

# Life Styles of Desert Litter-Dwelling Microarthropods: a Reappraisal Based on the Reproductive Behaviour of Cryptostigmatid Mites

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*Studies in a series of Chihuahuan Desert litter and soil habitats confirmed that reproductive activity was most pronounced following the major rainfall, as in the Mojave Desert. Immediately after the summer rains, evidence was found of considerable breeding activity in more than 60% of the oribatid species studied in the former desert.*

*Experiments were conducted in which plots under creosotebush (*Larrea tridentata*) were watered weekly or monthly from June 1981 to June 1982. Microarthropods were sampled monthly from 20 g aliquots of litter from watered plots and from untreated controls. The continuous rainfall regime caused no change in patterns of activity — particularly reproductive activity — of the soil microarthropods.*

*The reproductive activities of four species of oribatid mites were analysed. Two *Passalozetes* species and *Jornadia larreae* showed a definite seasonality in egg production, centred on the period of natural rainfall in the desert (July and August). These three species have life-history strategies which are geared to predictable natural rainfall and were not disrupted by experimental watering. *Joshuella striata* behaves rather differently and it may be no coincidence that it is common to both the Mojave and Chihuahuan deserts. In both it shows a peak in egg production from December to February, the period of natural rainfall in the Mojave. After watering, the pattern becomes bimodal, with a second peak from August to October, about the period of natural summer rainfall in the Chihuahuan Desert.*

*In die loop van proewe wat van Junie 1981 tot Junie 1982 uitgevoer is, is grond waarop "kreosootbos" (*Larrea tridentata*) groei weekliks of maandeliks besproei. Mikroartropode uit 20-g-monsters van plantreste afkomstig van besproeide veld sowel as van onbehandelde kontroleveld is maandeliks getoets. Die gereelde besproeiing het geen verandering in die patroon van aktiwiteit — veral voortplantingsaktiwiteit — veroorsaak nie.*

*Die voortplantingsaktiwiteit van vier spesies van oribatied-mite is ontleed. Die eierproduksie van twee *Passalozetes*-spesies en *Jornadia larreae* was klaarblyklik seisoengebonde en het hoofsaaklik in die woestyn se natuurlike reënseisoen (Julie en Augustus) plaasgevind. Hierdie drie spesies beskik oor 'n lewensgeskiedenisstrategie wat op die voorspelbare natuurlike reënval ingestel is en wat nie deur eksperimentele besproeiing beïnvloed is nie. *Joshuella striata* gedra hom anders en dit is waarskynlik nie toevallig dat hy in die Mojave- sowel as die Chihuahua-woestyn voorkom nie. In albei hierdie gebiede bereik dié spesie se eierproduksie 'n hoogtepunt van Desember tot Februarie, die natuurlike reënseisoen in*

*die Mojave. Ná besproeiing word die patroon egter bimodaal, met 'n tweede piek van Augustus tot Oktober, wat ongeveer die natuurlike somerreënseisoen in die Chihuahua-woestyn is.*

## Introduction

Hot deserts are conventionally considered to be 'pulsed' environments. Biological activity, triggered by rainfall events which are variable in timing and magnitude, should be stochastic in nature, i.e. random with respect to its timing during the annual cycle and with its intensity. Selection in such environments should favour 'opportunistic' species which can 'track' their environment and respond rapidly, by recruiting a new generation of individuals, during the temporary favourable period afforded by a rainfall event. This is consistent with the ideas that (1) hot desert systems conform to the 'trigger-pulse-reserve' paradigm enunciated by Noy-Meir,<sup>1</sup> and (2) selection in such environments favours *r*-strategists.<sup>2,3</sup> The criteria associated with *r*-selection were applied to selected numbers of soil-dwelling mites (Acari) studied in the Mojave Desert of southern California,<sup>4</sup> and it was concluded that, on balance, they behaved in the way that theory would have predicted. It was demonstrated, for example, that:

1) Total microarthropod numbers showed a peak during the nine months of the study, which coincided exactly with the month of maximum rainfall (December).

2) A second, and smaller, peak occurred about four months later (April and May).

3) Both of these peaks were more pronounced in litter-dwelling microarthropods, as opposed to those living in the underlying mineral soil.

4) These population peaks were caused by the recruitment of juveniles into populations rather than the re-activation of dormant adults. This was particularly true of two species of oribatid mites, *Joshuella striata* (which was the most abundant oribatid), and *Haplochthonius variabilis*. *J. striata* recruited in December and January and contributed significantly to the winter peak of total microarthropod numbers. *H. variabilis* recruited in April and May and was mainly responsible for the second peak.

5) A third species of mite, the prostigmatid *Spinibdella cronini*, which was a predator on the juveniles of both *J. striata* and *H. variabilis*, has two recruitment periods, one in January (which coincided with recruitment in the prey species *J. striata*), and a second in April/May (coinciding with recruitment in *H. variabilis*).

6) The age structure of the populations of all three of these species over the study period suggested that the life cycles were completed — from egg to adult — in a matter of weeks rather than months.

7) An astigmatid mite, *Glycyphagus* sp., which is phoretic as an hypopus on insects, occurred in relatively high numbers in the mineral soil in December and, thereafter, virtually disappeared.



Fig. 1. Map showing the distribution of deserts in the southwestern part of the U.S.A. and northern Mexico.

All of these observations suggested that *J. striata*, *S. cronini*, *Glycyphagus* sp. and, to a lesser extent, *H. variabilis*, showed characteristics associated with 'opportunistic' species consonant with their identification as *r*-strategists. Moreover, the data available on their life histories, although not conclusive, pointed in the same direction.

This study on the soil microarthropods of a Mojave Desert site certainly appeared to support the belief that these animals 'tracked' their environment in an opportunistic manner. Immediately, the question must be asked: do the conclusions arrived at from this study have a universality, i.e. can they be applied to all soil ecosystems in hot deserts? Of course, there is no ready answer to this question, since virtually nothing is known, at this level of taxonomic expertise, about the species composition of the soil fauna of

the Sahara, the Namib, the Arabian or the Australian deserts, for example. However, studies carried out subsequently on the soil fauna of sites in the Chihuahuan Desert of New Mexico suggest that the conclusions derived from the Mojave study require a re-appraisal.

### Sites and methods

The main study site is located on the Jornada Experimental Ranch, a facility of New Mexico State University situated 40 km NNE of Las Cruces, Dona Ana County, New Mexico (Figs 1 and 2). A detailed description of the site is given by Kamill *et al.*<sup>5</sup> For the purposes of the present paper, it is sufficient to note that studies reported here were conducted on an alluvial piedmont supporting the growth of creosotebush (*Larrea tridentata*) on the lower bajada (valley slope) and a mixed vegetation along the margins of arroyos (outwash channels) and on the higher slopes of the bajada. This vegetation included scattered clumps of juniper (*Juniperus monosperma*), Apache plume (*Fallugia paradoxa*), desert oak (*Quercus grisea*) and black grama grass (*Bouteloua eriopoda*). Litter samples (113 cm<sup>2</sup>) were taken from beneath each of these vegetation types and, in addition, from beneath salt bush (*Atriplex* sp.) in White Sands National Monument, some 150 km east of the Jornada site. Samples from each vegetation type were replicated five times and microarthropods were extracted using a modified Tullgren funnel. This work was carried out immediately after heavy summer rains in this part of the Chihuahuan Desert, and was designed as a pilot survey of the soil microarthropods occurring in a variety of litter types. Some of the results of this survey are presented here, and these relate exclusively to mites belonging to the order Cryptostigmata (oribatid mites). These mites were identified to species where possible, and counts were made of adult males and females, of gravid females and of the numbers of eggs present in each of the latter.

During 1980–82, attention was focused on experimental plots under creosotebush on the Jornada. These plots were set up to test the findings of Whitford *et al.*<sup>6</sup> that simulated rainfall events produced an immediate increase in numbers of microarthropods recovered from litter samples so treated.

Rainfall amendments were delivered through a sprinkler system regulated to supply water at the rates of (1) 6.25 mm (= 0.25 in) per week, or (2) 25.40 mm (= 1 in) per month. Each of these treatments was replicated three times, as was the unwatered control. Creosotebush litter, confined in screen cylinders, was placed in 20 g aliquots on the soil surface under creosote bushes, randomly selected within each plot. These aliquots were sampled twice each month during the study period, which extended for approximately one year during 1981 and 1982. Each month, litter samples were taken twice, the day before water amendments and, again, three days after the treatment (on all plots including the control). The samples were replicated five times for each treatment and microarthropods were extracted using modified Tullgren funnels. Mineral soil beneath the litter was also sampled to a depth of 10 cm. These samples yielded very few microarthropods even in treated plots and are not considered further in this analysis.

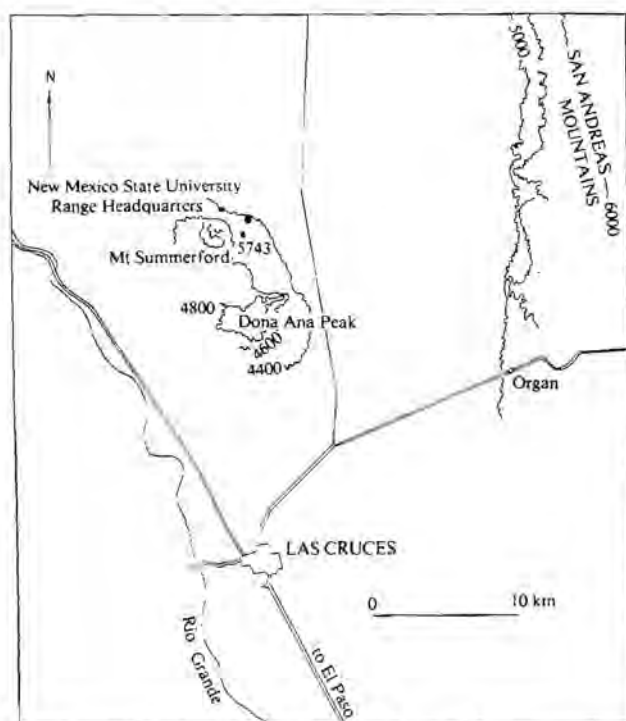


Fig. 2. Map showing the location of the study site in relation to other geographical and topographical features in the vicinity of Las Cruces, N. Mexico.

Table 1. Cryptostigmata Inferiores: Numbers of males and females present in five litter samples taken from each of six litter types.

	<i>Atriplex</i>	<i>Fallugia</i>	<i>Juniperus</i>	<i>Quercus</i>
<i>Hoplophthiracarus</i> sp.				2♂♂
<i>Cosmochthonius plumatus</i>	4♂♂ 1♀		1♂	
<i>Sphaerochthonius splendidus</i>	2♂♂	2♂♂ 11♀♀		
<i>Camisia horrida</i>			2♂♂	
<i>Trhypochthonius tectorum</i>				210♀♀

No examples were taken from *Bouteloua* or *Larrea*.

**Results**

*The pilot survey*

A total of thirty species of Cryptostigmata belonging to seventeen families was recorded from the six litter types sampled in 1979. A check-list is given in Appendix I.

The analysis of reproductive data is split up into three sections which conform more or less to the natural groupings of Cryptostigmata families: the Inferiores, the Superiores Apterogasterina and the Superiores Pterogasterina.

*Cryptostigmata Inferiores*

Table 1 provides data on the numbers of males and females collected from the six litter types for the five species belonging to this section. Not too much can be read into these data since, except in the case of *T. tectorum*, the numbers recovered are low. However, the following observations are perhaps worth making:

- 1) Two of the sites, *Bouteloua* and *Larrea*, did not yield any Inferiores.
- 2) One hundred and ninety-one (90%) females of *T. tectorum* were gravid, and the number of eggs per female averaged slightly less than 2 (1.78). No males were recovered, suggesting that this species is probably parthenogenetic.
- 3) The one female recovered of *C. plumatus* was gravid and contained a single egg.
- 4) None of the eleven females of *S. splendidus* was gravid.

*Cryptostigmata Apterogasterina*

A breakdown of the numbers of males and females of the eleven apterogasterine species in the six litter types is given in Table 2. Three of these species, *Plesiodamaeus* sp., *Ramusella elliptica* and *Scapheremaeus obliterated*, need not concern us for they occurred either in low numbers and/or none of the females was gravid. The single female of *Cymbaeremaeus* sp. collected from the *Juniperus* was gravid and contained a single egg but this lone individual can hardly be regarded as substantial evidence that breeding activity is occurring in this population at large. The remaining seven species are represented by at least several females at one or more of the sites, and they deserve further scrutiny. To this end, Table 3 has been constructed to show (a) the percentage of females that are gravid, (b) the average number of eggs per gravid female, and (c) the main site of breeding activity, if this can be identified. The species are listed in decreasing order of the percentage frequency values of gravid females.

If we define an active breeding population as one in which at least 50% of the females are gravid, we can place three species, *Damaeus* sp., *Tectocephus velatus* and *Oppia* sp., in this category. *Damaeus* sp. was collected only from the *Fallugia* site and although the number of females recovered was only six, five of these were gravid. Further, the number of eggs per gravid female was considerably higher than that of the other two species considered here as active breeders and this is taken as further evidence that reproductive out-

Table 3. Cryptostigmata Apterogasterina: Frequency (%) of gravid females, average number of eggs per gravid female and main breeding site, where applicable.

	Gravid females (%)	Average number of eggs/gravid female	Main breeding site
<i>Damaeus</i> sp.	83	7	<i>Fallugia</i>
<i>Tectocephus velatus</i>	75	2	All except <i>Bouteloua</i> and <i>Juniperus</i>
<i>Oppia</i> sp.	50	2	<i>Juniperus</i>
<i>Oppiella</i> sp.	35	1	
<i>Microzetes auxiliaris</i>	13	1	
<i>Joshuella striata</i>	10	2	
<i>Machadobelba</i> sp.	6	4	

put could be high at this time of year in this species. *T. velatus* was apparently breeding at all of the sites investigated except the *Bouteloua* site, where it did not occur at all. This rather general pattern of distribution, embracing five of the six sites, accords with its ubiquitous distribution on a cosmopolitan scale. *Oppia* sp. was not breeding in the *Bouteloua* site despite the fact that there was a large preponderance of males in the samples.

*Cryptostigmata Pterogasterina*

Reproductive data relating to the species assigned to this section are given in Tables 4 and 5. The numbers of females of *Passalozetes californicus*, *P. neomexicanus granulatus*, *Areozetes* sp., *Zygoribatula heteroporosa* and *Peloribates hammeri* were too low to allow firm conclusions to be drawn regarding the reproductive activity of these populations as a whole (Table 4). However, it is worth noting in passing that in all of these cases except *P. neomexicanus granulatus*, the females collected were gravid. The two females of *P. californicus* contained two and three eggs, respectively, *Areozetes* sp. two eggs each, *Z. heteroporosa* seven eggs and *P. hammeri* three eggs. These species are clearly following the trend demonstrated by several of the remaining nine species of Pterogasterina for which more substantial data are available (Table 5). With the exception of the nominate form of *P. neomexicanus* and *Galumna* sp., all of these 'higher' oribatids show evidence of considerable breeding activity in these sites at this time. Further, it will be evident that species preferences for a particular breeding site vary. Only the very exposed *Bouteloua* site was not favoured by any of the species, and *Jornadia larreae* and possibly *Peloribates* sp. restricted their breeding populations to a single site. Finally, it may be noted that egg output per individual gravid female is much higher, generally, in the Pterogasterina than in the Apterogasterina.

*Simulated rainfall experiments*

Counts of total microarthropods recovered from 20 g aliquots of

Table 2. Cryptostigmata Apterogasterina: Numbers of males and females present in five litter samples taken from each of six litter types.

	<i>Atriplex</i>	<i>Bouteloua</i>	<i>Fallugia</i>	<i>Juniperus</i>	<i>Larrea</i>	<i>Quercus</i>
<i>Joshuella striata</i>	10♂♂ 8♀♀	4♂♂ 1♀		3♂♂ 2♀♀		
<i>Plesiodamaeus</i> sp.						1♂ 16♀♀
<i>Damaeus</i> sp.			1♂ 6♀♀			
<i>Microzetes auxiliaris</i>				15♀♀		
<i>Tectocephus velatus</i>	9♂♂ 17♀♀		42♀♀	1♂ 86♀♀	9♀♀	45♀♀
<i>Oppia</i> sp.		244♂♂ 3♀♀	1♂ 1♀	33♂♂ 27♀♀	3♂♂	
<i>Oppiella</i> sp.			8♀♀	4♀♀		1♂ 5♀♀
<i>Ramusella elliptica</i>	1♀					1♀
<i>Machadobelba</i> sp.			7♂♂ 16♀♀			
<i>Cymbaeremaeus</i> sp.				1♂ 1♀		
<i>Scapheremaeus obliterated</i>			3♂♂			

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Table 4. Cryptostigmata Pterogasterina: Numbers of males and females present in five litter samples taken from each of six litter types.

	<i>Atriplex</i>	<i>Bouteloua</i>	<i>Fallugia</i>	<i>Juniperus</i>	<i>Larrea</i>	<i>Quercus</i>
<i>Passalozetes californicus</i>		1♂ 1♀		1♀	2♂♂	
<i>P. neomexicanus</i>		14♀♀				
<i>P. neomexicanus granulatus</i>		1♂		1♀	2♀♀	
<i>Scutovertex</i> sp.	13♂♂ 8♀♀		4♂♂ 9♀♀	7♂♂ 7♀♀	2♀♀	
<i>Areozetes</i> sp.	2♀♀					
<i>Hemileius initialis</i>				49♂♂ 22♀♀		61♂♂ 29♀♀
<i>Jornadia larreae</i>			1♀	1♀	77♂♂ 141♀♀	
<i>Schelorbates pallidulus</i>	1♂ 17♀♀			12♂♂ 19♀♀		
<i>Zygoribatula heteroporosa</i>				2♂♂ 1♀		
<i>Peloribates europaeus</i>		1♀		19♂♂ 5♀♀	5♂♂ 10♀♀	
<i>P. hammeri</i>				4♂♂ 1♀		
<i>Peloribates</i> sp.			1♀	4♂♂ 4♀♀		
<i>Galumna</i> sp.	1♀	2♀♀	11♀♀	2♂♂ 202♀♀		1♀
<i>Pilogalumna</i> cf. <i>bloemfonteinensis</i>						25♂♂ 108♀♀

litter, on a monthly basis, from June 1981 to June 1982, are graphically represented in Fig. 3. Here, treatment effects are plotted separately. It will be evident from this graph that simulated rainfall, applied at the rate of 6.25 mm each week, and at the more concentrated but discontinuous rate of 25.40 mm each month, did not produce significantly higher numbers of microarthropods than did the unwatered control plot. Nor were treatment effects significant when individual groups of microarthropods were considered. This is illustrated by the data obtained for the Cryptostigmata, which are typical of other microarthropod taxa (Fig. 4).

On the other hand, the Cryptostigmata do decrease overall during the period of the experiment, irrespective of treatment, and this, perhaps, requires further analysis. Since treatment effects were insignificant, these data were pooled to allow general comparisons to be made between the results of 'before' and 'after' watering treatment.

Attention was therefore focused on the population dynamics of the four numerically dominant species of Cryptostigmata occurring in this Chihuahuan Desert site: *Passalozetes neomexicanus*, *P. californicus*, *Joshuella striata* and *Jornadia larreae*. *J. larreae* is a new genus and species for which the Jornada site is the type locality. Similarly, *P. neomexicanus* is a new species and formal descriptions of this and *J. larreae* are being published elsewhere.<sup>7,8</sup>

Table 5. Cryptostigmata Pterogasterina: Frequency (%) of gravid females, average number of eggs per gravid female and main breeding site, where applicable.

	Gravid females (%)	Average number of eggs/gravid female	Main breeding site
<i>Hemileius initialis</i>	100	5	{ <i>Juniperus</i> { <i>Quercus</i>
<i>Jornadia arreae</i>	100	6	<i>Larrea</i>
<i>Peloribates</i> sp.	100	10	<i>Juniperus</i>
<i>Peloribates europaeus</i>	90	6	{ <i>Juniperus</i> { <i>Larrea</i>
<i>Schelorbates pallidulus</i>	83	4	{ <i>Juniperus</i> { <i>Atriplex</i>
<i>Pilogalumna</i> cf. <i>bloemfonteinensis</i>	65	6-12	{ <i>Fallugia</i> { <i>Quercus</i>
<i>Scutovertex</i> sp.	60	4	{ <i>Atriplex</i> { <i>Fallugia</i>
<i>Passalozetes neomexicanus</i>	14	2	
<i>Galumna</i> sp.	0.5	2	

The data relevant to this analysis are presented in the form of histograms (Figs 5 and 6), and before we examine these in detail some points of explanation are required:

- 1) The data are divided, essentially, into two sets: those obtained immediately prior to watering, and those taken three days after watering. Given the premise that we are monitoring the immediacy of the biological response, we can regard the data obtained from 'before watering' as a control against which can be measured the effect of the moisture variable — the 'after watering' effect.
- 2) In each case, and for each treatment, counts were made of adult males and females, and the number of eggs in gravid females.
- 3) The data have no statistical significance since collections from

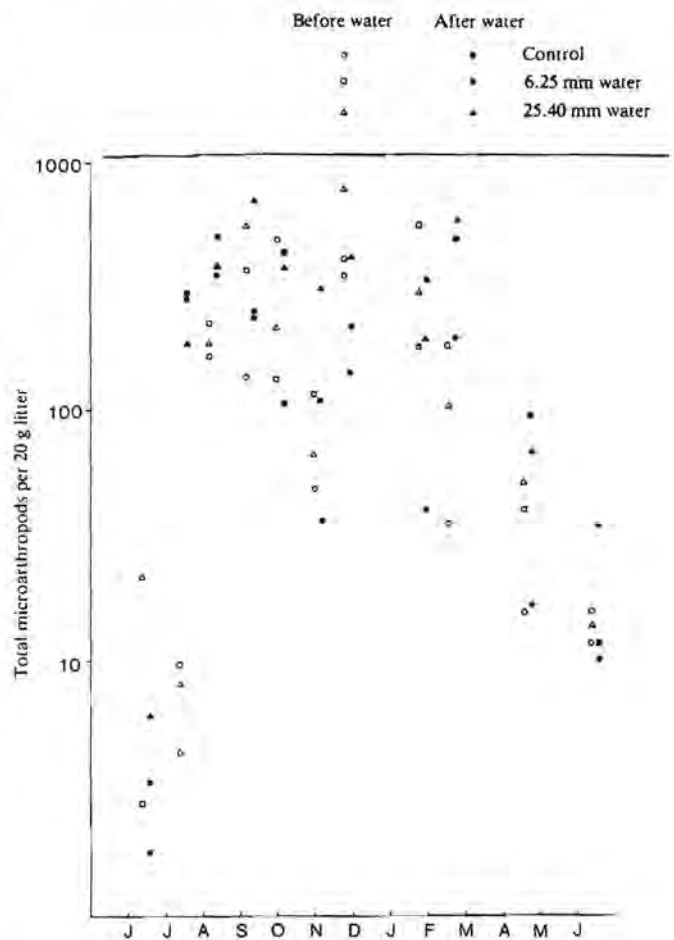


Fig. 3. Counts of total microarthropods from control and treated plots in the simulated rainfall experiment.

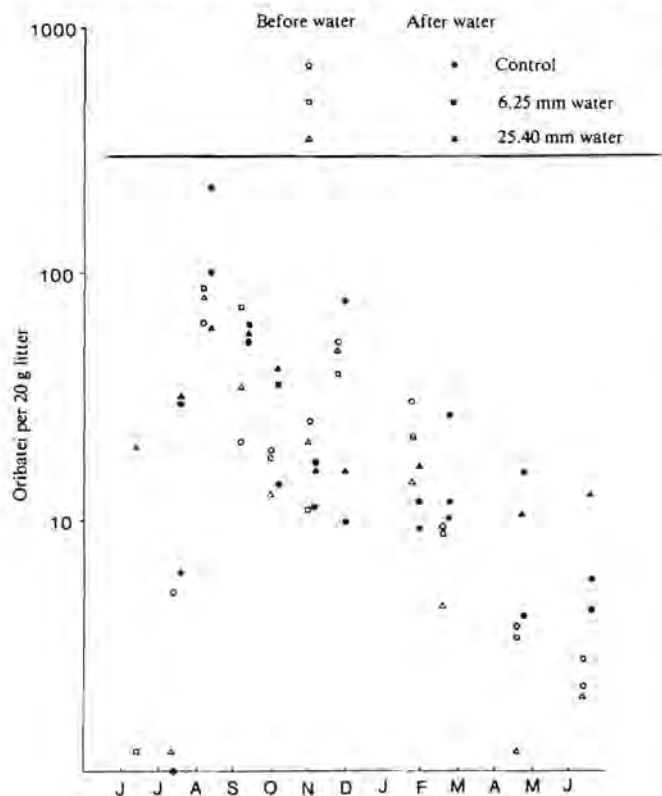


Fig. 4. Counts of Cryptostigmata from control and treated plots in the simulated rainfall experiment.

litter and mineral soil (15 replicates of each) on each sampling date were pooled in the laboratory.

4) However, certain trends are apparent — so apparent in fact, that perhaps they do not require statistical confirmation.

Given these conditions and qualifications, what conclusions can we derive from these data?

#### The control plots

As is evident from Fig. 5, the two *Passalozetes* species show definite seasonality in egg production. *P. neomexicanus* starts to produce eggs in July and reaches maximum production in the following month. Egg production ceases after August. In the case of *P. californicus*, egg production occurs over a rather more extended time period (July to September). *Jornadia larreae* also shows a definite peak in egg production centred on the month of August. In contrast, egg production in *Joshuella striata* occurs, for the most part, in the period December to January. This coincides with maximum activity of females — but neither of these events coincides with the period of seasonal rainfall in the Chihuahuan Desert. *Passalozetes neomexicanus* also times its egg production to coincide with the appearance of the maximum number of females in the population, but this timing is coincident with the summer rainfall event. *P. californicus* behaves in a somewhat similar, if attenuated, way, although this species is much less abundant than *P. neomexicanus*. On the other hand, the period of maximum egg production in *Jornadia larreae* (August) does not coincide with the period of maximum adult female activity.

#### The treated plots

The data provided in Fig. 6 indicate that the effect of watering the plots is to intensify the seasonality of the breeding response, at least in the case of *P. neomexicanus*, *P. californicus* and *J. larreae*. The breeding response of *J. striata* assumes bimodal properties — a peak that corresponds to the natural summer rainfall event in the Chihuahuan Desert, and a second peak that occurs in February.

## Discussion

The studies described above provide some interesting insights into the survival strategies adopted in certain hot deserts. They also pose some questions that cannot, at the moment, be answered. The hypothesis being tested here is that the cryptostigmatid mite populations in question 'track' their environment in an opportunistic way such that they respond immediately to rainfall events (the presumed 'trigger') by recruiting a new generation of individuals. The results of the pilot survey, conducted in 1979, are consistent with this hypothesis, particularly with respect to the 'higher' Cryptostigmata Pterogasterina, which represented the majority of the soil microarthropods surveyed. Further, five of these dominant pterogasterines were breeding at more than one site (Table 5). This is a 'bet-hedging' strategy which ensures that if part of the population becomes eliminated due to unfavourable conditions in one habitat, the species will survive in an alternative (and possibly more favourable) habitat. This implies a degree of non-specialization which is consistent with the idea of *r*-selection. The results of more detailed analyses of reproductive activity of selected species, carried out in 1981/82 on simulated rainfall plots, are not entirely consistent with this view. On plots regarded as controls, *Passalozetes neomexicanus*, *P. californicus* and *Jornadia larreae* behave as would be expected by having peak egg production coincident with the summer rainfall period (Fig. 5). At this time, the adult female population is high in the case of *P. neomexicanus* and *P. californicus*, as would be expected. However, the peak in egg production in *J. larreae* (August) occurs some three months before the start of the period of maximum female activity (November). There is no immediate or obvious explanation for this discrepancy. *Joshuella striata* provides a strikingly different picture from *Passalozetes* spp. and *J. larreae* as far as its reproductive activity is concerned. *J. striata* is distributed across the winter rainfall desert of southern California to the summer rainfall desert of New Mexico. There is some evidence that the Chihuahuan Desert site studied here is of relatively recent origin (McBrayer, personal communication) — perhaps more recent than the Californian Mojave site from which *J. striata* was first recorded and described.<sup>9</sup> If this is indeed the case, then perhaps we can regard *J. striata* as a recent coloniser of the Chihuahuan Desert, retaining an in-built tendency to react to winter rainfall events, even in the summer rainfall desert of New Mexico.

The results from samples taken after rainfall amendments are even more surprising. Our initial assumption that these mites are *r*-strategists implies the expectation that they would reproduce opportunistically with each rainfall event. The seasonality observed in the samples taken before wetting should be replaced by a much more stochastic pattern of reproductive behaviour, without any evidence of seasonal peaks. Quite the reverse is the case, at least in three of the four species selected for detailed study (Fig. 6). The seasonality of the breeding response in *P. neomexicanus*, *P. californicus* and *J. larreae* is intensified rather than attenuated in the watered plots. The breeding response of *J. striata* has bimodal characteristics: a peak that corresponds to the natural summer rainfall event in the Chihuahuan Desert, and a second peak that occurs in February. This second peak approximates to the time that this species recruits in the winter rainfall desert of the Mojave.<sup>10</sup> *J. striata* would appear to be rather labile in its response to rainfall events — as it would have to be if it were to become a successful coloniser of both winter and summer rainfall deserts.

## Concluding remarks

The conclusion that appears to emerge from the analyses presented above is that the species studied in detail have acquired, through the process of natural selection, life-history strategies that are geared to predictable rainfall events in late summer (*Passalozetes* spp. and *Jornadia larreae*) or winter (*Joshuella striata*). These strategies are identified with natural rainfall events and in the case of *Passalozetes* spp. and *Jornadia larreae*, cannot be

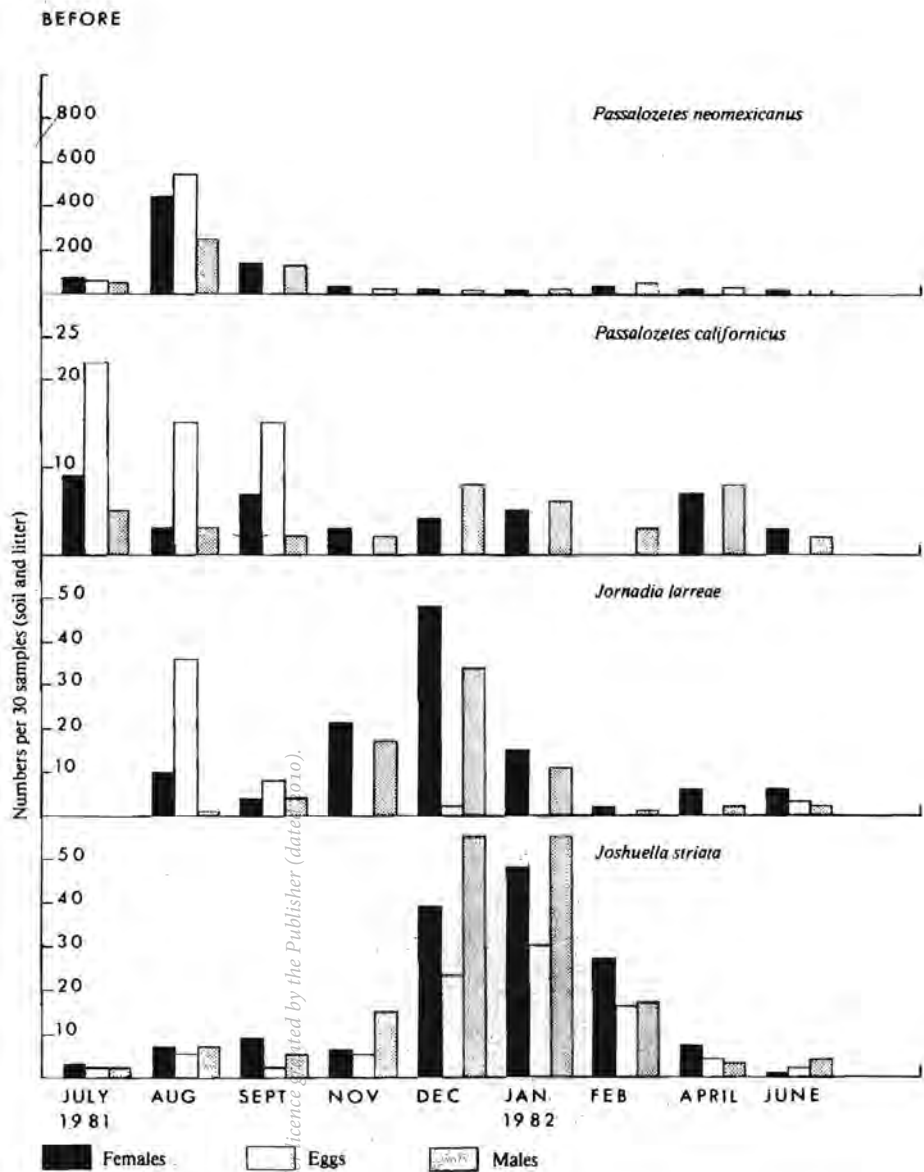


Fig. 5. Numbers of adults and eggs of four species of Cryptostigmata recovered from *Larrea* plots before watering for the period July 1981 to June 1982.

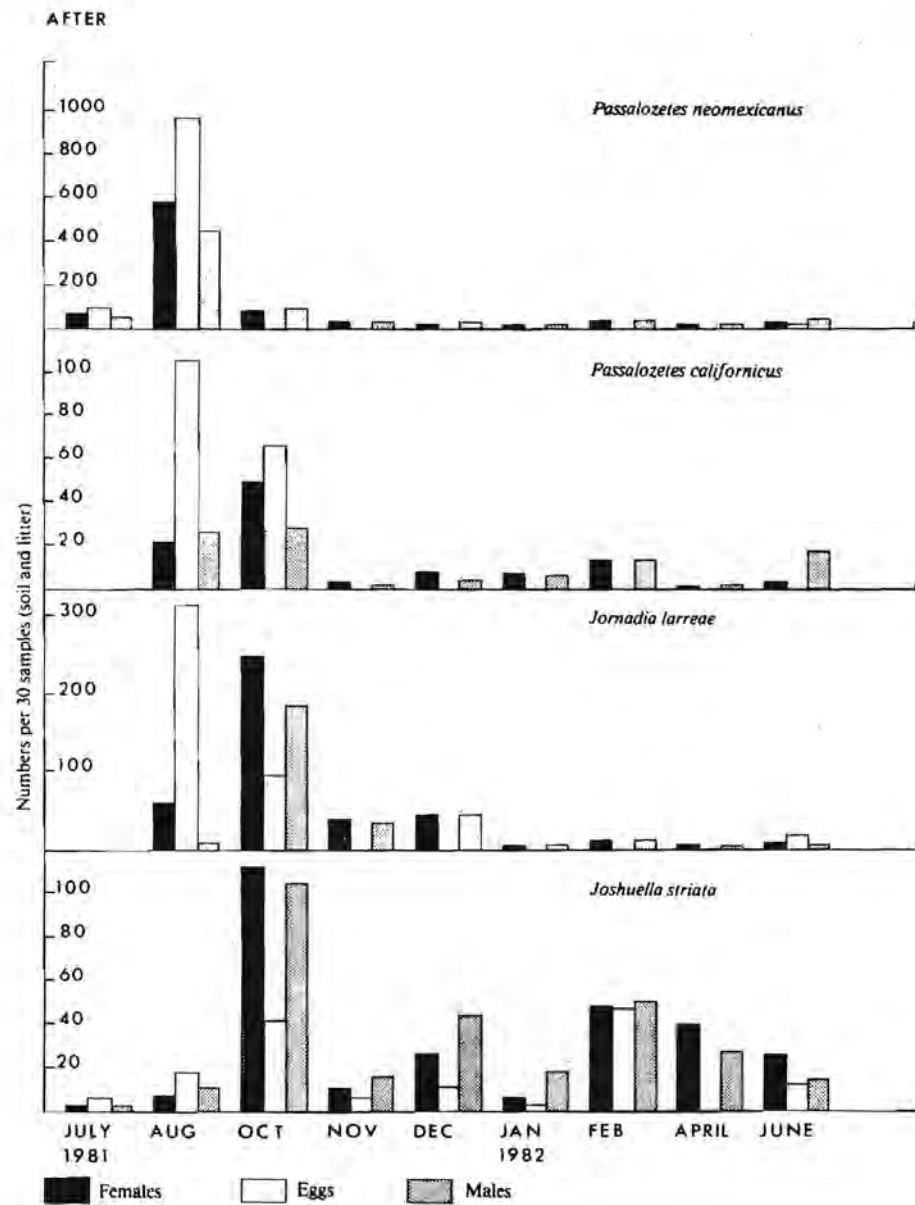


Fig. 6. Numbers of adults and eggs of four species of Cryptostigmata recovered from *Larrea* plots after watering for the period July 1981 to June 1982.

disrupted by perturbations to the system. This conclusion must cast doubt on the belief that these strategies are, unequivocally, the products of *r*-selection.

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### Appendix I

Cryptostigmata recorded in the litter and soil under six species of desert shrub (*Atriplex* sp., *Bouteloua* sp., *Fallugia paradoxa*, *Juniperus* sp., *Larrea tridentata*, *Quercus* sp.) in southern New Mexico, August 1979.

#### 'Lower' Cryptostigmata

- Phthiracaridae  
*Hoplophthiracarus* sp.
- Cosmochthoniidae  
*Cosmochthonius plumatus suramericanus* Hammer
- Sphaerochthoniidae  
*Sphaerochthonius splendidus* (Berlese)
- Camisiidae  
*Camisia* cf. *horrida* Hermann
- Trhypochthoniidae  
*Trhypochthonius* cf. *tectorum* (Berlese)
- 'Higher' Cryptostigmata (Apterogasterina)
- Gymnodamaeidae  
*Joshuella striata* Wallwork  
*Plesiodyamaeus* sp.
- Damaeidae  
*Damaeus* sp. sensu Grandjean
- Microzetidae  
*Microzetes auxiliaris appalachicola* Jacot
- Tectocephidae  
*Tectocephus velatus* (Michael)

#### Oppiidae

- Oppia* sp.  
*Oppiella* sp.  
*Ramusella (Insculptoppia)* cf. *elliptica* (Berlese)
- Machadobelbidae  
*Machadobelba* sp.
- Cymbaeremaeidae  
*Cymbaeremaeus* sp.  
*Scapheremaeus* cf. *obliteratus* Hammer

#### 'Higher' Cryptostigmata (Pterogasterina)

- Passalozetidae  
*Passalozetes californicus* Wallwork  
*Passalozetes neomexicanus* Wallwork et al.  
*Passalozetes neomexicanus granulatus* Wallwork et al.
- Scutoverticidae  
*Scutovertex* sp. nov.
- Oribatulidae  
*Areozetes* (genus close to)  
*Hemileius* cf. *initialis* (Berlese)  
*Jornadia larreae* Wallwork & Weems  
*Schelorbates* cf. *pallidulus* (C.L. Koch)  
*Zygoribatula* cf. *heteroporosa* Wallwork
- Haplozetidae  
*Pelorbates* cf. *europaeus americanus* Jacot  
*Pelorbates hammeri* Wallwork  
*Pelorbates* sp.
- Galumnidae  
*Galumna* sp.  
*Pilogalumna* cf. *bloemfonteinensis* Engelbrecht

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