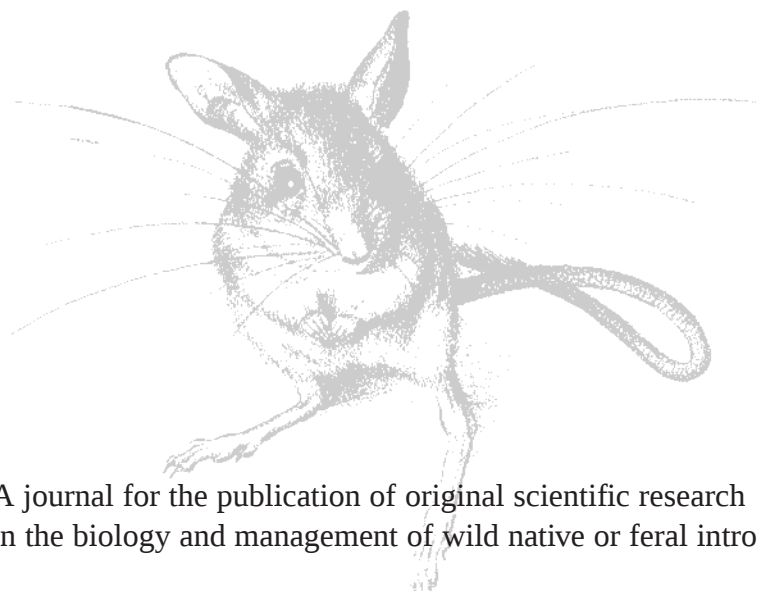

CSIRO PUBLISHING

Wildlife Research

Volume 26, 1999
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Long-term dynamics of rodent populations in arid Australia: the influence of rainfall

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Abstract

Populations of rodents were studied for periods of 7–9 years at each of three sites in arid Australia. All species fluctuated dramatically in abundance, being absent or in low numbers during droughts but erupting after significant rainfall. Strong correlations were obtained between capture rates and cumulative monthly rainfall residuals, with time lags, that had been modified by an exponential decay function to model the post-rain depletion of resources. The introduced *Mus domesticus* erupted within only two months of exceptional rainfall at one site, whereas the native rodents *Notomys alexis*, *Pseudomys hermannsburgensis* and *P. desertor* generally responded 3–10 months after rain. The faster response of *M. domesticus* reflects its high reproductive potential compared with the native rodents, and perhaps greater immigration. Differences in magnitudes and delays in response to rainfall among the native species were due probably to differences in initial population sizes and times available for response and, for *P. desertor*, to between-site differences in the quality or quantity of food resources. Population declines in all species during dry periods probably followed resource shortages.

Despite the usually strong linkage between rainfall and population dynamics, rain failed to trigger population responses in rodents for prolonged periods at two of the sites, and was not clearly associated with an eruption of *P. hermannsburgensis* at the third. The lack of a population response at one site was attributed to predation, but events at the other two remain unexplained. We conclude that long-term studies should play an important role in describing temporal changes in rodent populations in arid Australia and, with field experiments, in evaluating how rainfall and other factors combine to effect the changes.

Introduction

Populations of rodents in arid environments often show great variation in size and composition over short periods of time. Increases in abundance usually follow rainfall, and probably reflect responses to rain-induced increases in the availability of food (Chew and Butterworth 1964; Brown and Heske 1990; Brown and Harney 1993). Increases can occur within just a month of rainfall (Boonstra and Redhead 1994), but are more common within several months to a year (Whitford 1976). In hyper-arid regions population increases can also be triggered by the flow of ephemeral creeks or even the appearance of advective fog (Withers 1983; Griffin 1990). With the subsequent onset of drought, populations can crash precipitously (Plomley 1972).

Biotic factors may also influence the population dynamics of desert rodents. In North America, for example, the numbers of several species of small granivorous rodents are often depressed by the presence of larger and competitively superior rodents (Brown *et al.* 1986; Heske *et al.* 1994) or by granivorous ants (Brown and Davidson 1977). In semi-arid Chile, predation has been demonstrated to depress rodent numbers, especially species with predictable population cycles (Meserve *et al.* 1993, 1996). Indirect and facilitatory interactions may also occur among rodents and other granivores (Thompson *et al.* 1991), but population-level effects have been little studied.

In arid Australia, rainfall is usually considered to be the major influence on populations of rodents (Finlayson 1939; Newsome and Corbett 1975; Dickman 1993; Predavec and Dickman

1994). There is, however, debate about the timing and amount of rain needed to trigger population increases, and the lag period before increases occur (Predavec 1994a; Southgate and Masters 1996). This perhaps reflects the short duration (<3 years) of most studies and the low probability that they will span extreme climatic conditions. Fire may also affect rodent populations in arid Australia by altering the structure of vegetation (Masters 1993), while observations by Newsome and Corbett (1975) and Corbett and Newsome (1987) suggest that predators speed population declines following eruptions.

In the present paper, we evaluate the population dynamics of four species of rodents in relation to rainfall at three sites in arid Australia. Field work was carried out for 7–9 years at each site, and covered periods of drought and exceptional rainfall.

Methods

Study sites

The first site, at Ethabuka station in the north-eastern Simpson Desert, Queensland (23°46'S, 138°28'E), is characterised by long parallel sand dunes up to 8 m high and 1 km apart. The dominant vegetation is spinifex, *Triodia basedowii*, which occurs from the dune valleys to just below the dune crests. Gidgee, *Acacia cambagei*, occurs on heavier clay soils in the swales, while smaller perennials such as *Eremophila* spp., *Grevillea stenobotrya*, *Crotalaria* spp., *Sida* spp. and other species of *Acacia* occur on the dune sides and crests (Dickman *et al.* 1993). Rainfall averages 196 mm per year (recorded at the nearest long-term weather station at Marion Downs, 120 km away), with more than 74% occurring between October and March. Maximum daily temperatures average 38°C in December and January, while minimum temperatures of 7°C or less occur in July (Bureau of Meteorology 1988).

The second site, 15 km west of Yulara, near Uluru National Park, Northern Territory (25°17'S, 130°55'E), is on a transitional sandplain of red clayey sand (Allan 1984). *Triodia basedowii* is again the dominant groundcover species, but scattered *Acacia* spp., *Grevillea* spp. and *Allocasuarina decaisneana* are also present (Masters 1993). Rainfall averages 279 mm per year, with 67% occurring between October and March. Average daily temperature maxima of 38°C occur in mid-summer, and minima of 3°C occur in July (Bureau of Meteorology 1988).

The third site is at Salt Beef Lake (20°50'S, 130°20'E), 40 km south of The Granites goldfields in the Tanami Desert, Northern Territory. The site is characterised by an area of wide, shallow drainage lines dominated by spinifex, *T. pungens*, and scattered ti-tree, *Melaleuca glomerata*. The adjacent sandplain is principally a hummock grassland of *Plectrachne schinzii* with shrubs such as *Acacia* spp. and *Eucalyptus* spp. (Gibson and Cole 1992). Rainfall averages 464 mm per year (recorded at the nearest long-term weather station at Rabbit Flat, 90 km away). As with the other sites, rain falls principally in the summer months, with 83% occurring between October and March. Average daily temperature maxima of 39°C occur in mid-summer, and minima of 6°C in July (Bureau of Meteorology 1988). Median monthly rainfall totals are well below average monthly totals at all sites, reflecting a skewed distribution of rainfall caused by infrequent periods of very high rainfall, particularly for the Simpson Desert and Uluru sites (cf. Morton 1982).

Study species

The spinifex hopping-mouse, *Notomys alexis* (30 g), occurred abundantly for part of the time at all study sites. This species is omnivorous, taking seeds, green plant material, invertebrates and some fungi (Murray and Dickman 1994a, 1994b). It is quadrupedal at low speeds but bipedal when moving fast. The sandy inland mouse, *Pseudomys hermannsburgensis* (12 g), also occurred abundantly at times at each study site. It takes a similar range of foods to *N. alexis* (Murray and Dickman 1994a, 1994b), but is entirely quadrupedal and able to climb to about 0.5 m in shrubs to obtain food. The desert mouse, *P. desertor* (25 g), occurred at all sites, but was not abundant enough at the Simpson Desert site to warrant detailed population analysis. It appears to be omnivorous at the latter site, but herbivorous in the Tanami and elsewhere in its range (Murray *et al.* 1999). The house mouse, *Mus domesticus* (12 g), occurred also at all sites, but was abundant, temporarily, only at Uluru; data from the other study sites are not presented. It is probably granivorous in the arid zone, but may be primarily insectivorous elsewhere (Watts and Morton 1983). Like the three species of native rodents, the introduced *M. domesticus* is nocturnal and shelters in burrows by day. Forrest's mouse, *Leggadina forresti*, was also captured at each site, but numbers were insufficient for analysis. A final species, the long-haired rat, *Rattus villosissimus*, was captured in the Simpson Desert only; its population dynamics have been described elsewhere (Predavec and Dickman 1994).

Census methods

In the Simpson Desert, rodents were live-trapped in pitfall traps (16 cm in diameter, 60 cm deep) each equipped with a 5-m drift fence of aluminium flywire to increase trap efficiency (Friend *et al.* 1989). Six grids of 36 traps each were established in March 1990, and opened 3–6 times a year from August 1990 until September 1997. Each grid covered 1.0 ha, with 20 m between traps in a 6 × 6 configuration. Grids were 0.5–2.0 km apart. At Uluru, animals were live-trapped in Elliott traps baited with a mixture of peanut butter and rolled oats. Six grids of 100 traps were established 400–1100 m apart, and opened 1–5 times a year from September 1987 to May 1992. Traps were placed in a 25 × 4 configuration, with 10 m between traps in a trapline and 40 m between traplines, each grid covering an area of 2.88 ha. From September 1992 to March 1995 trapping took place on two larger grids of 200 traps, which were opened 3–4 times a year. Traps were placed in a 25 × 8 configuration with 20 m between traps in a trapline and 60 m between traplines, each grid covering 5.04 ha. Finally, in the Tanami, animals were live-trapped in Elliott traps baited as above. Three lines of 25 traps were established in June 1981 in *Triodia* habitat, with an additional three lines being established in *Plectrachne* habitat in January 1982. Traps were spaced 20 m apart within a trapline, with traplines separated by a minimum of 500 m. Traps were opened once or twice a year until February 1989.

In each study site traps were opened for 3–4 consecutive nights per trip and checked once or twice a day. Captured animals were weighed, checked for sex and reproductive condition, given a unique mark by toe- or ear-clipping, and then released at the point of capture. Recapture rates were low, especially in the Simpson Desert (<10% for *N. alexis* and *P. hermannsburgensis*), and hence precluded the use of population estimators. Because of this, and because of the different methods and intensity of sampling at each study site, we have presented data on population fluctuations in standardised form as captures per 100 trap-nights (one trap-night = one trap open for one night). Mean capture rates are presented per site, ± s.e., using grids as replicates (traplines for the Tanami site). Detailed analyses of population composition or reproduction are not presented here, but are referred to in Masters (1993, 1997), Predavec (1994a, 1994b) and Dickman *et al.* (1995).

Rainfall

Records of monthly rainfall during the study periods were obtained from rain gauges at or near the Uluru and Tanami sites, and from the weather station on Marion Downs 120 km east of the Simpson Desert site. Comparison of Marion Downs rainfall with unofficial rainfall records from Ethabuka homestead, 15 km south of the site, shows good agreement between the two, particularly with regard to major rainfall events. Marion Downs rainfall records are used here, however, because they are more complete. Long-term means were derived from monthly rainfall records from 1913 to 1995 for Marion Downs, 1964 to 1983 for Uluru, and 1969 to 1995 for the Tanami.

Analysis and statistical evaluation

Given the likely complex and little-understood relationship between rainfall and small mammal abundance in arid environments, no *a priori* model exists to support a particular comparison of these two variables. Previous workers (Masters 1993; Predavec 1994a; Southgate and Masters 1996) have correlated capture rates of rodents with cumulative monthly rainfall residuals (CMRR). The CMRR (Sutherland *et al.* 1991) is the cumulative difference between the actual and long-term mean monthly rainfall for a site, and is especially effective in identifying droughts. In preliminary analyses, we calculated Pearson's product-moment correlation coefficients for comparisons of capture rates of rodents with CMRR for the same months, and with the CMRR for each of the previous 12 months, to detect any delays in population responses to rain. Probability values for these multiple comparisons were modified using the Dunn-Sidak correction (Sokal and Rohlf 1995).

Use of the CMRR is strictly appropriate, however, only when data are distributed normally (Sutherland *et al.* 1991; see also Srikanthan and Stewart 1991). The measure is thus biased by exceptional rainfall events, which are relatively common in arid Australia (Morton 1982), the measure being then insensitive to subsequent periods of drought. To address this, we fitted an exponential decay function to CMRR values (CMRR(exp)), to model the probable decline of the effects of heavy rain with time from the event. We used data on the rate of decline of seed biomass in sand at Ethabuka following heavy rain in early 1992 (Predavec 1994b) to estimate a rate of decline for rain-induced resources over subsequent months of low rain. This calculation yielded a decay rate of approximately 20% per month (i.e. seed density dropped by 20% per month), which was used to modify the CMRR function. Specifically, residual values were multiplied by 0.8 before being carried over to the next month, so that the effects of heavy rainfall decayed exponentially with time. Given that the modified values

declined after rainfall in the same way as a major food resource of the study species, they were expected to better reflect the biological effects of rain than CMRR alone. Capture rates of rodents were correlated with CMRR(exp) values for the same months and, as before, with values lagged from 1 to 12 months. Probability values for multiple comparisons were again modified using the Dunn–Sidak correction (Sokal and Rohlf 1995).

As an alternative approach to removing seasonal effects, the average capture rates for each species over the entire year March to February were correlated with the preceding summer's rainfall (October to March). Summer rains dominate in northern arid regions of Australia (Williams and Calaby 1985) and often initiate widespread seeding of desert plants (Jacobs 1982; Westoby *et al.* 1988).

We note that in using parametric correlation analysis to describe associations between rodents and rainfall, consecutive sample points suffer from lack of temporal independence. In the present study, we use correlation analyses primarily as descriptive tools and not as tests of hypotheses, so that dependency is not as critical. This approach follows that of other workers (as above; see also Holbrook *et al.* 1997). Alternative methods of time-series analysis such as autoregressive modelling commonly use one data point per year and require long periods (>>10 years) for reliable interpretation (e.g. Bjornstad *et al.* 1995; Krebs 1997). Our data were insufficient for analysis by such methods.

Results

Simpson Desert site

Over the seven years of the study, heavy summer rainfall was recorded at the beginning of each of the years 1991, 1992, 1995 and 1997, with smaller winter rains in 1990 and 1996, resulting in large fluctuations in CMRR(exp) (Fig. 1). Capture rates of *P. hermannsburgensis* and *N. alexis* fluctuated dramatically over this period (Fig. 1). Both species peaked in August 1991, six months after CMRR(exp) had peaked in February, the wettest month of the entire study (303 mm). Rodent populations declined subsequently in a similar fashion to CMRR(exp). The smaller summer rains of 1991/92 were followed by an equally large peak in *P. hermannsburgensis* populations in August 1992, while *N. alexis* peaked two months earlier at higher densities than it had achieved the previous year. In contrast, heavy rains in early 1995 appeared to have no effect on populations, while rains in early 1997 saw a small increase in *P. hermannsburgensis* but no response from *N. alexis*.

Although CMRR(exp) alone did not explain all the variation in abundance exhibited by the two rodent species, capture rates were correlated highly with CMRR(exp) with a time lag of 6 months ($P < 0.01$) (Fig. 2a). In comparison, unmodified CMRR did not correlate with capture rates for either species for any time lag. Following the February 1991 rain, CMRR increased dramatically and remained high for the rest of the study (Fig. 3). Rodent populations, however, increased sharply to peaks in 1991 and 1992, but then declined dramatically, remaining relatively low for the rest of the study. With low monthly rainfall averages, CMRR did not decline after such a substantial increase, even though little further rain fell for several years.

Correlations of annual capture rates with the preceding summer rainfall were non-significant for both *P. hermannsburgensis* and *N. alexis* (see Table 1). This partly reflects the lack of response of both rodent species to periods of high rainfall in the summer of 1994/95, and to a lesser extent, the summer of 1996/97.

Uluru site

Fig. 4 shows the capture rates for *P. hermannsburgensis*, *N. alexis*, *P. desertor* and *M. domesticus* plotted alongside CMRR(exp) over the course of the study. March 1989 was by far the wettest month of the study, with 419 mm of rain, resulting in a sharp peak in CMRR(exp). All four rodent species showed significant population increases within two months, although, for *P. hermannsburgensis* in particular, populations may have already been rising due to lighter rains the previous year. Populations peaked in all species 2–12 months after the peak in CMRR(exp), and declined subsequently following the decline of CMRR(exp). A further eruption of *P. hermannsburgensis* occurred in the latter half of the study through 1993 and 1994 (Fig. 4a). However, this eruption was not preceded by substantial rainfall.

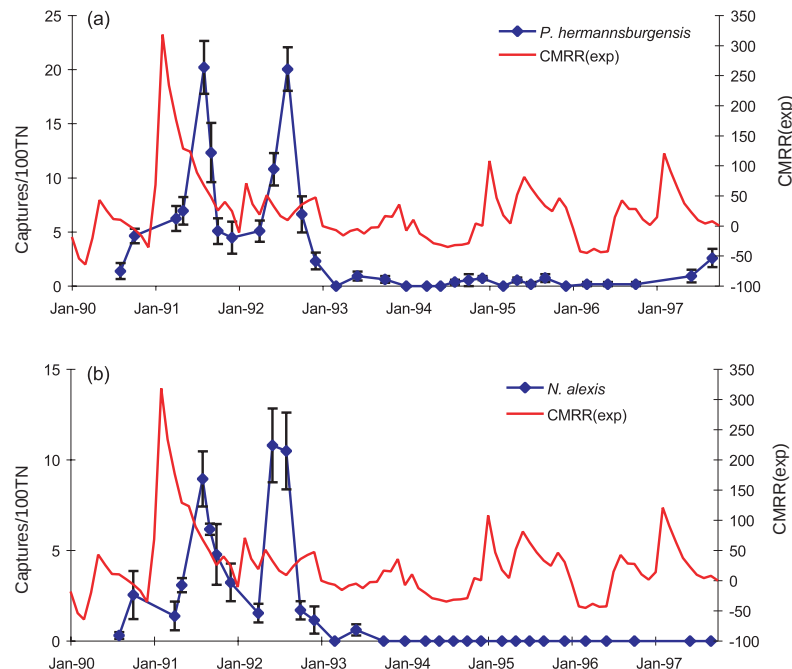


Fig. 1. Captures per 100 trap-nights (TN) for *Pseudomys hermannsburgensis* (a) and *Notomys alexis* (b) from August 1990 to September 1997 at the Simpson Desert site (mean $\pm$ s.e.). Also shown is the cumulative monthly rainfall residual modified by an exponential decay function [CMRR(exp)].

For all species except *P. hermannsburgensis*, capture rates were correlated highly with CMRR(exp) ($P < 0.01$), with time lags of 0–12 months (Fig. 2b). The strongest correlations for native species were lagged at least 3–4 months, whereas for *Mus domesticus*, the strongest correlations were lagged by only 0–2 months. Similarly, capture rates of all species except *P. hermannsburgensis* were also correlated with CMRR ($P < 0.01$), with time lags of 0–10 months, although correlations were generally weaker than for CMRR(exp). Only average annual capture rates for *N. alexis* and *M. domesticus* were correlated with the previous summer's rain ($P < 0.05$ for *N. alexis*, $P < 0.01$ for *M. domesticus*; Table 1).

Tanami Desert site

Fig. 5 shows the capture rates for *P. hermannsburgensis*, *N. alexis* and *P. desertor* plotted alongside CMRR(exp) over the course of the study. February and March 1982 were two of the wettest months of the study, resulting in a peak in CMRR(exp) in March 1982. All three rodent species showed significant increases in populations, climaxing 4–10 months later. As at the other sites, rodent populations declined subsequently, following the decline of CMRR(exp). Smaller peaks in CMRR(exp) occurred later in the study, particularly as a result of rains in 1983, 1984, 1986 and 1987. Small increases in all rodent populations occurred in 1984; however, the later rains appeared to have little effect.

Capture rates were correlated significantly with CMRR(exp) only for *P. desertor*, with a time lag of 3–4 months (Fig. 2c). There were no correlations of CMRR with capture rates of any species for any time lag. For all three species, however, average annual capture rates were correlated with the previous summer's rain ($P < 0.01$ for all species; Table 1).

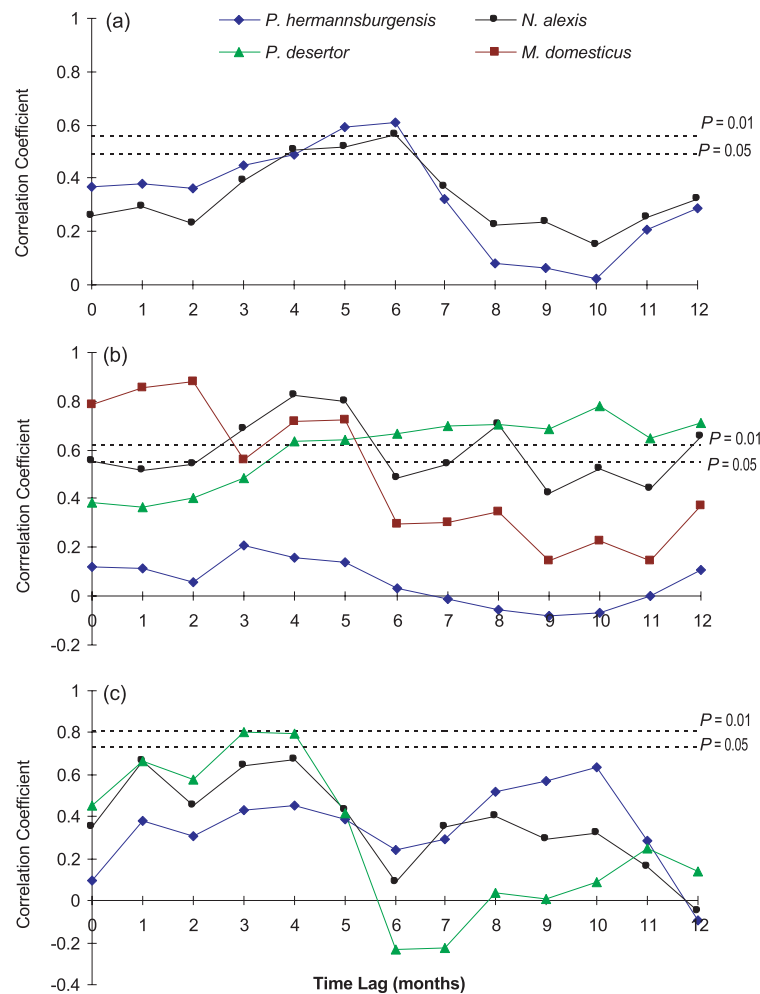


Fig. 2. Correlation coefficients (r) for comparisons of CMRR(exp) with rodent capture rates for the Simpson Desert (a), Uluru (b) and Tanami Desert (c) sites, for time lags of 0–12 months. Critical values for r represent Dunn–Sidak corrected P -values for 13 multiple comparisons (Sokal and Rohlf 1995).

Discussion

Rainfall was clearly a major correlate of rodent numbers in each of the three study sites, although factors other than rainfall were important at certain times. The 3–12-month lags in population maxima following rain for the three species of native rodents were similar to lags documented for these species in previous studies (Newsome and Corbett 1975; Dickman 1993; Predavec 1994a; cf. Southgate and Masters 1996), and generally similar to the population lags of rodents in other arid environments (Beatley 1969; Whitford 1976). With the exception of *P. hermannsburgensis* at Uluru, the rapidity of population increases of *M. domesticus* contrasted with the generally slower responses of the native species, but was similar to that reported for *M. domesticus* elsewhere (Watts and Aslin 1981). At Watarrka National Park, Northern Territory, Southgate and Masters (1996) described population changes of *M. domesticus*, *N. alexis* and *P. hermannsburgensis* that correlated best with CMRR when lagged by 9–15 months. We

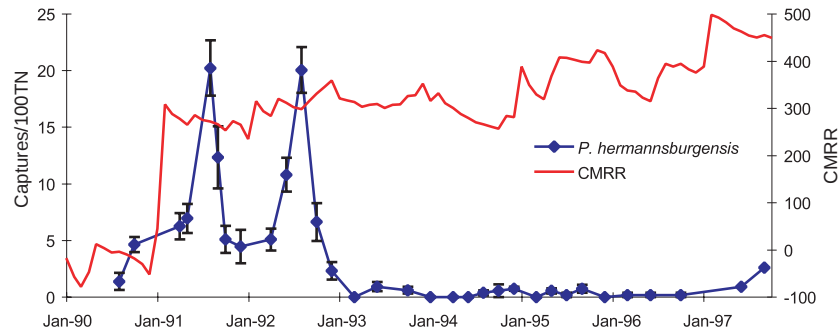


Fig. 3. Captures per 100 trap-nights (TN) for *Pseudomys hermannsburgensis* (mean $\pm$ s.e.) at the Simpson Desert site, as for Fig. 1, compared with the cumulative monthly rainfall residual (CMRR).

Table 1. Correlation coefficients for the average annual capture rates of *Pseudomys hermannsburgensis*, *Notomys alexis*, *P. desertor* and *Mus domesticus* with the previous summer's rainfall for the Simpson Desert, Uluru and Tanami Desert sites

*, $P < 0.05$; **, $P < 0.01$

Species	Simpson Desert d.f. = 6	Uluru d.f. = 6	Tanami Desert d.f. = 6
<i>P. hermannsburgensis</i>	0.593	0.128	0.907**
<i>N. alexis</i>	0.537	0.760*	0.854**
<i>P. desertor</i>		0.630	0.855**
<i>M. domesticus</i>		0.943**	

also found generally high correlations of capture rates of rodents for the 12 months following previous summer rainfall, especially for the Tanami Desert site where sampling had been carried out longest.

Despite some concordance between our results and those of other workers, rainfall appeared to have variable effects between sites, species, and times. Between-site variation was manifested by differences in the time each species took to reach peak densities following rain, and in differences in amplitudes of population fluctuations. Variation in response time was greatest for *P. hermannsburgensis*, which showed lags of 10 months at the Tanami site, 6 months in the Simpson Desert and only 2 months for the initial eruption at Uluru. It was least (4–6 months) for *N. alexis*. To some extent, variation in response time could be expected because the frequency of trapping differed between the three sites; actual trough and peak populations could have been missed, especially at the Tanami site where sampling was least intense. In addition, correlation coefficients often differed only slightly between adjacent lag periods (see Fig. 2), so that differences in lag periods of 1–2 months may be more apparent than real. However, the 8-month discrepancy between sites for *P. hermannsburgensis* is striking. The slower response for this species in the Tanami could have been due to the generally low population size at this site (capture rate $< 1/100$ trap-nights prior to increases; Fig. 5a). By contrast, above-average winter rains falling prior to eruptions at the other sites meant that populations of this rodent were already increasing, well before the major summer rains occurred (Figs 1a, 4a). Furthermore, the Tanami site also received above-average rainfall for most summers during the study period (Fig. 5). Although *P. hermannsburgensis* is omnivorous (Murray and Dickman 1994a), it is possible

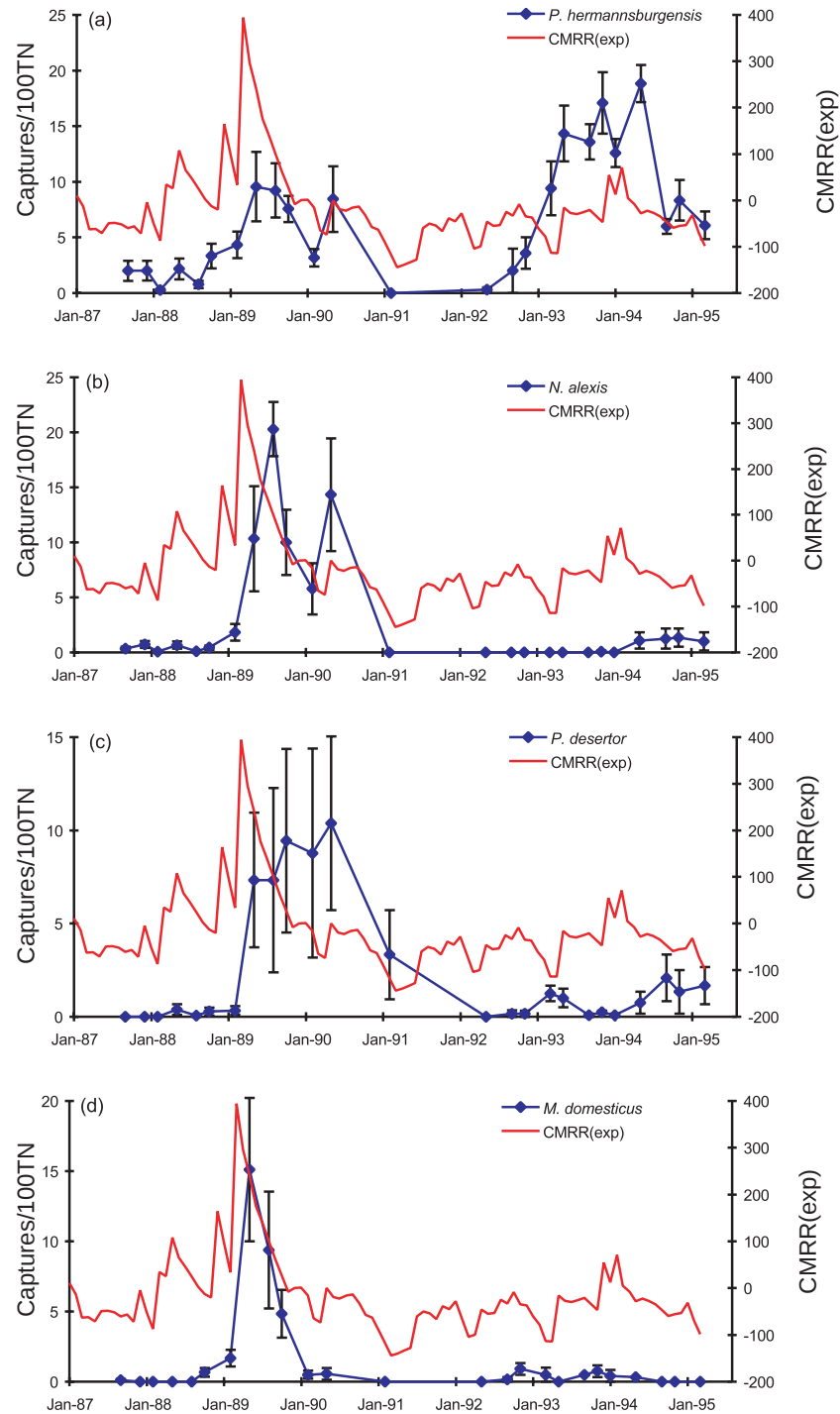


Fig. 4. Captures per 100 trap-nights (TN) for *Pseudomys hermannsburgensis* (a), *Notomys alexis* (b), *P. desertor* (c) and *Mus domesticus* (d) from September 1987 to March 1995 at the Uluru site (mean $\pm$ s.e.). Shown also is the cumulative monthly rainfall residual modified by an exponential decay function [CMRR (exp)].

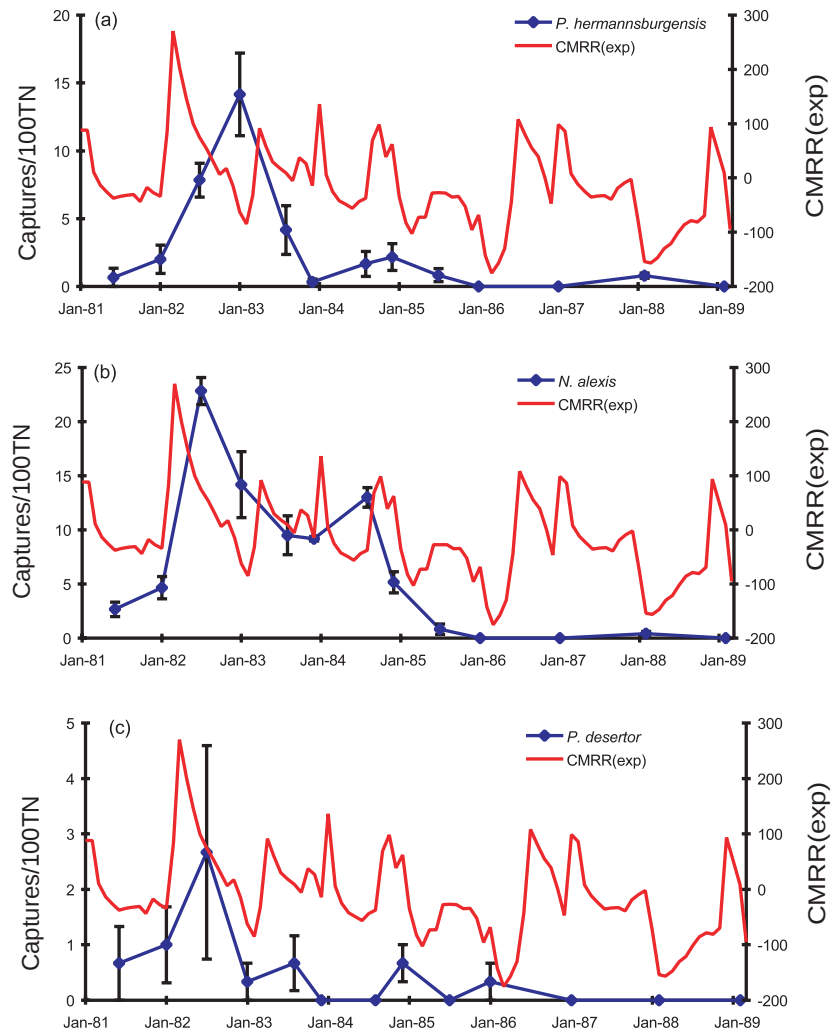


Fig. 5. Captures per 100 trap-nights (TN) for *Pseudomys hermannsburgensis* (a), *Notomys alexis* (b) and *P. desertor* (c) from June 1981 to February 1989 at the Tanami Desert site (mean $\pm$ s.e.). Shown also is the cumulative monthly rainfall residual modified by an exponential decay function [CMRR (exp)].

that the annual heavy rains resulted in long-term depletion of seed banks or other resources so that populations were progressively dampened and recoveries prolonged.

Differences in capture rates between trough and peak populations of each species also varied between sites. While all species disappeared from trap records on some occasions, *M. domesticus* achieved high numbers only at Uluru, while *P. desertor* achieved high numbers only at the Uluru and Tanami sites. Maximum capture rates of *N. alexis* were 11–23 captures per 100 trap-nights between sites; only those for *P. hermannsburgensis* (14–20 captures per 100 trap-nights) were relatively constant. Because different trapping methods were used at the different study sites, some variation in capture rates may have been due to different trap-efficiencies. For example, failure to record increased numbers of *M. domesticus* and *P. desertor* after rainfall at Ethabuka could have arisen if these species avoid pitfall traps or seldom enter the more open

microhabitats where pits are often located (Dickman 1992; Read 1992). However, comparisons of pitfall and Elliott traps at Ethabuka have shown that pitfalls efficiently capture all the study species, especially when equipped with drift fences (CRD, personal observations). Since *M. domesticus* and *P. desertor* also use similar microhabitats to those favoured by *P. hermannsburgensis* (McNaught 1994; Murray and Dickman 1994a), which had its highest capture rates at Ethabuka, the different trapping methodologies used between sites probably did not bias capture rates unduly. Given the very low densities of *M. domesticus* at the Ethabuka and Tanami sites, and of *P. desertor* at Ethabuka, there may have been insufficient time for populations to respond to the temporary improvements in conditions brought about by rain (Andrewartha and Birch 1954). Alternatively, the quality of resources may vary between sites, especially in relation to rain. *P. desertor* appears to be generally herbivorous in most parts of arid Australia (Watts 1972; Happold 1983; Murray *et al.* 1999), and is presumably able to increase rapidly in numbers if rainfall stimulates growth of its food plants (Newsome and Corbett 1975). At Ethabuka *P. desertor* may be generally limited in abundance by a paucity of its favoured food plants, and appears to be omnivorous (Murray *et al.* 1999). In such marginal sites, rainfall may do little to promote population growth.

Interspecific differences in population growth after rainfall presumably reflect differences in reproductive potential or immigration. The rapid response of *M. domesticus* following exceptional rainfall at Uluru (Fig. 4d) was apparently due primarily to increased reproduction (Masters 1993), although increases elsewhere have been attributed largely to immigration or to both processes together (Newsome 1969a, 1969b; Newsome and Corbett 1975; Southgate and Masters 1996). In south-eastern Australia, Saunders and Giles (1977) proposed that eruptions of *M. domesticus* required dry periods prior to rain to diminish predators, parasites and pathogens of the rodents. However, the two years prior to the eruption of *M. domesticus* in May 1989 were unusually wet (Masters 1993), providing more support for the notion that increases in numbers of rodents generally follow prolonged wet periods after a long dry (Southgate and Masters 1996). The general scarcity of *M. domesticus* accords with the conclusions of Read (1992) and Masters (1993) that it is a poor coloniser of spinifex grasslands and does not persist during dry periods.

The delayed population increases of the native rodents following rainfall probably reflect their reduced reproductive potential compared with *M. domesticus*, and possibly also more limited immigration. Species of *Notomys* and *Pseudomys* are characterised, with other 'old endemic' rodents, by smaller litter sizes, longer gestations and longer time to sexual maturity than more-recently-arrived species of rodents (Watts and Aslin 1981; Yom-Tov 1985). Analysis of the eruptions of *N. alexis* and *P. hermannsburgensis* at Ethabuka indicates that local population increases were due primarily to reproduction, with immigration from the regional pool playing a secondary role (Predavec 1994a, 1994b; Dickman *et al.* 1995). Limited evidence suggests that reproduction also played a major role in producing eruptions of *N. alexis*, *P. hermannsburgensis* and *P. desertor* at Uluru (Masters 1993); this accords with studies of these species in other parts of arid Australia (Newsome and Corbett 1975; Reid *et al.* 1993; Southgate and Masters 1996).

Despite the apparent importance of reproduction in stimulating population increases, and similarities in the reproductive potential of the three species of native rodents (Watts 1979, 1982; Watts and Aslin 1981; Breed 1990), interspecific differences in the speed of response to rainfall remained. At Uluru *P. desertor* took longer to reach peak densities than either of the other native species, while at the Tanami site *P. hermannsburgensis* showed the slowest response (Figs 4c, 5a). Fig. 4c suggests that *P. desertor* did respond relatively quickly following rain, and that the lag time of 10 months was only a marginally better fit than lags of 3–4 months. In view of the large standard errors associated with the capture rates of *P. desertor* on the Uluru grids, no real difference in lag times between species may therefore be indicated. In the Tanami, however, the relatively delayed response of *P. hermannsburgensis* to rainfall is difficult to interpret. Again, more frequent sampling of populations at this site might have revealed this delayed response to be more apparent than real.

Following previous studies, we assume that rainfall provided free water and enhanced plant growth, hence fuelling reproduction and perhaps also immigration (Newsome and Corbett 1975; Stafford Smith and Morton 1990; Predavec 1994a). Rain may also enhance the accessibility of buried seeds (Johnson and Jorgensen 1981), perhaps by increasing their smell; hydrated seeds also are more vulnerable to foragers than dry seeds when buried in dry sand (Vander Wall 1993). There is some evidence that invertebrate biomass also increases after rain, perhaps as a secondary response to the flush of vegetative growth (Fisher and Dickman 1993). Since invertebrates are favoured by *N. alexis* and *P. hermannsburgensis* (Murray and Dickman 1994b) and taken by many other species of desert rodents (Murray *et al.* 1999), rainfall appears to increase the abundance and availability of all important food groups.

Declines of rodent populations during drier periods may be dictated by shrinking food resources, especially seeds (Predavec 1994a). This notion is supported by the generally high correlations that we found between lagged capture rates and our CMRR statistic, which was modified by an exponential function derived from actual rates of seed decay (Predavec 1994b). However, other factors may also influence declines. Newsome and Corbett (1975) argued that predation is an intense modifier of population dynamics for both *M. domesticus* and native species of rodents in arid Australia, and suggested that predation could both speed rates of decline and prolong population troughs. We have no data on predator abundance at the Tanami or Uluru sites, but return to predation at Ethabuka below. Further hypotheses explaining declines of desert rodents have been proposed, including nutrient limitation (Morton and Baynes 1985), social suppression of reproductive activity at high population density (Breed 1979), disease (Carstairs 1974; Munger *et al.* 1983), and damage to food stores by too-frequent heavy rain or contamination by mycotoxins (Valone *et al.* 1995). We have no data to test the first two hypotheses. However, we saw no evidence of disease during declines of any of the present study species, and can reject the food-store hypothesis on the grounds that no Australian desert rodents appear to cache food (Watts and Aslin 1981; but cf. Baker *et al.* 1993).

Although capture rates usually increased after good rainfall and decreased during drought, this was not always the case. *P. hermannsburgensis* erupted at Uluru in 1993 and 1994 in the absence of significant rainfall (Fig. 4a). In contrast, populations of all species failed to respond to heavy rainfall in 1986 and 1987 in the Tanami (Fig. 5), and neither *N. alexis* nor *P. hermannsburgensis* showed marked increases after rain in the summers of 1994/95 and 1996/97 at Ethabuka (Fig. 1). Over the longer periods studied here, rodents could have been affected by successional changes in the structure of vegetation, or by sporadic events such as fire (Fox 1982; Masters 1993). At Ethabuka the mean cover of spinifex did increase from 6% to 25% over the course of the study, but the major surge in late 1991 (Haynes 1996) did not coincide with either the initial increases in rodent populations or with their long-term declines. Fire did occur on some of the Tanami trapping sites during the study, and on some of the Uluru sites in 1986 just prior to the study. However, this could not account for the unanticipated eruption of *P. hermannsburgensis* at Uluru in 1993/94, or the lack of response of all species across all trapping sites regardless of fire to the 1986 and 1987 rains in the Tanami.

A further possibility is that the intensity of predation differed over the course of sampling at each site (cf. Newsome and Corbett 1975). Following exceptional rainfall at Ethabuka in early 1991, feral cats (*Felis catus*) increased in abundance and red foxes (*Vulpes vulpes*) arrived at the site for the first time (Dickman 1996a). From mid-1991 until late 1992 a major component of the diet of these predators was long-haired rat (*Rattus villosissimus*), which reached peak population numbers over this period (Predavec and Dickman 1994; Dickman 1996b). With the decline of all rodents in late 1992 and the virtual disappearance of *R. villosissimus*, the diets of both predators switched to include *N. alexis* and *P. hermannsburgensis* as a higher proportion of the diet (Dickman 1996b; PSM, unpublished). Despite declines in the abundance of foxes and cats since 1993, it is likely that predation pressure has continued to suppress recoveries of the very low density populations of *N. alexis* and *P. hermannsburgensis* even with significant rainfall in the summers of 1994/95 and 1996/97. Field experimental studies will be essential to test the predation hypothesis, and are now being undertaken (PSM, unpublished). It is possible

that increased predation also suppressed rodent populations in the Tanami from 1986, but no data are available to evaluate this.

The eruption of *P. hermannsburgensis* at Uluru in 1993–94 is more difficult to interpret. Although on-site rainfall was below average prior to the eruption (Fig. 4a), rain did fall in the surrounding region in mid–late 1992. This may have triggered population increases if the study area experienced a flush of new resources due to moisture run-on (Stafford Smith and Morton 1990). Light rains on-site in mid-1993 and the summer of 1993/94 (Fig. 4a) may have added further resources. It is unclear, however, why this species should respond but *N. alexis*, *P. desertor* and *M. domesticus* should not. Winter rains at the site in 1988 saw *P. hermannsburgensis* populations increasing, while other populations showed little response until much heavier rains fell during the following summer. Perhaps this species is able to respond to small increases in resources and, without sufficient follow-up rain, other, potentially competing, rodent species are not. Perhaps also, eruptions of *P. hermannsburgensis* may be amplified in periods of reduced competition. There are, however, few data available to test these possibilities.

In summary, our findings provide strong general support for the notion that rainfall drives the dynamics of rodent populations in arid Australia. However, factors other than rainfall can have over-riding effects at certain times, and these are likely to be discovered only via long-term studies that cover periods of extended rainfall and drought, and by studies that manipulate target factors experimentally. In future studies, we suggest specifically that direct measurements be made of the resources available to, and used by, rodents during periods of stasis and change, and that study sites be large enough to distinguish the contributions of reproduction, mortality and dispersal to population change. Hypotheses that predict the effects of food, water, predation and competition on population size should also be tested experimentally by manipulating levels of each factor and comparing the responses of treatment populations with those of replicated controls. Such studies have been pursued successfully on rodents of the Americas (e.g. Brown *et al.* 1986; Meserve *et al.* 1996), and will be essential to produce a more mechanistic understanding of rodent population dynamics in arid Australia.

Acknowledgments

We thank the innumerable coworkers and volunteers who have assisted with fieldwork over many years at our study sites, especially P. Banks, H. Braak, H. Brunner, J. Cole, F. Downey, A. Glen, P. Higgs, G. McNaught and B. Tamayo. We are also indebted to David and Paula Smith and family for their continuing support and interest in our work on Ethabuka station, and to the Anangu and Warlpiri peoples for access to the Uluru and Tanami study sites, respectively. Funding for work at the Simpson Desert site was provided by the ARC and ANCA. S. Gresser helped to prepare the manuscript, and critical comments were provided by L. Sutherland, E. Tasker and L. Twigg.

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Manuscript received 1 April 1997; accepted 9 June 1998