Aust. Wildl. Res., 1988, **15**, 435–50

Fox Control and Rock-Wallaby Population Dynamics

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Abstract

The population dynamics of five remnant rock-wallaby populations (*Petrogale lateralis*) persisting on granite outcrops in the central wheatbelt region of Western Australia were monitored over a six year period. From 1979 to 1982 all populations remained relatively static or declined for unknown reasons, but circumstantial evidence implicated fox predation. A fox control program was implemented in 1982 on two outcrops and was maintained for four years with the result that the two resident rock-wallaby populations increased by 138 and 223%. Two rock-wallaby populations occupying sites not subjected to fox control declined by 14 and 85%, and the third population increased by 29%. It was concluded that the fox has probably been a significant factor in the demise and decline of native mammals in the past, and that surviving populations are still at risk. Control of predation pressure on nature reserves was shown to be feasible from a management perspective.

Introduction

The European red fox (*Vulpes vulpes*) was introduced into Victoria in the late 1860s and was first recorded in Western Australia (W.A.) in 1912. During the next 25 years, foxes were recorded in all regions of the state except the North Kimberley region and most islands. The present distribution appears to be relatively stable as it is similar to that in 1934 (King and Smith 1985).

During and following this colonisation phase by the fox, the State's mammalian fauna changed profoundly with a number of small to medium sized species becoming rare or extinct. Considering the above association and the fox's known predatory instincts, it is tempting to incriminate the fox as a major cause of the demise and decline of many native mammals. However, the situation is confounded by the effects and complex interactions of other factors such as habitat destruction and fragmentation, changes in the fire regime, rabbit plagues, disease, and climatic changes.

In 1978 we carried out a survey of rock-wallabies (*Petrogale lateralis*) in the central wheatbelt region of W.A. (Fig. 1). The survey revealed that at one site the population had become extinct, and at two other sites the numbers were judged to be dangerously low. In response to this situation, investigations were commenced in 1979 in an effort to establish the cause(s) for the declines of rock-wallaby populations in the area.

These investigations, conducted over the period 1979–82, revealed that the total number of wallabies for the area was relatively stable (about 75–100 individuals). The reproductive rate was high, there was no evidence of disease, and it was clearly evident from handling trapped animals that individuals were invariably fit and healthy, and did not suffer excessive weight loss during drought. Given the above scenario, i.e. recent population extinctions or declines, ongoing recruitment, but no population growth over three years, it was evident

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that there was a cause of mortality which was unrelated to the known biological and environmental factors.

A compelling body of circumstantial evidence implicated predation by foxes as a primary factor (Kinnear *et al.* 1984). These data, and evidence from Christensen (1980), prompted this investigation which documents the effects of fox control, and the lack of control, on the dynamics of five rock-wallaby populations over a six-year period.

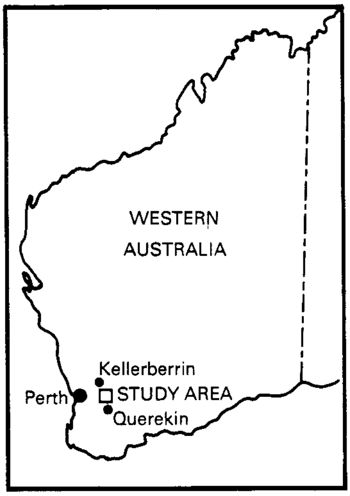

Fig. 1. Location of the principal study area where five remnant populations of rock-wallabies persist in the central wheatbelt region of Western Australia. The Querekin remnant is found approximately 40 km SE. of the study area.

Materials and Methods

The Study Area

The principal study area (Fig. 2) comprises a cluster of granite outcrops located south of Kellerberrin (210 km east of Perth). This area (approx. 150 km^2) now consists of established cereal and sheep farms which surround the outcrops, thus creating a situation comparable to an island system. Four outcrops which carry rock-wallaby populations, Nangeen Hill, Mt Caroline, Mt Stirling and Tutakin, are Nature Reserves, and a fifth population resides on private property (Sales' Rock). Kokerbin Rock carried a population until 1969–70. Outside this study area a sixth population (Querekin Rock) also persists on private property (approx. 40 km south-east, near the town of Shacklelton).

Population Survey Methods

In 1978 all sites were inspected on foot for presence of rock-wallabies. The most reliable evidence or rock-wallaby occupation was the presence of faecal pellets (scats) which are distinctive and readily distinguished from other resident macropods (i.e. the kangaroos, *Macropus robustus* and *M. fuliginosus*). Each site was mapped according to the distribution of scats, and details regarding the topographical features of the site were recorded. The small Tutakin population was not discovered until 1983.

Experimental Design

The purpose of the experiment was to test the following hypothesis: if fox predation was a significant factor affecting the population dynamics of rock-wallabies, relaxation of predation pressure would result in population growth until another factor intervened. The study area was partitioned as follows. On two nature reserves (Mt Caroline and Nangeen Hill) the fox was to be controlled. At Sales' Rock, Tutakin Reserve, Mt Stirling and at Querekin Rock there was to be no fox control. It was assumed that all wallaby populations were closed to immigration and emigration. During the seven years of the study, no evidence came to our notice that suggested otherwise.

Census Methods

A trap was designed and constructed by one of us (R.N.B.) that allowed us to repeatedly catch rock-wallabies without risk and undue trauma to all concerned. This trap is fully described by Kinnear *et al.* (1988).

Traps were set up at appropriate sites on a given outcrop wherever rock-wallaby scats were evident; a free-baiting period preceeded a given trapping session and following this period, the traps were baited and set before dusk, cleared of animals at approximately 2300 hours, rebaited and again cleared at 0600 hours next morning.

Trapped animals were held in hessian bags and processed in a nearby caravan as follows: all animals were weighed to the nearest gram, and small numbered tags were affixed in each ear; details of sex, dentition, reproductive status, pes length and body condition were recorded. Pouched young were examined and data on their sex, pes length, and stage of development were recorded. After processing, all animals were released near the point of capture. Rock-wallabies recaptured during a given trapping session, were released immediately at the trap site.

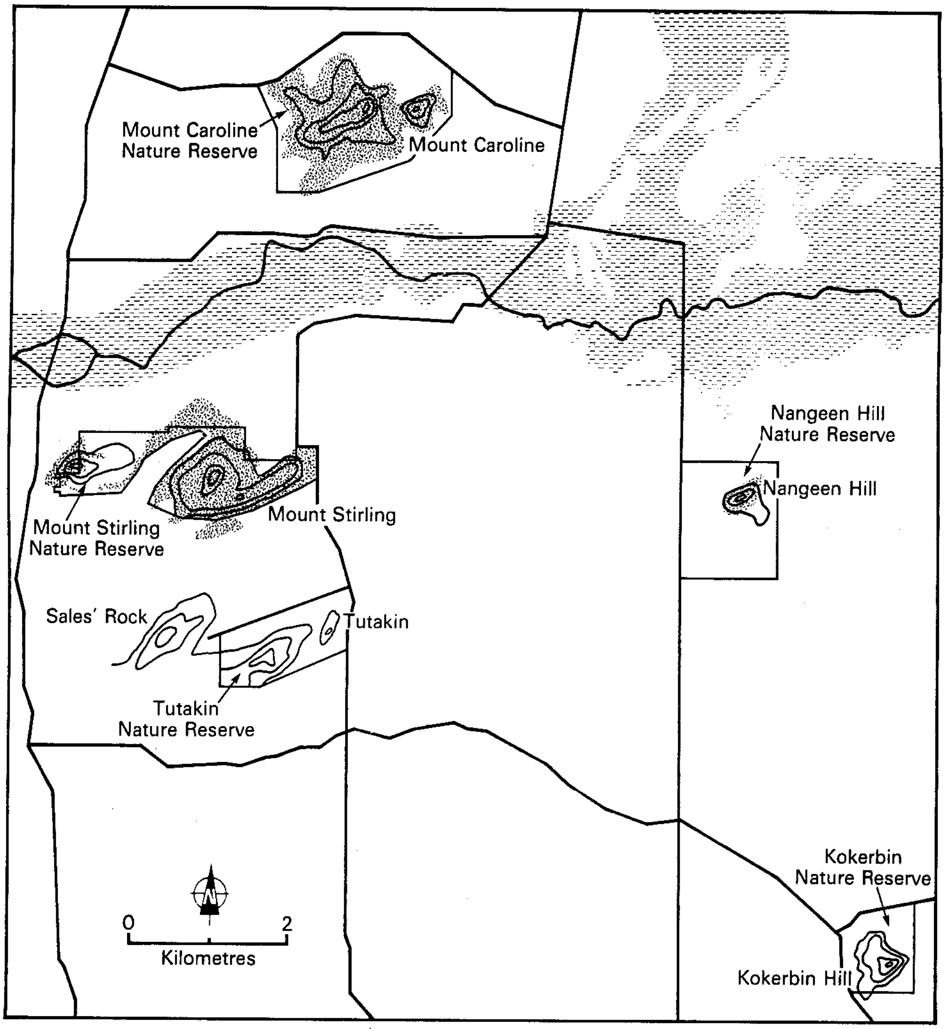

Fig. 2. The principal study area: five sites: Mt Caroline, Nangeen Hill, Mt Stirling, Tutakin, and Sales' Rock, support rock-wallaby populations. Kokerbin Hill carried a population until 1969–70. All sites are completely isolated by farmlands.

Initially (1979–82), a trapping session proceeded until the last three nights yielded only recaptures. This routine was adopted on the assumption that we had caught all of the trappable population. However, as population numbers increased on Nangeen Hill and Mt Caroline, and the use of the available habitat by rock-wallabies expanded, it became necessary to set out more traps over a wider area and to extend the trapping periods.

Population estimates were made prior to the implementation of fox control. The details are as follows: for Nangeen Hill and Sales' Rock, yearly population censuses of the respective rock-wallaby populations were made during the period 1979–82; the other sites were censused less frequently. After the 1982 census, fox control programs commenced on the designated reserves. Censuses were repeated in 1984 and 1986.

Population Analyses

Population estimates were based on frequencies of capture models as described by Caughley (1977). Three zero-truncated frequency distributions—Poisson, negative binomial, and geometric, were fitted to the mark-recapture data by adapting the algorithm listed in Caughley (1977; Appendix Table 3) to microcomputers (Fortran 77, Lahey Computer Systems, Vers. 2.11).

Fox Control

Initially (1979), fox control by shooting was attempted, but it was soon apparent that the method was impracticable. Nontheless, whenever possible, foxes were shot in the control areas particularly in the paddocks bordering Nangeen Hill Reserve. The toxin '1080' (sodium monofluoroacetate) was then selected following the recommendations of King *et al.* (1981), who showed that, while the fox is extremely susceptible to '1080', much of the W.A. fauna is naturally tolerant to it (Aplin *et al.* 1983; McIlroy *et al.* 1985).

Baiting trials were conducted on Nangeen Hill and Mt Caroline during the dry seasons of 1980–83 according to the following procedure: the perimeter firebreaks of Nangeen and Mt Caroline reserves where ploughed and graded by suitable implements, and colour-coded pegs were installed at 50 or 100 m intervals around the perimeter. Baits were laid at dusk near pegs, and next morning all peg sites were inspected for evidence of interest by foxes as indicated by footprints readily visible in the sandy soil.

In addition to the inspections of bait sites, a procedure which involved the recording of tracks made by foxes on the graded firebreaks was implemented. The rationale of the method was based on the expectation that if a baiting procedure was effective, track counts would diminish accordingly. For a given bait trial, the firebreaks were graded before dusk and next morning the number of fox tracks intercepted by an observer travelling along the firebreak were recorded with reference to the nearest colour-coded peg. Generally, a prebaiting sequence of track counts was made and, after baiting, a follow-up post-baiting sequence of track counts was made to assess bait performance. The effectiveness of the baiting regime was also assessed by periodic searches of Nangeen Reserve and the surrounding countryside for fox remains.

Results

Bait Trials

There were two objectives of the bait trials: (i) to determine the types of bait which were most palatable to foxes, and (ii) to determine how frequently the baits should be applied. Meat (40–50 g, 4·5 mg '1080') was the most attractive bait type tested. However, after rain the toxicity of meat baits was always uncertain, and it therefore became important to find a bait that would remain potent under wet conditions. Eventually, we learned that intact raw fowl eggs were readily taken by foxes, and so from June 1983, eggs dosed with 4·5 mg '1080' were used during the wet season.

The second objective, i.e. the determination of the baiting frequency, has not been resolved. Our original intent was to bait at a level which would maintain a reserve free of fox tracks for extended periods, but it was soon realised that this was an unrealistic goal. For example, in order to achieve zero track counts, we found it necessary to lay fresh meat baits for several consecutive days, but such an investment in baiting appeared to be unproductive as the periods of zero or low fox activity were of a surprisingly short duration.

Initially, such findings generated the impression that fox control was not a feasible proposition. However, as time passed, it became evident from the cumulative count of dead foxes that the baiting program was in fact effective. In essence, poisoned foxes were being quickly replaced by immigrant foxes which in turn were meeting the same fate.

This conclusion is evident from the data presented in Fig. 3. This map covers the period from Jan. 1983 to 31 Aug. 1986, during which 226 foxes were knowingly destroyed—43 by shooting, 183 by poison baits. From Nov. 1985 to 31 Aug. 1986, 75 foxes were poisoned on Nangeen Reserve, a rate on average, of almost two foxes per week.

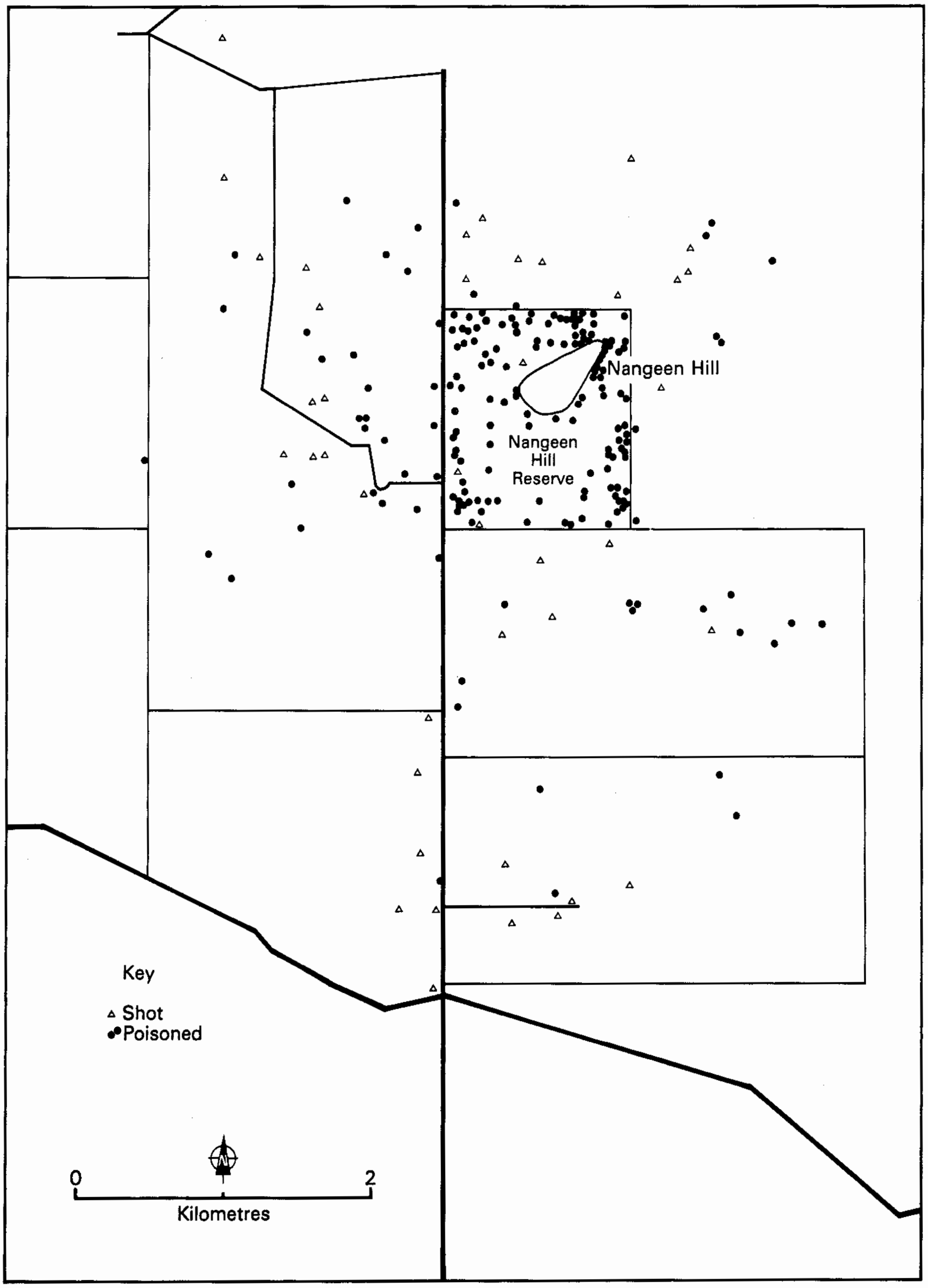

Fig. 3. Nangeen Hill Reserve and the surrounding farmland. The 183 closed circles mark the locations where the remains of poisoned foxes were found. The 43 open triangles represent locations where foxes were shot. Data collected during the period Jan. 1983 to 31 Aug. 1986.

Table 1. Census data and some population attributes for all populations for the period 1979–86

Year	Month	Trap clearances[A]	Total captured including repeats	Total captured excluding repeats	Adjusted census estimates[B]	Sex M	Sex F	Fj[C] (%)	Sex-adjusted M	Sex-adjusted F
				Nangeen						
1979	Mar.	–	19	12	18	6	6	83	7	11
1980	Mar.	–	48	20	21	7	13	31	7	14
1981	Apr.	187	97	20	26	8	12	67	10	16
1982	Mar.	238	75	25	29	9	16	75	11	18
1984	Mar.	350	165	45	51	21	24	54	23	28
1986	Mar.	572	346	69	69	32	37	35	32	37
				Mt Caroline						
1979	Oct.	–	16	9	10	4	5	60	5	5
1982	Apr.[D]	136	3	3	13	2	1	0	8	5
1984	May	225	26	11	22	7	4	50	14	8
1986	Apr.	862	167	42	42	26	16	81	26	16
				Sales' Rock						
1979	July	–	20	18	32	9	9	89	15	17
1980	Mar.	–	63	33	34	15	18	58	15	20
1981	Apr.	187	101	22	22	7	15	53	7	15
1982	Apr.	204	77	22	22	7	15	73	7	15
1984	Mar.	350	133	37	37	14	23	61	14	23
1986	Apr.	572	241	44	44	20	24	79	20	24
				Querekin						
1980	July	–	17	7	7	2	5	40	2	5
1983	July	–	8	5	5	2	3	66	2	3
1986	Sept.	32	1	1	1	0	1	0	0	1
				Tutakin						
1983	Apr.	60	14	6	7	4	2	50	4	3
1986	Apr.	114	15	6	6	2	4	100	2	4

[A] Number of traps × nights × 2.
[B] Includes animals known to be alive (KTBA), but not captured during a given trapping session.
[C] Females with pouched young.
[D] Trapping success rate low because of rain and the abundance of new growth.

When it was realised that the immigration rate of foxes was so high, a decision was made in June 1983 to alter the baiting program as follows: the Nangeen Hill Reserve baiting effort was henceforth maintained at a high level in order to afford as much protection as possible; eggs were used during the wet season, and both eggs and meat baits during the drier months. Baits were laid throughout the reserve, and from January to May, multiple applications per month were routinely made.

Mt Caroline was baited less intensively to test whether it was possible to achieve fox control at a more practicable level, i.e. a level which would not make excessive demands on reserve management resources. Accordingly, from December 1983 to May 1986, a 30-month period, baiting activities simply consisted of laying 140–160 eggs once per month, at 50 m intervals mainly on the firebreak perimeter of the reserve.

Age Estimates

The methods used to estimate the age of rock-wallabies by measuring pes length and dental characters (e.g. number of molars and molar height) were not particularly sensitive, but nonetheless were useful, especially for improving the census estimate (see below). We were able to establish over the six year period of trapping, that a rock-wallaby with three level molars was 2–3+ years old, and an animal with the fourth molar half erupted or more, was 4+ years old. An individual with a 'full mouth', i.e. four level molars, was 6+ years old. On applying these criteria to the 1986 trapping results, some Nangeen rock-wallabies were 12+ years old.

Census Results

A summary of the results obtained by trapping the five populations over the period 1979–86 is presented in Table 1. The total number of rock-wallabies captured for a given trapping period (excluding repeats) has been adjusted where necessary in order to account for animals not trapped, but which, by inference, were known to be alive (KTBA) at the time.

Adjustments to census totals were made for tagged rock-wallabies that had avoided capture for one or more trapping sessions and then were recaptured. Adjustments were also made to previous census totals, when mature untagged wallabies were caught and whose ages were estimable according to the above aging criteria.

Fig. 4 compares the adjusted census results for the five populations—three subjected to no fox control, and two afforded the benefits of control. The differences are pronounced; Nangeen and Mt Caroline populations registered 138 and 223% increases, while Sales increased by only 29%. Tutakin and Querekin declined by 14 and 85% respectively.

Frequency of Capture Analyses

The results obtained from fitting the three frequency distributions to the data from all populations except Querekin are summarised in the Appendix (Tables 1–3).

Data from both Nangeen and Sales' Rock which extend from 1979 to 1986 are included for completeness, but it should be recalled that the trapping procedure was still under development in 1979 and to a lesser extent during 1980.

The estimates for the years 1980–82 for Nangeen Hill fit the Poisson distribution well and generate population estimates which are very similar to the census values. The Negative binominal fits 1984 and 1986. The Geometric distribution produced estimates that were consistently higher than the census estimates.

All distributions generated very high population estimates for Sales' Rock for the years 1979–80. The Poisson fitted the years 1981–82 and 1984, and produced population estimates similar to the census values. The negative binominal fitted 1986 and the population estimate was in good agreement with the trapping census. The geometric distribution fitted poorly and produced high population estimates.

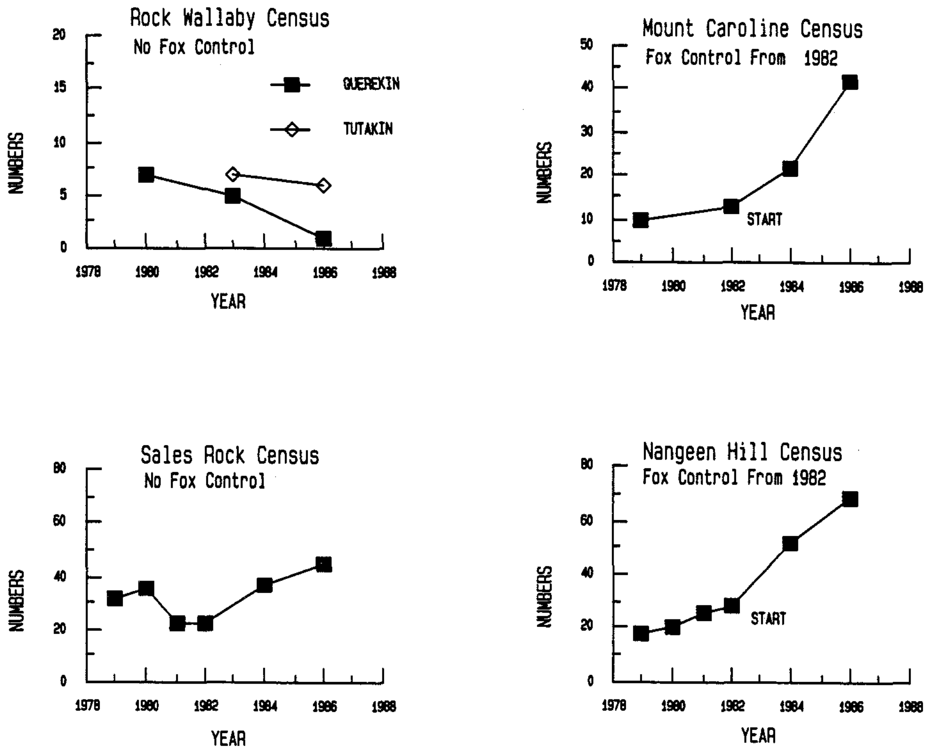

Fig. 4. Adjusted census estimates (see also Table 1) for the two populations where the fox was controlled (Nangeen Hill and Mt Caroline) and the three populations with no fox control (Sales' Rock, Tutakin and Querekin). Full-time systematic fox control began in May 1982. Experimental baiting trials were conducted on Mt Caroline and Nangeen Hill during the dry season periods Nov.–April, 1980–82, which may have afforded some protection from predation.

The negative binominal fitted Mt Caroline data for 1984–86 and the Poisson fitted the Tutakin distribution.

Rock-wallaby Survival

Survival data for Nangeen and Sales' Rock are presented in Fig. 5. The samples were trapped in 1980 and the mortality rate was calculated according to Caughley (1977, p. 151)

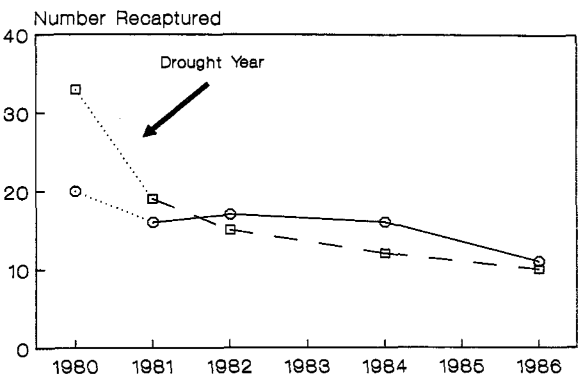

Fig. 5. Plots of rock-wallaby survival for Nangeen Hill (—⊖—) and Sales' Rock (—⊟—). Samples were marked in 1980 (March) which was subsequently declared a drought year (see comments in the Discussion).

over the period 1981–86. The slope of the Sales' sample (−0·123) differs from zero ($0 \cdot 01 < P < 0 \cdot 025$) and the proportion dying per year from 1981 onwards is 0·12.

The effect of drought (1980) is clearly evident particularly in the case of the Sales' population (see Discussion).

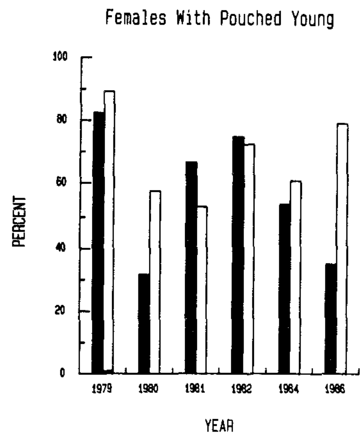

Fig. 6. Reproductive data: proportion of female rock-wallabies with young on Nangeen Hill (solid bars) and Sales' Rock (open bars) for the period 1979–86. The low 1986 value for Nangeen is associated with the population increase and signs of heavy grazing.

Reproductive Effort

Reproductive data for all populations are found in Table 1. For most years the reproductive effort was high and this potential for increase was fully expressed by the populations subject to fox control. Fig. 6 illustrates the percentage of females carrying pouched young for Sales' Rock and Nangeen Hill. The pes length range for pouched young indicates that breeding was not seasonal (Fig. 7).

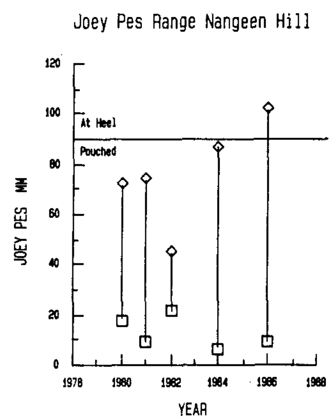

Fig. 7. Pes length range (□, minimum; ◇, maximum) for pouched young. The wide range indicates the lack of seasonal breeding for most years.

It is also likely that reproductive effort was affected by heavy grazing in 1986 as the reproductive status (and body condition, see Fig. 8) of the Nangeen population differed from previous years with the exception of 1980, a drought year. Females with pouched young comprised 35% of the female sample, which is appreciably lower than the Sales' Rock population (79%, Fig. 6).

Body Condition

By 1986, there were obvious signs of heavy grazing by the Nangeen population, and this aspect is reflected in the weight losses of mature (6+ years old) wallabies caught in 1984 and 1986 (Fig. 8*b*; paired '*t*' test, $0 \cdot 01 < P < 0 \cdot 025$). On Sales' Rock, there were never any signs of heavy grazing comparable to Nangeen, and there were no significant weight losses of mature individuals trapped during 1984 and 1986 (Fig. 8*a*; $0 \cdot 10 < P < 0 \cdot 25$).

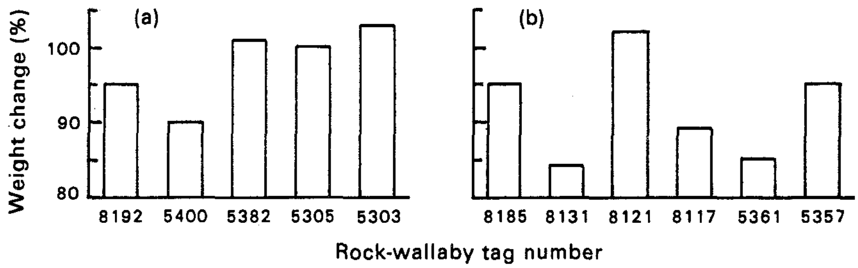

Fig. 8. Weight changes of mature individual rock-wallabies (6+ years) caught in 1984 and 1986. Sales' Rock (*a*) comparisons were not statistically different and there were no signs of heavy grazing. Nangeen Hill (*b*) registered a significant weight loss (paired '*t*' test, $0 \cdot 01 < P < 0 \cdot 025$) which is associated with the population increase and heavy grazing.

Discussion

Predation Pressure and Habitat Utilisation

The population increases of the two populations subject to fox control are reminiscent of the classical response of a population to the removal of a limiting factor affecting growth (Fig. 4). In the case of the Nangeen population, there was some evidence based on weight changes (Fig. 8*b*), that imply that, by 1986, the population was becoming resource limited with respect to food.

On release from predation, we observed not only a population increase, but also an increase in the use of the habitat. This response was clearly evident from our trapping effort (Table 1), when traps were set according to the distribution of scats. After two years of baiting, it became necessary to enlarge the trapping area and to increase the number of traps. This was particularily so for Mt Caroline in 1986, when it became necessary for logistical reasons to partition the reserve into two areas which were then censused separately in sequence using all available traps.

It was also noted that during the period prior to fox control on Nangeen Hill Reserve, animals were rarely observed far from shelter but, with baiting, the sightings increased and it became commonplace to observe rock-wallabies foraging away from the rock.

Our surveys of rock-wallaby populations in the wheatbelt (and elsewhere throughout the state), have shown that the remnant populations of rock-wallabies coexisting with the fox are invariably found in situations where the habitat provides protective shelter and food nearby. The species now persists only on sites which, in essence, are serving as refugia. This was readily evident from a survey of sites known to have carried populations in the wheatbelt; an inspection of these historical sites revealed shelter to be strikingly inadequate when compared to the present pattern.

Census Estimates: Validity of Results

The development of the Bromilow trap (Kinnear *et al.* 1988) was a significant achievement as it enabled us to safely trap on a sustained basis, without risk and without inducing wholesale trap avoidance behaviour (see frequency of recapture analyses, Appendix Tables 1–3). Our census estimates relied solely on trapping and this meant that if a tagged individual was never caught again, it was assumed to be dead. This assumption appears reasonable, particularly for the populations not subject to fox control. For example, with the Sales' population, major KTBA adjustments (Table 1) were only necessary for the initial 1979 trapping session when we failed to capture 14 wallabies because the trapping technique was not yet perfected. Thereafter it was necessary to make only one additional adjustment—an individual tagged in 1979 escaped capture in 1980, but was caught on all subsequent occasions.

In the case of the small populations, Querekin and Tutakin, the evidence suggests that we were enumerating the populations. These populations remained localised and concentrated in small 'break-away' areas of the outcrop which afforded protective shelter. In 1983, the Querekin population was kept under surveillance by the wildlife photographers, B. A. and A. G. Wells, who observed from concealed positions five individuals, including an individual with distinctive features (B. A. and A. G. Wells, pers. comm.); not long afterwards, the site was trapped and five were caught including the distinctive individual.

In summarising the fitting of trapping data to frequency distributions [see also, Eberhardt (1969)], it is generally apparent that both control and experimental populations responded to trapping in a similar manner. At lower population densities, the Poisson applies, and with population growth, the negative binominal becomes appropriate. This pattern lends support to the interpretation that the population estimates are valid, and that the differences between populations are not due to differences in trappability.

Predation and Drought Interactions

It is likely that fox predation poses a greater threat during severe drought. In 1980 the study area was declared drought affected (rainfall for the Nangeen area 54% of the Kellerberrin average; G. McDonald, pers. comm.), and associated with this event was a marked decline of the Sales' population (Fig. 5). Under drought conditions, one would expect a rock-wallaby to be more vulnerable to predation when foraging, if obliged to forage away from shelter. The alternative strategy (foraging close to protective shelter) would lower the predation risk, but would increase the risk of malnutrition or starvation. It is possibly significant that the Kokerbin population (Fig. 2) became extinct during a drought affected year 1969–70. It also follows that the interaction of fox predation and severe drought would be very strong at high rock-wallaby densities and also, if the drought were prolonged.

The Nangeen Hill population did not decline following the 1980 drought affected year, probably because the population was already low, and because foxes were being actively hunted and shot which may have afforded the population some protection.

Survival and Mortality

Fig. 5 illustrates rock-wallaby survival from samples marked in 1980. The effect of drought is particularly apparent for the Sales' population, but it is not known whether the mortality was due to a higher level of predation pressure or physiological stress resulting from the drought. We suggest that the former is probably a factor because, during the entire course of the study, we never observed any signs that rock-wallabies were severely stressed nutritionally or otherwise.

It is obvious from Fig. 7 that, for Nangeen Hill and Sales' Rock, predation was directed at juveniles. Adult survival was similar for both Sales and Nangeen both during the pre-baiting period and following the implementation of the baiting program. However, this example does not indicate that fox predation is *focused solely on juveniles*. The Querekin population decline represents adult mortality in the absence of drought. One would expect that juvenile mortality would be density dependent and that juveniles would be competitively disadvantaged, should protective shelter be limiting. The recovery of the Sales' population following drought is possibly a result of increased survival due a lower level of competition for protective shelter.

It should be noted that in calculating the percentage population changes for all populations after four years of fox control, the highest census value for the period 1979–82 was used as a reference value. For the Sales' population, the 1980 value of 34 wallabies represents a population size attainable under predation pressure, but not sustainable in a drought year when the population declined to 22. By 1986 the Sales' population recovered to reach a level of 44 animals. The recovery creates the impression of a larger net increase than was actually realised; i.e. in reality, the Sales' population registered a net increase of only 10 animals (from 34 to 44). In contrast, under fox control, Nangeen Hill increased by 40, and Mt Caroline by 29 (from 13 to 42).

Predation and Population Genetics

Under predation, rock-wallabies cannot maintain populations at levels believed necessary to maintain population fitness and genetic variance (Frankel 1983; e.g. prior to fox control it was estimated that the five closed populations, consisted of a total of 75–100 animals). Small closed populations are susceptible to genetic deterioration due to drift and inbreeding, and with regard to the latter point, an electrophoretic survey of some of the populations in 1980 detected very little variation (Kinnear *et al.*, unpublished work). It is not yet clear if predation by foxes contributed to this lack of variation, but this possibility may need to be considered by wildlife managers.

Concluding Remarks

How much damage the fox has done to Australian wildlife in the past will never be known, but it seems reasonable to conclude from this study that the fox not only contributed to the decline and extinction of populations (Kinnear *et al.* 1984), but also profoundly affected the range and distribution of many species. It is our view that the ecology of the surviving populations of small-to-medium sized macropodids is atypical because of fox predation. It is probable that today, populations can only persist in refugia that may be quite atypical of a species' actual niche requirements. In terms of the Hutchinson (1978) concept of the niche (see also, Kinnear 1985), fox predation affects the dimensions of a species' *realised niche* by exaggerating the requirements for protective shelter and need for food to be nearby. Niche theory predicts that a release from predation would relax the requirements for shelter and the proximity of food, and thus permit the expansion of the realised niche, which is precisely what was observed (i.e. greater use of the habitat when the fox was controlled).

It is also important to realise that the fox still exercises predation pressure on populations and therefore remains a threat to some surviving species. Unfortunately, a more prevalent belief in the conservation community is that, while the fox may have caused damage in the past, a presumed state of equilibrium now exists with respect to the surviving fauna. This view would appear to be true for some of the rock-wallaby populations described in this study, but it should be stressed that the equilibrium is a precarious one. Under predation, the populations are too small to have long-term viability and, moreover, the predation threat effectively isolates the populations reproductively (apart from fragmentation *per se*) and thus promotes inbreeding. Furthermore, when subject to predation, the populations are more susceptible to adverse environmental conditions such as severe and prolonged drought.

This study has shown that control of predation pressure is possible, and it is encouraging that the baiting program as exercised on Mt Caroline (one application of baits/month on the reserve perimeter) afforded adequate protection as judged by the rate of population increase (Fig. 4). There are also reasons to believe that control efforts can be reduced even further (Kinnear and Onus, in preparation).

More research on fox control with emphasis on optimising the baiting procedure is currently in progress. In the long-term the ultimate solution would be some method of biological control.

Acknowledgments

A project of this nature would not have been possible without the cooperation and goodwill of the local farming community. It is a pleasure to acknowledge this, and we therefore thank the following families: McDonald, Sales, Johnston, Cole, Hammond, Hadlow, Canova, Langdon and Crook. J. Turner made some important contributions during the early stages. The cooperation of the APB and in particular, H. Lieuwes, D. King and A. Oliver is gratefully acknowledged. A fruitful discussion with A. R. Main led us to test eggs as a bait. We are grateful to A. Burbidge, P. Christensen, A. Friend, D. King and A. Kinnear for their constructive comments on drafts of the manuscript. N. Caputi provided statistical advice. Finally, certain actions taken by B. K. Bowen during the initial stages of the project made this study possible.

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Appendix Table 1. Population estimates and goodness of fit statistics for recapture frequencies from Nangeen Hill

Year	Trapped	KTBA	Estimate	χ^2 value	d.f.	Fit
		(*a*) Poisson fit and population estimates				
1979	12	18	19	0·996	1	NS
1980	20	21	23	1·261	2	NS
1981	20	26	20	3·124	2	NS
1982	25	29	27	4·978	3	NS
1984	45	51	46	24·87	5	$P<0·001$
1986	69	69	70	42·32	7	$P<0·001$
		(*b*) Negative binomial fit and population estimates				
1979	12	18	58	–	0	–
1980	20	21	22	–	0	–
1981	20	26	20	8·487	1	$P<0·005$
1982	25	29	31	11·73	2	$P<0·005$
1984	45	51	53	7·101	3	NS
1986	69	69	77	10·14	6	NS
		(*c*) Geometric fit and population estimates				
1979	12	18	31	0·453	1	NS
1980	20	21	34	3·633	1	NS
1981	20	26	25	5·077	2	NS
1982	25	29	37	2·950	2	NS
1984	45	51	62	2·401	3	NS
1986	69	69	86	12·18	6	NS

NS, not significant.

Appendix Table 2. Population estimates and goodness of fit statistics for recapture frequencies from Sales' Rock

Year	Trapped	KTBA	Estimate	χ^2 value	d.f.	Fit
			(a) Poisson fit and population estimates			
1979	18	32	94	–	0	–
1980	34	35	45	1·109	2	NS
1981	22	22	22	8·502	5	NS
1982	22	22	23	3·586	3	NS
1984	37	37	38	6·482	4	NS
1986	44	44	44	20·302	7	$P<0{\cdot}005$
			(b) Negative binominal fit and population estimates			
1979	18	32	55	–	0	–
1980	34	35	63	2·689	1	NS
1981	22	22	23	23·70	4	$P<0{\cdot}001$
1982	22	22	22	–	0	–
1984	37	37	39	51·36	4	$P<0{\cdot}001$
1986	44	44	46	10·37	6	NS
			(c) Geometric fit and population estimates			
1979	18	32	171	–	0	–
1980	34	35	73	1·087	2	NS
1981	22	22	28	10·76	3	$P<0{\cdot}025$
1982	22	22	30	9·574	2	$P<0{\cdot}01$
1984	37	37	51	9·882	4	$P<0{\cdot}05$
1986	44	44	54	5·442	5	NS

NS, not significant.

Appendix Table 3. Population estimates and goodness of fit statistics for recapture frequencies

Year	Trapped	KTBA	Estimate	χ^2 value	d.f.	Fit
(i) **Mt Caroline**						
		(a) Poisson fit and population estimates				
1984	11	22	13	1·463	1	NS
1986	42	42	43	17·63	5	$P<0·005$
		(b) Negative binominal fit and population estimates				
1984	11	22	19	1·442	1	NS
1986	42	42	49	5·327	4	NS
		(c) Geometric fit and population estimates				
1984	11	22	18	0·326	1	NS
1986	42	42	56	3·058	5	NS
(ii) **Tutakin**						
		(a) Poisson fit and population estimates				
1983	6	7	7	1·050	1	NS
1986	6	6	7	1·681	1	NS
		(b) Negative binominal fit and population estimates				
1983	6	7	7	–	0	–
1986	6	6	50	–	0	–
		(c) Geometric fit and population estimates				
1983	6	7	10	1·951	1	NS
1986	6	6	9	0·465	1	NS

NS, not significant.

Manuscript received 23 February 1987; accepted 15 January 1988