Seasonality of some Chihuahuan Desert soil oribatid mites (Acari: Cryptostigmata)

J. A. Wallwork, Miranda MacQuitty,
School of Biological Sciences, Queen Mary College, University of London, UK

Solange Silva and W. G. Whitford
Department of Biology, New Mexico State University, Las Cruces, NM, USA

(With 12 figures in the text)

1. Reproductive strategies of four species of oribatid mites were investigated in the Chihuahuan Desert from 1981 to 1984.

2. Breeding activity coincided with the summer rainfall period in three of the four cases: *Passalozetes neomexicanus, P. californicus* and *Jornadia larreae*. This pattern was not changed by the application of simulated rainfall at other times of the year. The strict seasonality of reproductive behaviour is interpreted as an outcome of strong selection pressure to recruit only when food quality and quantity and microclimate are most favourable.

3. *Joshuella striata* showed a more flexible pattern which was essentially bimodal. Periods of egg production occurred in winter and also during the summer rainfall period. This pattern is consistent with the known distribution of this species in winter- and summer-rainfall deserts in south-western USA.

Contents

Introduction

Many desert plants and animals time their periods of reproductive activity to coincide with periods of natural rainfall (Noy-Meir, 1973; Crawford, 1981; Louw & Seely, 1982; Wallwork, 1980, 1982). In this respect, they conform to the 'trigger-pulse-reserve' paradigm defined by Noy-Meir (1973) to describe responses of desert organisms. Since rainfall 'triggers' are stochastic in timing and magnitude, it may be expected that periods of reproductive activity of desert organisms would be unpredictable.

If desert organisms respond to rainfall 'triggers' (*sensu* Noy-Meir, 1973), then modification of climate by imposition of regularity in rainfall should result in shifts in reproductive patterns. However, if organisms have evolved reproductive physiologies linked to the 'predictable' rainfall season, then reproduction should remain seasonal. In a study imposing climate modification on a series of plots in the Chihuahuan Desert, we found that, during the first year of study, four species of soil-dwelling oribatid mites reproduced during the predictable season of rainfall

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(Wallwork, Kamill & Whitford, 1984). If the superimposed artificial rainfall were to result in a shift in reproduction, that response was not likely to occur during the first year. We therefore continued the climate modification and reproduction studies for an additional two years. This paper reports the results of that study, together with baseline data on the population dynamics of oribatid mites and selected species.

Study site and methods

The study site was located on the Jornada Long-Term Ecological Research site on the New Mexico State University ranch 40 km NNE of Las Cruces, New Mexico. The long-term average rainfall in this area is 225 mm yr^{-1}. Summers are hot with maximum air temperatures between 35–40 °C from mid-May to mid-September. Rainfall is predominately summer rainfall from convectional storms. The probability of cumulative rainfall of more than 25 mm, based on 119 years of precipitation data, is greater than 0·6 in July, August and September, 0·30 in October and less than 0·2 for the remainder of the year (Houghton, 1972). Rainfall was recorded by a tipping bucket rain gauge and clear vue rain gauges located within 100 m of the study plots.

We established 9 plots on an area where creosotebush, *Larrea tridentata* (D.C. Cov.) occurs as a monotypic dominant shrub. The soil is a loamy sand with a calcium carbonate deposition layer (caliche) at approximately 70 cm depth. The 'rainfall supplemented' plots were set up with an irrigation system that provided sprinkler-delivered water above the shrub canopy to mimic natural rainfall as closely as possible. The irrigated plots thus received the natural rainfall plus the scheduled supplement. Three plots received 1″ (= 25 mm) every 4 weeks, 3 plots received ¼″ (= 6 mm) per week and 3 plots received no additional water.

In 1981 and 1982, soil microarthropods were extracted from the litter remaining in open-bottom screen cylinders that originally contained 20 g of *L. tridentata* litter. The litter and a small quantity of mineral soil was carefully transferred to plastic bags for transport to the laboratory. The cylinders with creosotebush litter had a surface area of 10 cm². Five cylinders from each irrigation treatment and control were collected
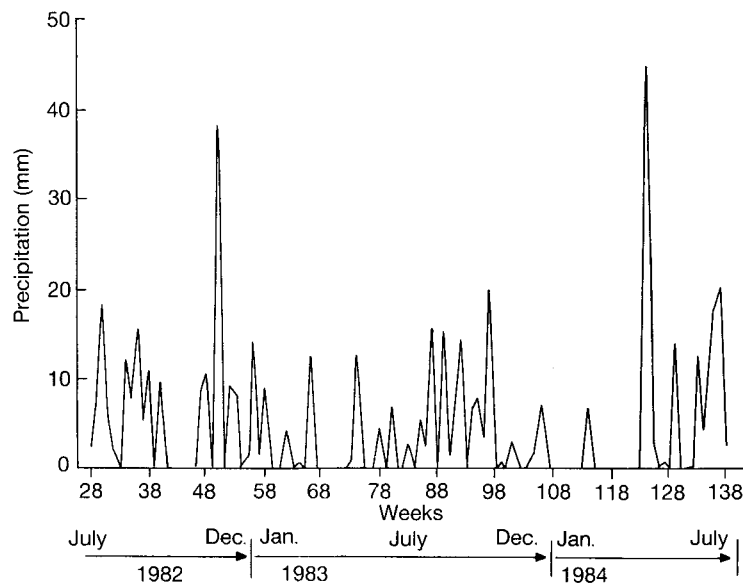

FIG. 1. Weekly rainfall data for the period July 1982 to July 1984 at the study site.

on each sampling date. In 1983 and 1984, 2 square screen enclosures 1·5 m each side were constructed around creosotebushes on each plot. We maintained a litter layer of 1 cm of *L. tridentata* litter collected from the surrounding area. We collected 12 cores of litter and soil (surface area 64 cm^2) to a depth of 8 cm. Cores and litter samples were collected 3 days after the application of the 25 mm simulated rainfall. The litter or litter and soil cores were placed in modified Tullgren funnels and mites were extracted into water for 72 h. The collection vials were removed from the funnels and the mites were identified, counted and transferred into 90% ETOH.

The number of eggs present in each gravid female was counted after the mites had been cleared in Hoyers for microscopic study. The data on clutch size were used as an index of fertility for comparisons between species and years.

Results

The rainfall events during the study are presented in Fig. 1. There are three important features of the rainfall during the period of this study:

1. A strongly clustered series of peaks from July through early October 1982 and August to October 1983. These are typical of the long-term, predictable season of rainfall for the northern Chihuahuan Desert.

2. Periods of low and intermittent rainfall occurring mainly during the spring.

3. Isolated and, at times, intense rainfall events such as those which occurred in December 1982 and May 1984. Such events are largely stochastic and reflect the short-term unpredictability of the rainfall pattern in this area. The May 1984 storm has been classified as a one in 100-year occurrence.

Effects of treatments

Densities of oribatids in all three treatments are generally higher in 1981 than in subsequent years (Fig. 2). Peaks in population density occurred in August and September in 1981, 1983 and
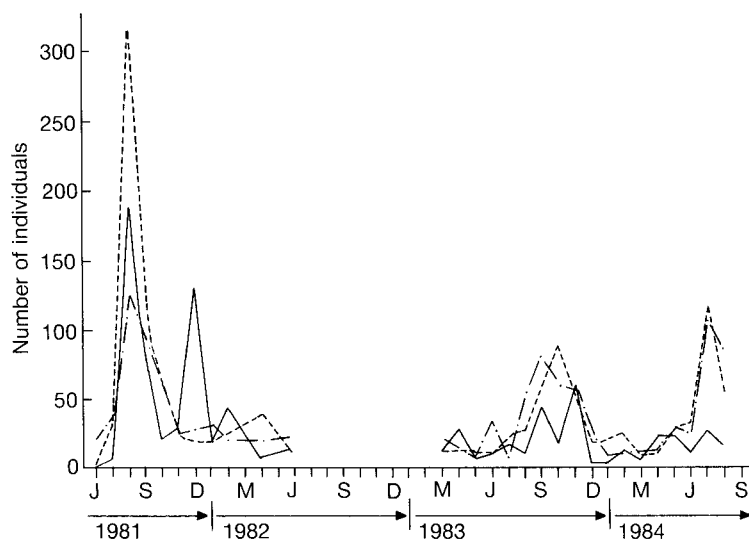

FIG. 2. Monthly population densities of oribatid mites for the period June 1981 to August 1984 on control (———), ¼″ amended (- - - - - -) and 1″ amended (-------) plots.
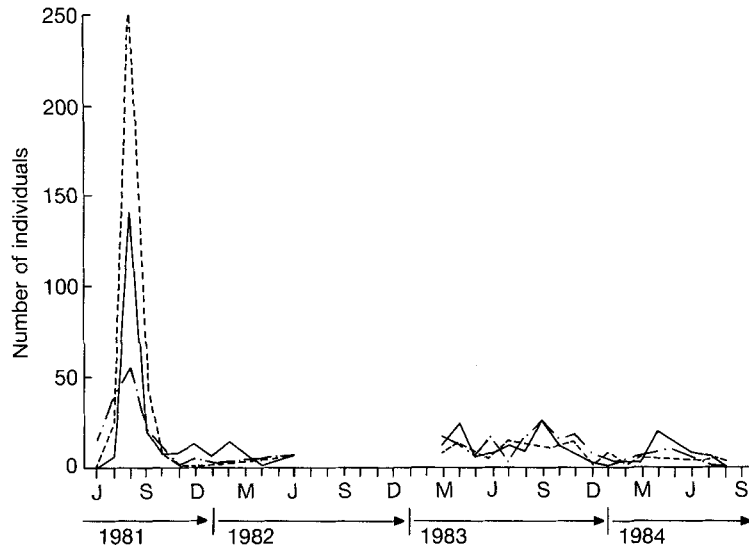
FIG. 3. Monthly population densities of *Passalozetes* spp. (*P. neomexicanus* and *P. californicus*) for the period June 1981 to August 1984 on control (———), ¼″ amended (- - - - - -) and 1″ amended (-·-·-·-·) plots.

1984 (i.e. the rainy season). There is an additional peak in the control in December 1981 which continued in an attenuated form into February 1982. With these exceptions, oribatid densities were generally higher in the rainfall-amended plots than in the controls.

Species comparisons

We examined population fluctuations of selected species of oribatids, concentrating on those that were numerically the most abundant: *Passalozetes neomexicanus* Wallwork, Weems & Kamill, *P. californicus* Wallwork, *Jornadia larreae* Wallwork & Weems, and *Joshuella striata* Wallwork. Unfortunately, the two species of *Passalozetes* were not separated during the counting of samples and must be considered as *Passalozetes* spp. for analysis of population fluctuations. We suggest that most of these were *P. neomexicanus*.

Passalozetes spp. contributed a large fraction of the density peaks of total oribatids that occurred during August 1981 in all three treatments (Figs 2 and 3). Subsequently, the number of *Passalozetes* spp. declined to very moderate levels in all three treatments.

Jornadia larreae consistently produced peak densities during the period of summer rainfall in 1981, 1983 and 1984 on the plots receiving rainfall amendments (Fig. 4). *Jornadia larreae* also contributed to the December 1981 peak of total oribatids on the control plots (Fig. 2) as well as the very small increase in numbers that occurred in April 1982 on the plots amended with 1/4″ rainfall (Fig. 2).

Joshuella striata was often as abundant on the control plots as it was on the plots that received amendments. Further, density peaks in all treatments were more widely scattered over the summer and winter. *Joshuella striata* made an important contribution to the December 1981 peak of total orbatids in the controls (Figs 2 and 5) and to the subsequent minor peak in February 1982.
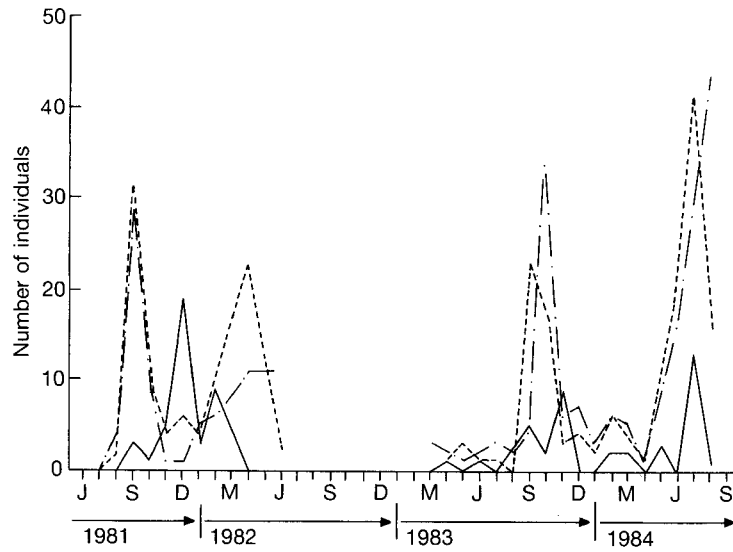
FIG. 4. Monthly population densities of *Jornadia larreae* for the period June 1981 to August 1984 on control (————), $\frac{1}{4}''$ amended (- - - - - -) and 1″ amended (------) plots.
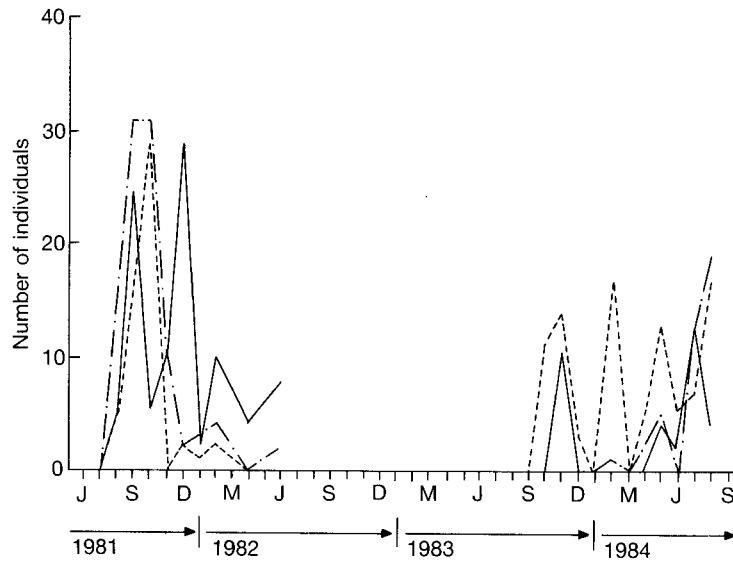

FIG. 5. Monthly population densities of *Joshuella striata* for the period June 1981 to August 1984 on control (————), $\frac{1}{4}''$ amended (- - - - - -) and 1″ amended (------) plots.

Reproductive biology

In 1981/82, data were obtained on the seasonality of breeding for *Passalozetes neomexicanus*, *P. californicus*, *Jornadia larreae* and *Joshuella striata* (Wallwork *et al.*, 1984). A pilot study conducted in 1979 on the Jornada site provided data on clutch sizes of many of the oribatid species occurring here, including the four just mentioned (Wallwork *et al.*, 1984). These four species were selected for intensive study in 1983/84.
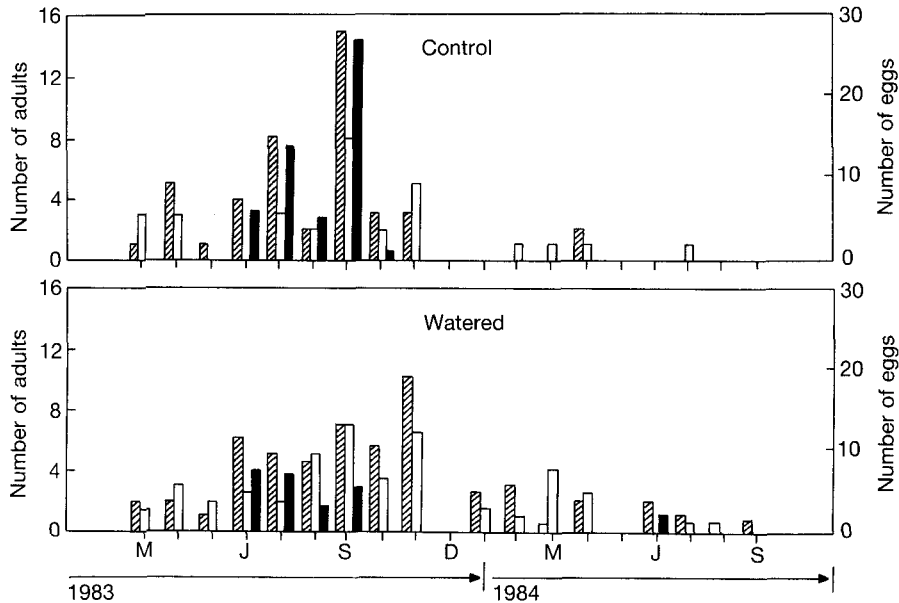

FIG. 6. Numbers of females (▨), males (□) and eggs in gravid females (■) of *Passalozetes neomexicanus* in control and water-amended plots (¼″ and 1″ data pooled) in 1983–84.

Passalozetes neomexicanus

The marked seasonality of breeding in this species noted in 1981/82 was repeated in 1983 (Fig. 6). Adult females occurred in the samples taken from watered plots throughout most of the study period. However, egg production was restricted to the months of June to September 1983 and was fairly evenly distributed throughout this period of time. A similar pattern occurred on the control plots, although here the number of adult females reached a peak in September, as did egg production (Fig. 6). Compared to 1981/82, when breeding was confined to the months of July and August (Wallwork *et al.*, 1984), the 1983 breeding season was extended in both the watered treatments and the controls, and a few individuals were reproducing in October in the latter. Inexplicably, though, population levels were low in 1984 and virtually no breeding activity was observed in either control or watered plots up to September 1984. Clutch size, based on the number of eggs present in gravid females, was two, and this agrees with the estimate reported previously for this species on this site (Wallwork *et al.*, 1984).
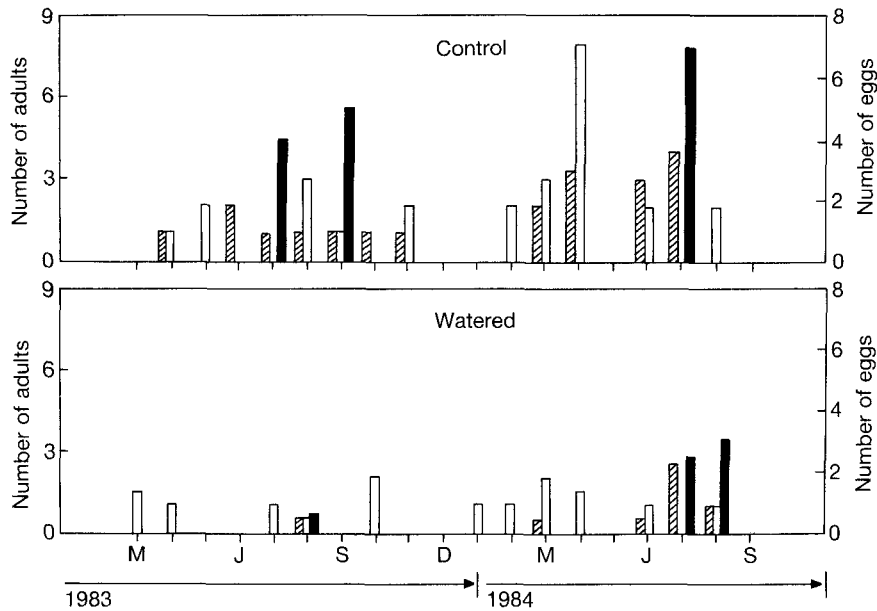
FIG. 7. Numbers of females (▨), males (□) and eggs in gravid females (■) of *Passalozetes californicus* in control and water-amended plots ($\frac{1}{4}''$ and $1''$ data pooled) in 1983–84.

Passalozetes californicus

The numbers of this species recovered in 1983 were somewhat lower than those collected in 1981/82; there was, however, an apparent increase in the summer of 1984. *Passalozetes californicus* is never as abundant as *P. neomexicanus* on the Jornada. Breeding activity was detected in July and September 1983 in the controls, and in August 1983 in the watered plots (Fig. 7). A similar pattern was shown in 1984. It can be assumed, therefore, that this species reproduces during the period July to September, and into October (taking into account the 1981/82 data). The pattern of reproductive activity described in 1981/82 for this species is confirmed by the data obtained in 1983/84. Data on clutch size are sparse in 1983/84; gravid females contained one to six eggs. The mean for the population (3·7) is close to previously recorded estimates (Wallwork *et al.*, 1984).

Jornadia larreae

Females of this species were less numerous in the 1983/84 samples than they were in 1981/82 and the data on breeding activity during 1983, depicted in Fig. 8, are hardly convincing if considered alone. In 1981, *J. larreae* showed a peak in egg production centred around August both in the control and watered plots and continuing through October on the watered plots. There is also evidence that breeding may commence as early as June 1982 on all treatments (Wallwork *et al.*, 1984). A period of egg production extending from June to September is not inconsistent with the 1983/84 data and provides some confirmation of the reproductive pattern described previously (Wallwork *et al.*, 1984). Furthermore, the juveniles of this species have been described (Wallwork & Weems, 1984) and were identified in the 1983/84 samples. A few protonymphs and deutonymphs were recorded from plots receiving $1''$ rainfall amendments in
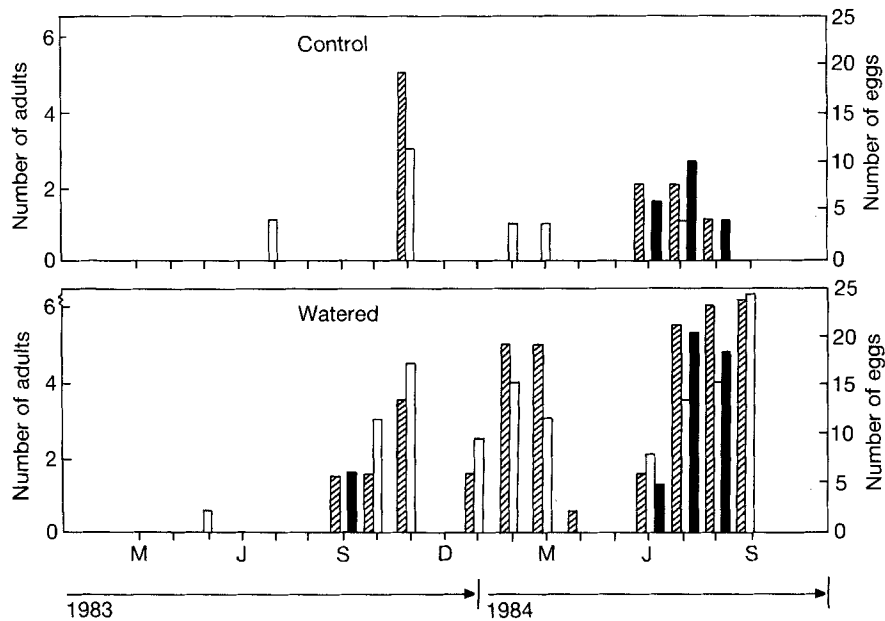
FIG. 8. Numbers of females (▨), males (□) and eggs in gravid females (■) of *Jornadia larreae* in control and water-amended plots ($\frac{1}{4}''$ and $1''$ data pooled) in 1983-84.

September 1983, and these developmental stages, together with tritonymphs, occurred in the samples from watered plots in January 1984. In July and August 1984, all post-embryonic stages, from larvae to tritonymphs were taken from all treatments in appreciable numbers. Protonymphs and deutonymphs outnumbered tritonymphs in these samples. These observations indicate that eggs produced at the beginning of the summer can develop to late nymphal stages in July and August and, certainly, this appears to be the case in 1984. A development time from the hatching of the egg to the tritonymph and, possibly, the adult of 4-6 weeks at this time of the year is not inconsistent with these data. Elsewhere, Wallwork (1980) has suggested short development times (i.e. of the order of weeks rather than months) for soil mites in a Mojave Desert site. Another feature of the 1981/82 pattern which was repeated in 1983/84 was the asynchrony between the period of maximum egg production (June and September) and a period when female activity was high (November to March), particularly on the watered plots (Fig. 8). Clutch sizes are consistent, each gravid female containing four to six eggs (mean clutch size = 5·0). This is in accord with the data reported previously (Wallwork *et al.*, 1984).

Joshuella striata

In the control plots in 1981/82, breeding activity was concentrated mainly in the period December to February, i.e. coincident with rainfall events in the Mojave, but not the Chihuahuan Desert. In the watered plots, breeding activity was bimodal with a second peak coincident with the summer rainfall (August through October). This was interpreted as indicating a rather more flexible pattern of reproduction than those shown by *Passalozetes* spp. and *Jornadia larreae*; a flexibility which would permit *J. striata* to be a successful colonist of both types of desert. In

1983/84, the few data that were available for the control plots indicated breeding activity occurring from August to November (Fig. 9), but a second peak (during winter), observed in 1982, was not shown in 1984. In the watered plots, gravid females occurred in samples collected from May to November 1983, and egg production reached a peak during the months of September and October. Gravid females were also present in January and February 1984 but breeding activity was less pronounced at this time than the winter peak of breeding that occurred in 1982 (see Wallwork *et al.*, 1984). There is some evidence that the breeding activity curve has retained its bimodal character in the watered plots in 1983/84, but it is much more attenuated than it was in 1981/82. The possible reasons for this difference between the years will be discussed later. Clutch sizes were slightly different (mean for controls = 3·25; mean for watered plots = 2·5) but this difference was not significant at $P = 0·01$.

Other oribatids

With the exception of *Aphelacarus acarinus* (Berlese), most of the other species were recovered in numbers that were too low to provide concrete data on their reproductive biology. Nevertheless, they yielded some information which is, perhaps, worth recording.

Aphelacarus acarinus occurred consistently during the spring and summer months but virtually disappeared from the surface litter during the winter (December to March). This was the case for all treatments throughout the period of the study (1981/82 and 1983/84). At no time during the period were any gravid females collected, so the breeding biology of this species remains a complete mystery. Weems (unpubl.) found that population levels remained relatively constant in mineral soil underlying the litter on watered plots during the winter months (December to February) of 1981/82. Conceivably, breeding could occur here, but no data are available to check this.
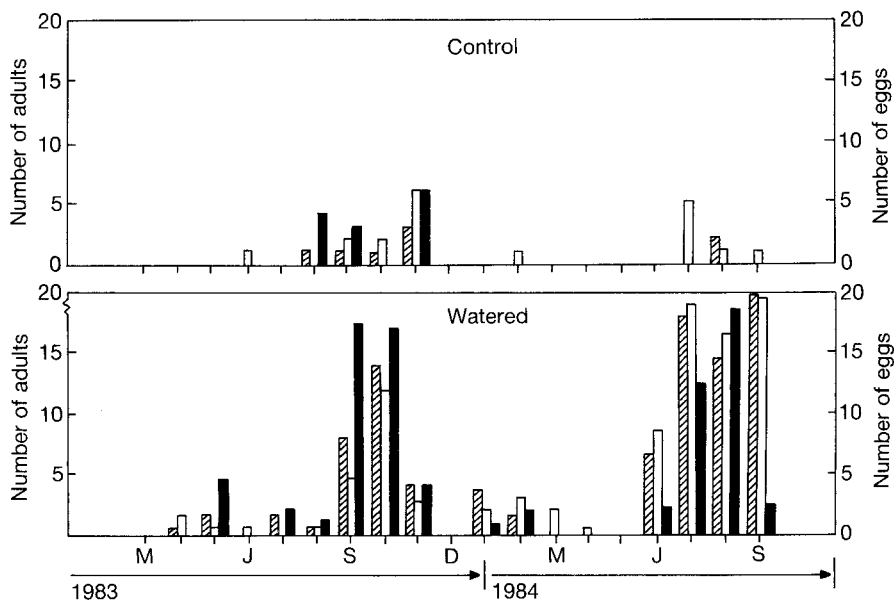

FIG. 9. Numbers of females (▨), males (□) and eggs in gravid females (■) of *Joshuella striata* in control and water-amended plots ($\frac{1}{4}''$ and $1''$ data pooled) in 1983–84.

Cosmochthonius plumatus Berlese was collected only in very low numbers in 1981/82 and no data are available on its breeding biology at this time. This species was almost completely absent from the control plots in 1983/84 but it appeared along with *C. emmae* Berlese, from which it was not distinguished, in appreciable numbers in the watered plots, particularly those receiving 1″ rainfall monthly, in late March 1983, and it was represented here until the early part of November. It was not recorded in any numbers during the winter and spring months, but reappeared in large numbers in the watered plots in June 1984 and continued to be abundant here through the remainder of the summer. But, like *Aphelacarus acarinus*, no gravid females were identified in this litter-dwelling population during 1983/84. The absence of *Cosmochthonius* spp. from the control plots may reflect an intolerance of the dry conditions that occur here. Its virtual absence even from the watered plots in spring 1984 may have been occasioned by the scarcity of rainfall during this time (Fig. 1). By the same token, breeding activity in the watered plots may be occurring among individuals living deeper in the profile (i.e. in the mineral soil) where humidities are likely to be higher than at the surface, and more stable. This is largely speculation, although *C. plumatus* was recorded from the mineral soil (down to a depth of 10 cm) during the 1981/82 sampling and was more abundant in the plots amended with 1″ rainfall than in the other treatments (Weems, unpubl.).

Brachychochthonius sp. was not recorded from the 1981/82 samples but this may have been due to its being misidentified as a juvenile. Gravid females, each containing a single egg, were present in samples taken in April, June, September, October and November 1983 and in June and July 1984. In all instances, except for the July 1984 record which relates to the $\frac{1}{4}$″ rainfall treatment, gravid females were taken only from the plots receiving 1″ rainfall amendment.

Peloribates sp. was collected only during 1984 and, then, only sporadically. Gravid females were present in March, April and July and showed no preference for any particular treatment. Clutch size varied between four and 12 during this period and this confirms the earlier findings of Wallwork *et al.* (1984). It is likely that two different species are present in the population studies in the *Larrea* site, namely *P. europaeus* Willmann and a species as yet unidentified. If these two species have slightly different breeding periods, this would account for the rather wide range in the timing of egg production (five months at least). Moreover, *P. europaeus* has an average clutch size of six, while the unidentified species averages ten eggs per gravid female (Wallwork *et al.*, 1984). A mixture of these two species in the populations studied would account for the rather large limits recorded for clutch size.

Zygoribatula cf. *heteroporosa* Wallwork was rare on the control plots in 1983/84, and only sporadic on the watered plots where it was apparently breeding in June and July 1984. Clutch size varied between five and ten.

Oppioids occurred in samples taken from all treatments in the period March to August 1983. They then became very infrequent until June and July 1984 when they were found only in the watered plots. Breeding activity was never observed in these small-sized species, but the possibility cannot be ruled out that this occurs at greater depths than those sampled in this study (i.e. the mineral soil). There may be parallels between the behaviour of oppioids and that of *Aphelacarus acarinus* and *Brachychochthonius* sp. in this regard.

Age structure

The proportions of adult oribatids and juveniles (not separated into species) in each of the monthly samples taken in 1981/82 and 1983/84 from the control and watered plots are depicted
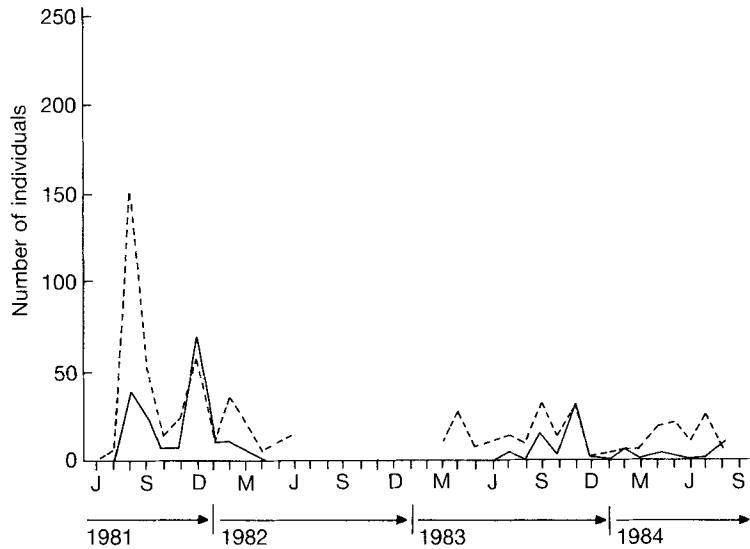
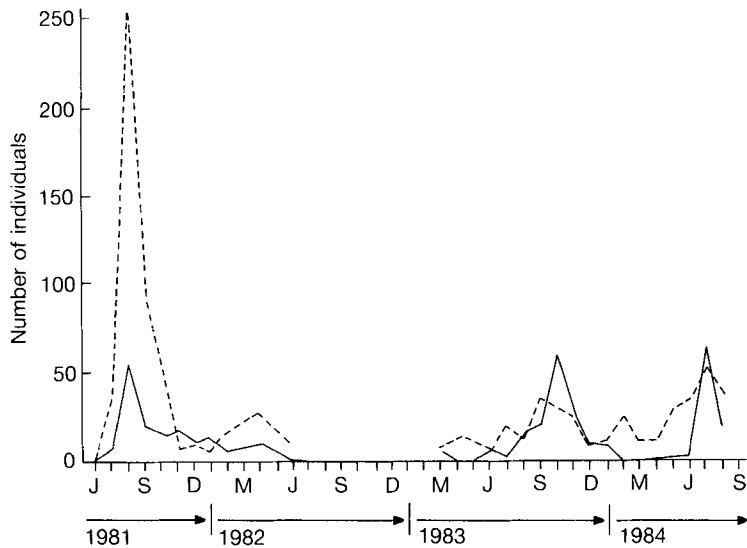FIG. 10. Numbers of adult (- - - -) and immature (———) oribatids in the control plots from 1981 to 1984.

FIG. 11. Numbers of adult (- - - -) and immature (———) oribatids in $\frac{1}{4}''$ rainfall-amended plots from 1981 to 1984.

graphically in Figs 10–12. One outstanding feature of these data, which confirms the findings of Wallwork (1980) on the soil microarthropods of a Mojave site, is that peak densities of juveniles were completely synchronized with peak densities in the adult population, i.e. there is no evident reproductive time lag. This generally holds true between years and between treatments. In particular, the age structure on the watered plots is virtually identical (cf. Figs 11 and 12) and recruitment is concentrated in the period of summer rains. An additional peak in adult and
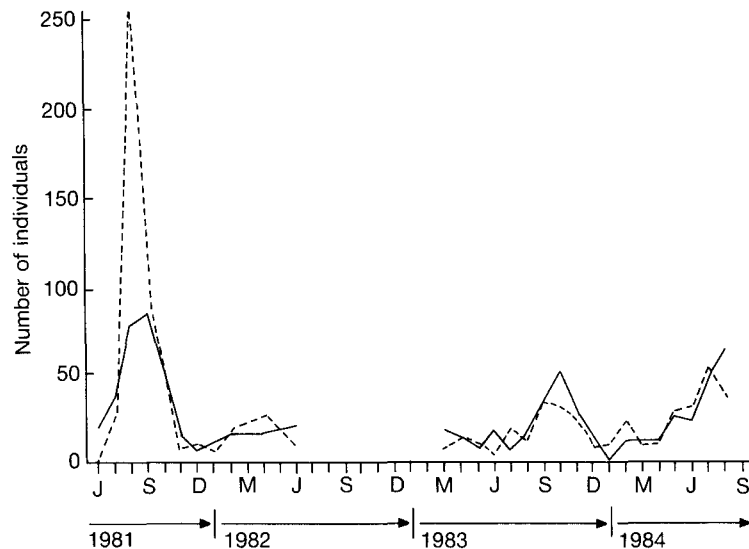
FIG. 12. Numbers of adult (- - - -) and immature (————) oribatids in 1″ rainfall-amended plots from 1981 to 1984.

juvenile numbers occurs in December 1981 and again in November 1983 on the control plots (Fig. 10). A comparison with Fig. 5 indicates that the adult peaks noted at these times reflect increases in numbers of *Joshuella striata*. Since this species was known to be producing eggs in December 1981 (Wallwork *et al.*, 1984) and in November 1983 (see Fig. 9) on the control plots, it appears likely that *J. striata* was making an appreciable contribution to the juvenile peaks observed at these times.

Discussion

In the cases of *Passalozetes neomexicanus, P. californicus* and *Jornadia larreae*, the patterns of reproductive activity occurring in 1981/82 were repeated in 1983/84 for the most part. These patterns are strongly seasonal and coincide with the period of summer rainfall, measured on a long-term basis in this part of the Chihuahuan Desert.

The winter of 1982/83 was atypical, but not entirely unusual, in that it was characterized by a series of rainfall events (Fig. 1). These events did little to disturb the patterns of reproduction shown by the two *Passalozetes* species and *Jornadia larreae*; patterns that we suggest have become established in a genotype by a long process of Natural Selection. Indeed, we would have made this prediction from the results obtained in 1981/82 when rainfall amendments, delivered at a time of the year 'outside' the period of natural rainfall, failed to produce any changes in the timing of the reproductive response. *Passalozetes neomexicanus* did commence breeding activity a month earlier in 1983 than in 1981 and the spring rains in 1983 may have been responsible for this. This we regard as 'fine tuning' on the part of this species. On the other hand, it is worthy of note that the clutch sizes produced by *Passalozetes neomexicanus, P. californicus, Jornadia larreae* and *Joshuella striata* in 1983/84 were identical to those reported from an earlier study (in 1979) from this locality.

As noted previously, *J. striata* is widely distributed in the deserts of the south-western part of the USA, from the Mojave to the Chihuahuan. Over this geographical range, rainfall patterns vary such that *J. striata* experiences winter rainfall (December to January) in the Mojave and mainly summer rainfall (July to September approximately) in the Chihuahuan Desert.

The breeding pattern of *Joshuella striata* does appear to be more variable, over the period of this study (1981–84), than the other three species considered here. We have suggested (see earlier) that this species is more flexible in its timing of reproductive activity than the others. In 1981/82, rainfall amendments converted an otherwise unimodal response curve (centred around the winter months) to one with bimodal properties (with both winter and later summer peaks). The spring rainfall in 1983 may have displaced this shift even further, with the result that the winter peak in breeding activity is suppressed in favour of a response that is related to the natural rainfall events occurring in the Chihuahuan Desert. This pattern is repeated in 1984, despite the fact that rainfall events during the spring months were less frequent and less intense than in 1983. This interpretation is consistent with the idea that this species is more flexible in terms of its reproductive strategy than the other three.

It cannot be assumed that all species of desert soil-dwelling oribatids exhibit the seasonality described above. Clearly, such strategies will minimize the energetic costs of reproduction in sexual species which can maximize egg production at times of the year when the population of adults (males and females) is large. Under these circumstances, the frequency of heterosexual encounters, and hence fertilization of eggs by males, will be high. In the case of *Passalozetes neomexicanus* and *Joshuella striata*, this generally holds true both on the controls and watered plots throughout much of the period of this study. The data obtained for *Passalozetes californicus* in 1981/82 also support this idea, but those available for 1983/84 are less conclusive. Interpretation of the data for *Jornadia larreae* presents something of a problem. Peak densities for adults occurred during the summers of 1981–84, but maximum egg production did not always occur at this time. There is no evidence to suggest that *J. larreae* is parthenogenetic and, indeed, adult males are as common as females at certain times of the year (Fig. 8). However, the clutch size for this species is relatively large compared with the other three considered here, and this could offset the low numbers of adults present during the breeding season. At the other extreme, the most 'primitive' species of Cryptostigmata, such as *Trhypochthonius tectorum*, *Cosmochthonius plumatus* and *Brachychochthonius* sp. produce one (*Cosmochthonius* and *Brachychochthonius*) or, at the most, two (*Trhypochthonius*) eggs at any one time. *Trhypochthonius tectorum* is certainly parthenogenetic (Wallwork *et al.*, 1984) and gravid females of *Brachychochthonius* were recovered from April to November 1983 and in June and July 1984. This suggests an extended breeding season occupying at least seven months of the year at this site. Such a long breeding season would be required to maintain population levels, in view of the small clutch size.

This study suggests that Chihuahuan Desert oribatid mites can be grouped as 'seasonal' breeders or 'climate' responsive breeders. Species of oribatids that have a restricted distribution like *Passalozetes neomexicanus* and *Jornadia larreae* are at the *k* end of the *r-k* continuum. They have evolved reproductive periodicity linked to the 'predictable' season of rainfall and do not respond reproductively to favourable moisture outside that season. *Joshuella striata*, a widely distributed North American desert species (Wallwork, 1982), exhibited both summer and winter egg production in response to supplemental rainfall. This species, therefore, more closely fits the trigger-pulse-reserve paradigm for desert organisms described by Noy Meir (1973) and is closer to the *r* end of the *r-k* continuum.

The advantages of evolving a seasonal breeding pattern in a seasonal desert are obvious.

Rainfall in deserts is generally considered to be unpredictable, but lack of predictability refers to quantities of rainfall, not to season. As shown earlier in this paper, there is a high probability of significant rainfall in the northern Chihuahuan Desert in late summer, July to September. If mites were to lay eggs in response to a large rain event in April or May, the probability that the soil would continue to be wet by rainfalls would be extremely low and survival of developing eggs and nymphs improbable. In addition, quantity and quality of food and moderate microclimate in surface leaf litter is a function of repetitive rainfall events, hence seasonal. These factors undoubtedly exerted strong selective pressure for 'seasonal' breeding in these oribatids.

The most important effect of rainfall supplementation for the seasonal breeders was to modify the leaf litter microclimate and extend the period of egg production. In species like *Jornadia larreae*, however, the supplemental water allowed egg production during one year when none was measured in unwatered plots, and in a subsequent year, resulted in considerably higher egg production. Thus, the effects of rainfall quantity and/or timing cannot be generalized to all species of oribatids included in this study.

Joshuella striata populations vary considerably through time, depending upon the rainfall. The absence of egg production and low populations of *J. striata* in unwatered plots in 1984 suggest that this species may fail to breed in some years. However, if summer moisture is adequate, there may be sufficient winter moisture in approximately one in five years for successful winter breeding in *J. striata*.

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