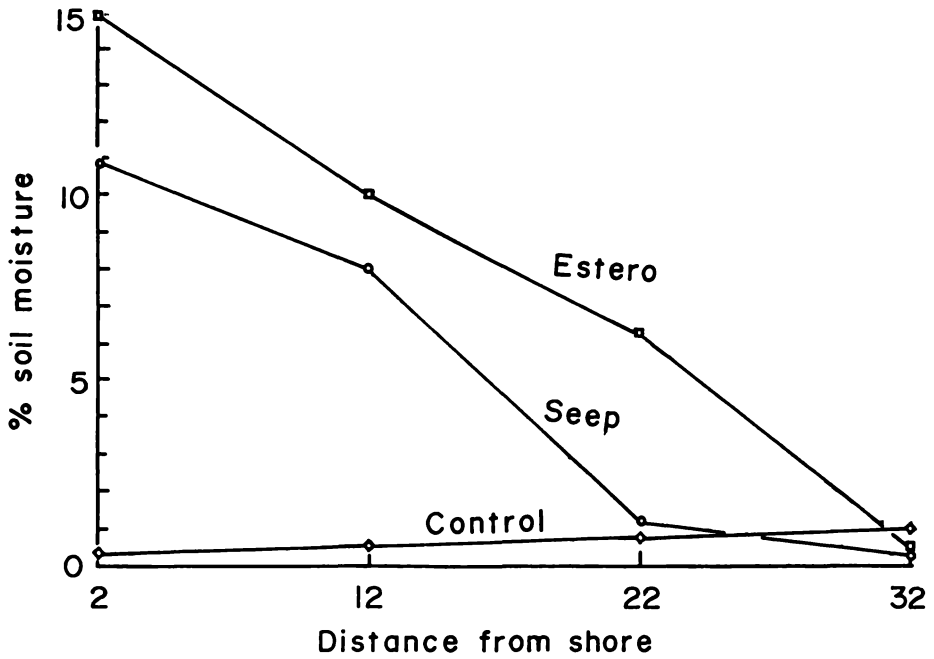


Fig. 5. Soil moisture gradients, representing single samples, for the estero, seep, and control sites.

densities or species richness of trapped arthropods when these were compared by regression analysis on a plot basis ($n = 12$) at all sites.

At each site, we also examined capture trends for carnivores and detritivores. Using data in Table 3, we found a significant inverse relationship between individuals of these trophic groups at the estero ($r = -0.52$, $p < 0.05$, Spearman rank correlation, 1-tailed test). No other correlations were significant.

Beta diversity

Species turnover between the estero and control sites was greater than between the estero and the seep and control sites (Table 4). A major contributing factor was the relative uniqueness of the carnivore assemblage at the estero. The lowest turnover observed was between detritivores at the estero and seep sites.

DISCUSSION

We found clear organizational differences among the surface-active arthropod assemblages at the three study sites. Moreover, all sites were surprisingly rich in species. Several years earlier, a more extensive study by Crawford (1989) at a dune-interdune site about 5 km to the east resulted in expected species numbers (also at $n = 80$) that ranged from < 5 to 18, compared to the 18-27 range in the present report. Thus, the presence of permanent water bodies (seep, estero) in a relatively confined, dune-associated landscape may promote relatively high numbers of surface-active species.

A specific, although untested, explanation for the estero's species richness may be that *Uca latimanus* is in some way acting as a "keystone species" (Paine 1969), since expected richness was significantly lower at the seep where *U. latimanus* did not occur. The possibility that the presence of this omnivore enhances species richness at the estero could be tested by constructing crab enclosures.

Assemblage organization was also most unique at the estero site, mainly due to the large population of crabs, and the many carnivores, particularly spiders and very small carabid beetles. The presence of crabs reflected the marine environment of the estuary. However, one *U. crenulata* was found dead in a control site trap some 300m distance from the estero, and bleached carapaces and claws of other *Uca* crabs were scattered between the control and estero sites. Perhaps intermediate swales become wet enough after winter rains to support a marginal inland crab population.

TABLA 4

Numbers of carnivores, detritivores, and total species* shared between study sites, and corresponding community coefficients.

Habitat pairs/ Arthropod groups	Number of species shared	Community coefficient (%)
Estero/Seep		
Carnivores	5	35.7
Detritivores	8	69.6
Total	14	49.1
Estero/Control		
Carnivores	2	17.4
Detritivores	4	36.4
Total	7	25.9
Seep/Control		
Carnivores	5	53.3
Detritivores	5	47.6
Total	9	43.9

* Data from Table 1, plus *Solenopsis* ants which occurred at all sites.

The dominance of carnivores at the estero, and the excess of carnivores at the seep relative to the control site, tend to support the observation of Crawford and Seely (1987) that carnivore:detrivore ratios are high in moist desert habitats. However, the presence of very small carnivorous carabid and staphylinid beetles close to the estero shoreline was unexpected. Possibly they rely on a high microfaunal density made possible by elevated soil moistures. Numerous small dipterans were present during sampling; their eggs and larvae are a potential food source. Also, although we did not trap many ants (other than *Solenopsis*), tiny individuals that also may be prey were often fairly abundant on the surface. Paarman et al. (1986) reported that larvae of certain carabids in the Sahara Desert prey on ants and their broods.

Since soil in the vicinity of the seep was also moist, the unique aspects of the estero assemblage must have resulted from factors other than moisture alone. We speculate that the occasional connection in El Niño years of the estero and Río Sonyita has over time resulted in a mixed, partly relic assemblage of hygrophilic riparian arthropods and *Uca* crabs.

In other respects, assemblage organizations at the three sites were relatively similar. Thus proportional distributions of species were roughly the same, although a comparatively small number of very abundant species was present at the estero. Also, isopods (*Tylos*) occurred at all three sites, although they were trapped most frequently at the control site and least often at the estero (and there only in traps farthest from the shoreline). According to Hamner et al. (1969), this species orients away from soil moisture and up an elevational gradient. Finally, no trophic or taxonomic group showed a correlation with plant cover at any site. This is consistent with results obtained from studies of ground-dwelling desert beetles (Thomas 1983, Parmenter and MacMahon 1984), *Tylos punctatus* (Wood, unpublished data), and several assemblages of surface-active desert arthropods (Crawford, 1989).

In general, and despite the similarities just discussed, results of this study support the hypothesis that horizontal moisture gradients influence organizational patterns of arthropod assemblages in a restricted desert ecosystem. Species richness, individual abundances, and carnivore:detrivore ratios all appear to increase along moisture gradients involving scales that change by an order of magnitude from 32m (transect length) to 0.5 - 1 km (distances between sites). Long-term studies would help to verify these apparent trends.

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