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Diurnal activity patterns and vertical migration in desert soil microarthropods

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With 3 figures

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1. Introduction

A number of taxa of desert invertebrates exhibit diel periodicities that allow them to avoid extremes in temperature or desiccation (Crawford 1981). This has been documented in desert soil microarthropods, with the highest populations occurring in the surface litter in the early morning (Whitford et al. 1981). Whitford et al. (1981) attributed the diurnal fluctuations of microarthropods in surface litter to migration from the moister mineral soil to the litter each day. Another valid hypothesis is that microarthropods enter a form of cryptobiosis or an inactive state during the day and thus cannot be extracted from litter bags. Cryptobiotic species would revert to an active state as temperatures drop and litter moisture increases during the night.

The objectives of this research were to test the "migration" and "cryptobiosis" hypotheses and to examine the effect of increased soil moisture and reduced soil temperature on activity patterns of microarthropods in surface litter.

2. Study area

The research was done on the Jornada Long-Term Ecological Research (LTER) site, 40 km NNE of Las Cruces, Dona Ana County, New Mexico. The vegetation is sparse, consisting of annual plants, with a few shrubs and subshrubs (Mackay et al. 1986). The average rainfall is 210 mm and air temperatures range from below 0 to 40 °C.

3. Methods

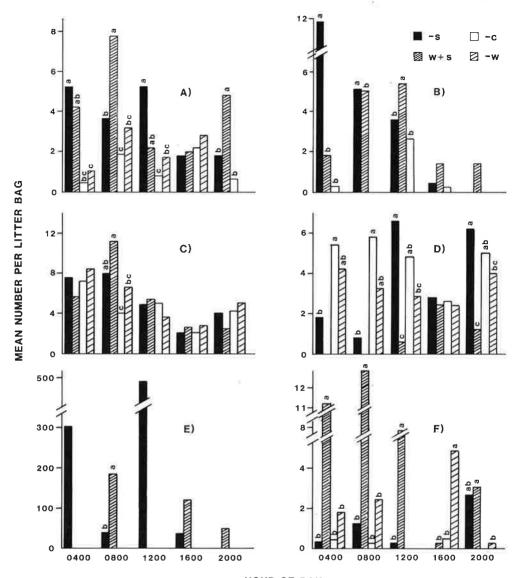
We established 4 plots each $3.5~\mathrm{m} \times 12.5~\mathrm{m}$ (MacKay et al. 1986). Two plots were shaded by dark green nylon netting and two of the plots were watered at irregular itervals with a sprinkler system. The design consisted of a shaded plot, a watered plot, a shaded and watered plot and a control plot. We documented that the shaded plots had reduced soil temperatures and the watered plots had increased soil moisture (MacKay et al. 1986).

We placed 70 fiberglass litterbags (15 cm×15 cm) each with fifteen grams of air dried creosote bush (Larrea tridentata) leaf litter in each of the plots. We retrieved the first group of bags on 15 August 1984, 3 months after placement in field, at 04:00, 08:00, 12:00, 16:00, 20:00 (5 bags from each plot) to document diurnal differences in the presence of microarthropods in the litter bags. Mites were extracted from the litter into water using modified Tullgren funnels for a 3 day period (Santos et al. 1978). A second group of bags was retrieved on 31 August 1984 at 04:00, 08:00, and 12:00 and extracted in a similar manner. In addition, soil samples (0—10 cm,5 cm diam.) were collected below the litter bags at 08:00 and extracted in a similar way. The third set of bags (15 from each plot) were retrieved on 14 September 1984 at 08:00. Soil samples were collected at 0—5 and 5—10 cm below each litter bag. Microarthropods were extracted from five bags from each plot in ad-

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HOUR OF DAY

Fig. 1. Diurnal changes in numbers of soil mites extracted from bags of creosotebush leaf litter collected at the Jornada LTER site in southern New Mexico on 15 August 1984 (MST). "S" indicates shaded plot, "W + S" indicates watered and shaded plot, "C" indicates control plot and "W" indicates watered plot. Those bars of each group of 4 with different letters are significantly different at the 5% level [ANOVA and Duncan's Multiple Range Test] (a) Bdellidae. — Spinibdella cronini (Baker et Balcock), (b) Cunaxidae — Cunaxa spp., (c) Eupodidae — Eupodes (?) sp., (d) Nanor-chestidae — Speleorchesters sp., (e) Tarsonemidae — Tarsonemus sp., (f) Oribatulidae — Jornadia larrea Wallwork et Weems.

dition to associated soil samples. A second group of litter bags was sprinkled with distilled water and placed at 20 °C for 18 hours and a third group was air dried. At 04:00 on 15 September, the moistened bags were removed from the incubator and placed on the extractors. If the mites were migrating into the soil under the litter bags during the day, we predicted that we would find high population densities in the soil at 08:00. If they were not migrating, numbers of individuals would be low. Furthermore, if the microarthropods were going into a cryptobiotic state during the day, we expected to extract greater numbers from the litter after it had been moistened and incubated at 20 °C until the following morning. After three days of extraction, the first group of bags was

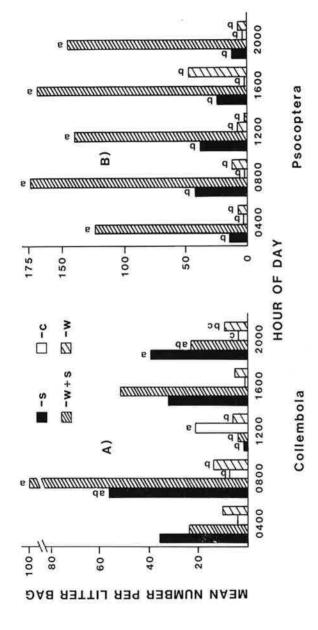


Fig. 2. Diurnal changes in numbers of insects extracted from creosotebush litter bags collected 15 August 1984. (a) Collembola — Isotominae and Neanurinae, (b) Psocoptera — Liposedis sp.

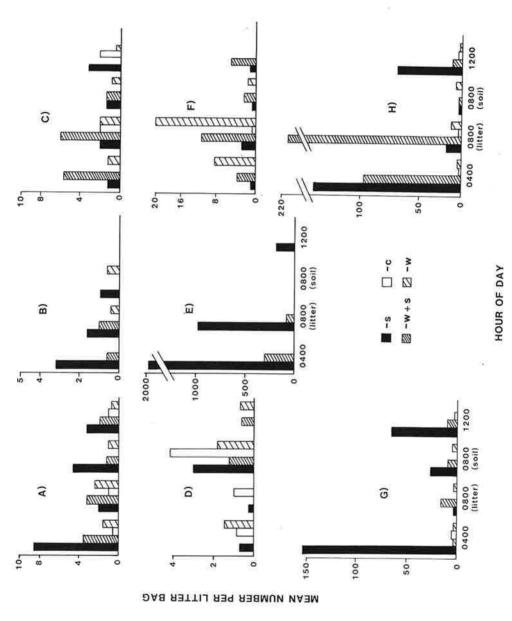


Fig. 3. Population density of soil mites and insects in and under (0—10 cm) crossotebush litter bags collected at the Jornada LTER site on 31 August 1984. Litter and soil under the litter bags were collected at 08:00. Symbols of the treatments are as in Figure 1: (a) Bdellidae, (b) Cunaxidae, (c) Eupodidae, (d) Nanorehestidae, (e) Tarsonemidae, (f) Oribatulidae, (g) Collembola, (h) Psocoptera.

sprinkled with water and placed at 20 °C for 24 hours and reextracted. We attempted to float the mites from the air dried litter using a sugar flotation sieving method (FRECKMAN et al. 1975). We did not obtain any microarthropods from the re-extractions of litter. We were also not able to separate mites from the litter by flotation, although we did observe some mites in the litter. Apparently those taxa which remain in the litter during the day cling to the litter. As a consequence, we did not include results of these two techniques in this paper.

The data were compared with ANOVA and Duncan's Multiple Range Test.

4. Results

Different numbers of microarthropods were extracted from litterbags collected at different times of the day (Figs 1 & 2 see also Whitford et al. 1981). Numbers of mites collected in the afternoon were reduced, especially Eupodes sp. and Speleorchestes sp. (Figs. 1c & 1d). The modification of soil moisture and temperature had an important effect on the numbers of mites extracted from litter bags (Fig. 1). There was an increase in population density of all 6 taxa in plots with reduced soil temperature. Only Jornadia larrea population densities increased in response to increased soil moisture alone. Most taxa showed increased numbers in the shaded and watered plot, especially Spinibdella cronini (BAKER & BALCOCK) and Cunaxa spp. Speleorchestes sp. population densities were lower in plots with reduced soil temperatures, and they occurred at highest densities in the control plot. Although increased soil moisture had little effect on mite populations, a combination of water and shade had an obvious effect, which was most pronounced in Spinibdella cronini and Cunaxa spp. Speleorchestes sp. population densities were lowest in the watered, shaded plot. Jornadia larrea showed an increased population density in this plot. Cunaxa spp., Tarsonemus sp. and I. larrea were virtually absent from the control plot, but were found in the modified plots, suggesting the importance of lowered soil temperatures for their populations.

The two taxa of insects, collembolans and *Liposcelis* sp. (Psocoptera), responded to soil temperature in a similar way to the mites (Fig. 2). A combination of shade and increased

soil moisture greatly increased the densities of both groups.

We found evidence for migration in some taxa, and lack of migration in other taxa (Fig. 3). Speleorchestes sp. and S. cronini were found in high populations in the underlying soil at 08:00. Cunaxa sp., Eupodes sp. and collembolans were found in low population densities in the soil. This evidence suggests migration, especially in the first two taxa. We found few or no Tarsonemus sp., J. larrea sp. and Liposcelis sp. in the soil, indicating that no migration occurred in these species.

We found an increase in extracted numbers of several taxa after the litter bags were incubated (Table 1). Exceptions were *Spinibdella* sp. and *Speleorchestes* sp. which showed no change, and *Cunaxa* sp. and *Eupodes* sp. which were virtually absent. The numbers of *Liposcelis* sp. extracted from incubated litter doubled, those of *Siteroptes* sp., *Speleorchestes* sp. and collembolans tripled or quadrupled. The density of these 4 taxa in the soil also increased. There was relatively little difference in microarthropod densities in the control plot after incubation of the samples. Most of the increase in density occurred in the shaded plot.

5. Discussion

Our original hypotheses are neither completely supported no rrejected by the data from this study. The data support both "diurnal migration" and "cryptobiosis" as adaptations that allow microarthropods to utilize the resources of leaf litter accumulations on the surface of a desert soil. Apparently some taxa have the physiological capacity to enter and emerge from some kind of cryptobiotic state while other taxa expend energy to move up through the soil column into the litter and back down into the soil. Seasonal vertical migration by microarthropods is well documented (USHER 1975, SCHENKER 1984, WHELAN 1985). Diurnal migration by soil acari has been suggested in deserts (WHITFORD et al. 1981) and in forests (METZ 1971). The data in this study are the first to our knowledge that suggest cryptobiosis as a mechanism available to soil acari for survival in a harsh environment.

The data from two independent experiments are consistent. The taxa that appear to migrate (S. cronini, Speleorchestes spp.) do not increase in numbers in the refrigerated sam-

Table 1. Effect of incubation before extraction on numbers of soil mites and insects extracted from crossotebush leaf litter bags, collected at the Jornada LTER site on 14 September 1984 at 08:00 nst

Taxon	No incubation			Incubation		
	litter	0—5 cm	5—10 cm	litter	05 cm	5—10 cm
Spinibdella cronini	1.0 ± .44	1.0 ±7	.8 ± .83	$^{1.0}_{\pm 1.2}$.6 ± .89	.2 ± .44
	(1.0 ± 1.22)	(0)	(.6 ± .89)	(0)	(0)	$^{(.4}_{\pm .54)}$
Cunaxa sp.	.83 ± .13	0	0	.2 ± .44	$\frac{.8}{\pm}$ 1.09	.8 ± .83
	(0)	(0)	(0)	$\frac{1}{4}$.89)	$\overline{(0)}$	(0)
Eupodes sp.	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Speleorchestes sp.	3.0 ± 4.12 (3.8 ± 1.14)	3.4 ± 1.67 (4.8 ± 4.08)	$2.2 \pm .83 $ (4.0 ± 1.73)	$\begin{array}{c} 1.6 \\ \pm .89 \\ (5.4 \\ \pm 4.50) \end{array}$	2.8 ± 1.64 (1.8 ± 1.3)	3.4 ± 3.13 (2.6 ± 2.19)
Siteroptes sp. (Pygme-	0	$^{1.6}_{\pm \ 2.3}$	$^{1.0}_{\pm\ 1.41}$.4 ± .54	$^{18.0}_{\pm\ 23.29}$	$^{6.2}_{\pm 11.69}$
phoridae)	(0)	$^{(2.0}_{\pm 1.22)}$	$^{(1.6}_{\pm\ 2.07)}$	(0)	(0)	(0)
Tarsonemus sp.	0	$12.0 \\ \pm 24.13$	0	0	$^{40.6}_{\pm 70.58}$	7.8 ± 15.81
	(0)	$\begin{array}{c} -6 \\ \pm 1.34 \end{array}$	(0)	(0)	$\begin{array}{c} -0.0 \\ \pm 15.65) \end{array}$	(4.2 ± 9.39)
Jornada larrea	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Collembola	$\frac{1.8}{\pm 3.03}$	0	$\begin{array}{c} 1.2 \\ \pm \ 1 \ 64 \\ 0 \end{array}$	9.0 ± 14.74 $(.8 \pm 1.78)$	$\begin{array}{c} 1.2 \\ \pm 1.3 \\ (.4 \\ \pm .54) \end{array}$	$.4 \pm .89$ (1.0 ± 2.23)
Liposcelis sp.	27.6 ± 35.4	$^{1.2}_{\pm}$ 1.78	$\begin{array}{c} .4 \\ \pm .89 \\ 0 \end{array}$	$\begin{array}{c} -42.2 \\ \pm 43.0 \\ (7.4 \\ \pm 15.99) \end{array}$	$\begin{array}{c} 4.8 \\ \pm 6.53 \\ (.2 \\ \pm .44) \end{array}$.2 ± .44 (.4 ± .89)

Note: Samples are of litter and at 2 depths under litter. The data are from bags from the shaded plot and control plot (parenthesis).

ples which suggests that these taxa are not capable of cryptobiosis (Fig. 3, Table 1). The densities of microarthropods that did not migrate (Tarsonemus sp., Collembola, Liposcelis sp.) were higher after the samples have been incubated at 20 °C, thus apparently emerging from a cryptobiotic state. We hypothesize that S. cronini, Cunaxa spp. and Eupodes sp. migrate diurnally and that they remain active in the litter for extended periods of time when litter temperatures are moderate, i.e. shaded. We further hypothesize that Tarsonemus sp., J. larrea, collembolans and Liposcelis sp. do not migrate diurnally. These taxa also remain active for longer periods of time in the litter that is shaded and maintained at moderate temperatures.

Our experimental design allowed us to compare the relative effects of soil moisture and soil temperature on population densities and activity of soil microarthropods. Usher (1976) argued that soil water was the most important environmental factor affecting soil microarthropod numbers. Loots & Ryke (1967) concluded that soil moisture was not always the most important factor. Data from this study show that for desert inhabiting microarthropods, soil temperature has more of an effect on relative population densities than

does soil moisture. This result is consistent with the findings of Steinberger & Whitford

(1984) and MACKAY et al. (1986).

We concluded that the active resident population of soil microarthropods in surface litter accumulations in a desert is a function of time of day, which affects diurnal migrant species, and litter temperature, which affects activity of species that are capable of cryptobiosis. Physiological studies of species that appear capable of cryptobiosis are needed before we can assess the flexibility that this adaptation allows its possessor with respect to utilization of the rich energy and nutrient sources characteristic of leaf litter accumulations. This is especially important in deserts where soil organic matter is often less than 1% by mass.

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We tested the hypotheses that diurnal variation in abundance of microarthopods extracted from soil surface litter in the northern Chihuahuan desert would be due either to the animals entering a cryptobiotic state or migrating to the deeper soil levels during the hot time of the day. We present evidence of migration in some taxa [esp. Speleorchestes sp. — (Nanorchestidae) and Spinibdella cronini (Baker et Balcock) (Bdellidae)]. Other taxa [Cunaxa spp. (Cunaxidae), Eupodes (?) sp. (Eupodidae), Isotominae and Neanurinae (Collembola), Liposcelis sp. (Psocoptera)] enter a cryptobiotic state and remain in the litter during the day. Experimental reduction of the soil temperature results in "migrating" taxa remaining in the litter for a longer period of time and the "cryptobiotic" taxa remaining active for longer periods of time. We also present experimental evidence for the lack of importance of soil moisture for desert soil microarthropods.

Key words: Acarina, Collembola, Psocoptera, desert, soil temperature, soil moisture, diurnal activity

patterns, vertical migration.