

# Compensatory responses by a fox population to artificial density reduction in a rangeland area in Western Australia

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## ABSTRACT

The capacity of a fox population to compensate for a significant reduction in density was assessed at two rangeland sites in Western Australia. The fox population at the treatment site was reduced to 26% of its original density using 1080 baits (sodium fluoroacetate) and the population at the control site was left undisturbed. Both populations were destructively sampled in 1997 after a full breeding season had elapsed after baiting. Additional data on the demographic characteristics of unbaited fox populations were collected in 1995 and 1996 from five additional sites that were outside the treatment and control sites. The ovulation rate in the treatment site was significantly higher than in the control and additional sites (7.2 corpora lutea/vixen versus 4.7 for the control site and 4.4 and 5.0 for the additional sites in 1995 and 1996, respectively), as was the implantation rate (6.1 implantations/vixen versus 3.9, 4.1 and 3.7), and litter size (5.4 versus 3.2, 3.8 and 3.2). The observed demographic differences in the treatment site are discussed in relation to the effectiveness of lethal baiting with 1080.

**Keywords:** baiting, compensation, control, effectiveness, foxes, reproduction

## INTRODUCTION

Foxes (*Vulpes vulpes*) are recognised as significant predators of small- to medium-sized native mammals in Australia (Kinnear et al. 1988, 1998, 2002; Dickman et al. 1993; Short & Smith 1994). They also cause direct economic losses to agricultural industries through predation on livestock (Saunders et al. 1995). Current strategies to control the impacts of fox predation rely heavily on lethal baiting with 1080 (sodium fluoroacetate; Saunders et al. 1995; Kinnear et al. 2002). Baits are delivered at regular intervals to ensure fox populations are maintained at sufficiently low densities to protect vulnerable species from predation (Orell 2004). When a baiting campaign is being planned it is important to understand how quickly fox populations may recover from the effects of lethal control so that expenditure on baiting operations can be optimised by reducing the frequency of bait delivery.

The reduction in abundance of any animal population tends to be countered through a series of density-dependent mechanisms, so that ultimately its original density is regained (Sinclair & Pech 1996). For example, reproductive output may increase when relatively more food becomes available to the remaining individuals. When the density of foxes is reduced by baiting, the ovulation rate may increase, juvenile and adult survival may increase, and the rate of barrenness and the age at which vixens first breed successfully may decrease (Englund 1980; Voigt & Macdonald 1984; Clark & Fritzell 1992; Barlow et al. 1997). If these responses are sufficiently large, and affect a significant proportion of the remaining individuals, then the effectiveness of the baiting program could be severely compromised.

The actual density reduction achieved in fox populations by baiting may be influenced by the type of social system operating within the exposed population (Caughley et al. 1992). In high density populations that experience abundant resources, dominance hierarchies tend to form and these are usually socially regulated (Macdonald 1983; Newsome 1995). The dominant vixen may suppress the reproduction of subordinate vixens and non-breeding vixens are common. If baiting is only partially effective in these populations breeding suppression could be disrupted and this may lead to a net increase in the number of vixens successfully breeding (Caughley et al. 1992).

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**Recommended citation:** Marlow NJ, Thomson PC, Rose K, Kok NE (2016) Compensatory responses by a fox population to artificial density reduction in a rangeland area in Western Australia. *Conservation Science Western Australia* 10: 3 [online]. <https://www.dpaw.wa.gov.au/CSWAjournal>

In contrast, in areas where resources are less abundant, such as semi-arid rangelands, the social system of foxes is more likely to be mated pairs (Marlow et al. 2000). In this breeding system virtually all adult vixens breed and there is little socially-regulated suppression of reproduction. Non-breeding vixens tend to be uncommon. The likely responses to control in such populations, in the absence of immigration or emigration, are increased reproductive output per vixen, and/or increased survival/recruitment of the cubs produced (Englund 1970; von Shantz 1984; Lindström 1988).

The potential capacity of a fox population to compensate for a reduction in density was assessed by subjecting a population to lethal control using 1080 baiting (Thomson et al. 2000). A single baiting event with 1080 fox baits was implemented and was predicted to remove approximately 75–90% of the population (Thomson & Algar 2000). It was reasoned that if this level of density reduction was imposed and immigration prevented, the expression of any compensatory demographic response should be facilitated, and thus our chances of detecting a response would increase.

In this paper we compare demographic data from a reduced-density fox population and an undisturbed population. Data from unbaited, intact populations in the same region from two previous years were also included. We quantify ovulation rates, implantation rates, resorption rates, litter sizes, yearling recruitment and the proportion of non-breeding vixens. The results are discussed in relation to ongoing lethal control strategies.

The experiment was undertaken at a very large scale relative to the home-range areas used by foxes (Saunders et al. 1995). This enabled important aspects of the foxes' ecosystem and community functioning to be monitored and enabled the population's response to the major perturbation to be quantified. This would not have been possible if the study had been undertaken at a smaller scale (Schindler 1998). A consequent constraint on the experiment was that it could not be exactly replicated due to the impracticality and expense of obtaining a second treatment area of similar size. It was prohibitive to arrange another similarly large area in which all landholders would agree to their land being aeri ally baited with 1080 baits that had the possibility of killing their dogs. Also, due to the variability across sites at the scale at which the baiting treatment was undertaken it was not possible to get true replication of fox control histories, land use or ecological conditions (see Schindler 1998). Despite the study areas not being replicated the results of this ecosystem-scale experiment are important to the understanding and management of fox populations at this scale and could not have been achieved from a replicated study undertaken at a moderate scale (Schindler 1998). The conclusions about community and ecosystem processes based upon data that have been collected in small-scale experiments can be flawed when they are extrapolated to the ecosystem

scale and erroneous management decisions may result (Schindler 1988).

## METHODS

### Study sites

The study was conducted in rangeland habitat near Carnarvon (24° 56' S, 113° 54' E), approximately 900 km north of Perth, Western Australia (Fig. 1; Thomson et al. 2000). The predominant land use of the area is sheep grazing and the major mixed-shrubland habitats chosen for the study sites are rated as highly productive for the region (7 ha/ sheep unit). Detailed descriptions of landforms and vegetation for the area are given in Payne et al. (1987).

The region has a semi-arid Mediterranean climate with an average annual rainfall of 220 mm. No effective rainfall (Beard 1976) fell in the study area in 1994. The drought broke just as the study commenced in June 1995 and 245 mm of rain was received during the remainder of the year. Above average rainfall occurred in 1996 and 1997 (287 mm and 254 mm, respectively).

Apart from highway transport, human activity across the study sites was centred on isolated homesteads (Fig. 1) and was largely confined to the checking of artificial watering points and occasional mustering of livestock. The fox population in the entire area was essentially unculled and undisturbed. There had been no organised fox control since the early 1980s when fur hunters operated in the area. Foxes were occasionally shot by kangaroo shooters but the impact of this on the population at the time the study commenced was assumed to be negligible. Rabbits were uncommon and patchily distributed in the area (N. Marlow, pers. obs.).

The treatment site (1000 km<sup>2</sup>) was centred 60 km south-east of Carnarvon (Fig. 1). This site was baited in August 1995 with dried kangaroo meat baits, each containing 3 mg of 1080. The baits were dropped from a Cessna 182 aircraft flying at 90 knots at a height of 500 feet along transects that were 1 km apart. A GPS (Garmin 12XL) and timer were used to ensure the nominal baiting rate of 5 baits km<sup>-2</sup> was achieved.

The treatment site was surrounded on its land boundary by a 15-km wide baited buffer zone (2180 km<sup>2</sup>) that was established to reduce immigration into the treatment site (Thomson et al. 2000). The buffer zone was initially baited at the same time and using the same regime as the treatment site. An unbaited 'control' site (610 km<sup>2</sup>) was centred 65 km north-east of Carnarvon (Fig. 1).

The baiting regime implemented in the treatment site in August 1995 resulted in higher than expected fox mortality (see below). The resulting density was too low to provide sufficient foxes for the subsequent comparison of reproductive output between this site and the control site that was to have taken place in 1996. Consequently, the baiting in the buffer zone that had been planned for February 1996 was cancelled and

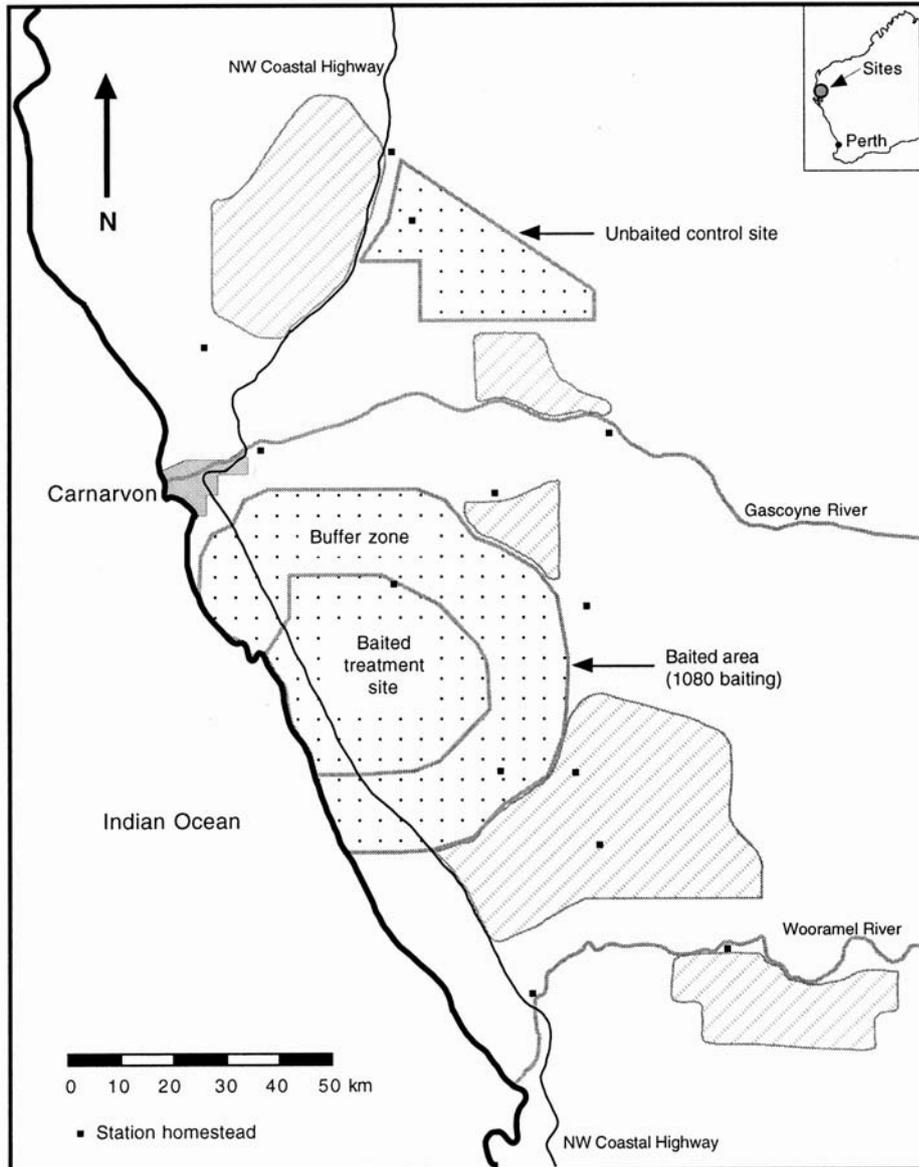


Figure 1. The spatial arrangement and extent of the study sites in Western Australia (after Thomson *et al.* 2000). The additional sites sampled in 1995 and 1996 are shown with grey cross-hatching.

some immigration into the treatment site was permitted during early 1996. By June 1996 sufficient foxes had recolonised the treatment site (i.e. 26% of the original density in August 1995; see below) and the buffer zone was again baited using the methods described above. Further baiting events were undertaken in the buffer zone in February 1997 and May 1997 to minimise further migration into the treatment site. The fox population in the treatment site then remained essentially undisturbed until the final destructive sampling was undertaken there and in the control site in 1997 (see below). It was recognised that the reproductive performance of immigrant vixens may not be equivalent to that of resident vixens.

Additional data on the breeding and density characteristics of unbaited fox populations were collected from five additional sites located outside the treatment and control sites (Fig. 1). Destructive

sampling (see below) was used to obtain fox carcasses from different areas within these five sites in both 1995 and 1996. Sampling undertaken in these sites during 1995 was positioned so as to minimise any potential impact it may have had on sampling undertaken in 1996.

### Density estimations

Fox density in the treatment and control sites was estimated from catch-per-unit-effort (CPUE) data from live-trapping (and release). Conventional trapping techniques (Fleming *et al.* 1998) and Victor Soft Catch® traps were used. Traps were set singly at approximately 0.5 km intervals along pre-determined tracks and were baited with a food lure (usually goat meat). When captured, foxes were examined and fitted with an ear-tag and radio-collar. CPUE data were used to derive a density estimate. To ensure the comparability

of estimates between years, trapping in each site was carried out at the same intensity and along the same transects each year. Trapping data were used to determine the pre-baiting and final densities of the fox populations in the treatment and control sites. They were also used in June 1996 to quantify the level of immigration into the treatment site (see below). Indices from trapping data were compared between sites using *Chi*-squared analysis.

The density of foxes in the treatment and control sites was also estimated using CPUE cyanide baiting at the end of the experiment. This technique involved placing wax capsules, each containing 1 g sodium cyanide, at 200 m intervals along pre-determined 20 km transects (Algar & Kinnear 1992). Cyanide baiting was also used to obtain CPUE estimates of fox density in the additional sites in 1995 and 1996 (Thomson et al. 2000). The transects used for cyanide baiting in the additional sites in 1995 and 1996 were separated by at least 4 km from the treatment and control sites. The CPUE density estimates of foxes in the treatment and control sites obtained from cyanide baiting were compared with those obtained in the additional sites in 1995 and 1996 using a one-way ANOVA.

### Final sampling

The fox population in the treatment site was left undisturbed for one year after immigration had returned the population density to 26% of the pre-baiting density. This interval would enable any compensatory changes in reproductive output, if present, to become evident. The fox populations at the treatment and control sites were then both destructively sampled between August and December 1997 to determine if any differences in reproductive output could be detected. Cyanide baiting, shooting and trapping were used to collect as many foxes as possible from both sites. Cyanide capsules were deployed for a single night to generate CPUE data and were then subsequently placed wherever fresh fox sign was observed (see Thomson et al. 2000). Opportunistic shooting was conducted from dusk until dawn, and foxes were shot with a .243 calibre rifle with the aid of a 100 W spotlight. Trapping was undertaken using Victor Soft-Catch® traps, set initially at 500 m intervals to enable CPUE densities to be estimated, and then wherever fresh fox sign was observed.

### Indices of condition and mange

Fox carcasses were weighed and differences in the weights of foxes between sites were compared using a one-way ANOVA. The extent of mange was scored as 1 ('none or slight', <10% hair loss) or 2 ('severe', ≥10% hair loss). Indices of 'none or slight' versus 'severe' mange were compared using *Chi*-squared analysis. Subcutaneous fat deposits were used as a nutritional index as outlined by Cavallini (1996) and were assessed as 1 (none or slight) or 2 (abundant). Fat scores of 'slight' versus 'abundant' were compared using *Chi*-squared analysis.

### Ageing

The snouts of foxes were collected for age determination. These were based on cementum annuli counts in teeth as described in Thomson et al. (2000) and using the techniques of Thomas (1977), Johnson et al. (1989) and Lieberman (1994). Individual foxes were then assigned to an appropriate annual cohort (see Marlow et al. 2000). The age structures of the populations sampled in the treatment and control populations in 1997 were compared with those of the additional sites in 1995 and 1996 through a series of two sample Kolmogorov–Smirnov tests.

### Reproductive parameters

The reproductive tracts of all vixens were examined in the field and the number of embryos or recent placental scars was recorded. Scars were classified as resulting either from resorptions or full-term births (Lindström 1981). At the time of our sampling, scars resulting from recent, late-term foetuses were very clear. Resorptions were unlikely to have been incorrectly scored, although late-term abortions may have been included in data on viable litter size (Harris 1979). Ovaries and embryos were collected and stored in 70% alcohol. Ovaries were later examined in the laboratory and the number of corpora lutea in each was counted. Vixens were classed as non-breeding if they failed to ovulate or become pregnant, or if they resorbed entire litters. Embryos were weighed and the timing of conception and parturition was deduced from embryo weights, using the methods and data described in Lloyd (1980). The sex of embryos was recorded if discernible and the sex ratio for in-utero cubs was calculated.

The ovulation rates, the number of implantations per vixen, resorption rates and litter sizes (number of actual or deduced viable embryos and including vixens which were non-breeding) were compared between populations using one-way ANOVA. A more comprehensive analysis of the data was precluded by the absence of replication of the treatment site.

Yearling recruitment was calculated by dividing the number of yearling vixens appearing in the sample population by the total number of viable vixen cubs produced in the preceding season. A 1:1 sex ratio at birth was assumed based on the ratio observed in litters collected during this study (see below). *Chi*-squared analysis was used to compare yearling recruitment between the treatment and control sites in 1997.

## RESULTS

### Population densities

Indices of population density, based on CPUE live-trapping data suggested that the original population density in the treatment site (before baiting in 1995) was not significantly different to that of the control site, albeit a year later in 1996 ( $\chi^2 = 1.2$ , d.f. = 1,  $P > 0.1$ ).

Respective capture data were 57 foxes in 190 trap nights (30% trap success), and 25 foxes in 104 trap-nights (24% trap success). Similarly, CPUE cyanide-baiting indices were not significantly different (ANOVA,  $F_{2,38} = 0.27$ ,  $P > 0.2$ ) between the control site ( $11.0 \pm 1.0$  per 100 bait stations; data from 14 transects), and the additional sites in 1995 ( $10.0 \pm 0.23$  foxes per 100 bait stations; data from 13 transects) and 1996 ( $8.8 \pm 0.76$  foxes per 100 bait stations; data from seven transects).

The number of foxes increased in the treatment site following immigration and the density of this population in June 1996 was 26% of its original density before it was baited in 1995 (Thomson et al. 2000). This was considered to satisfactorily represent a fox population with 'reduced density' commensurate with that resulting from a single 1080 baiting event (i.e. 74%; see Thomson & Algar 2000). Over this period, there was no substantial change in the density of the fox population in the control site (Thomson et al. 2000). The density of foxes in the treatment site in June 1996 was significantly lower than that of the control site and those of the additional sites sampled in 1995 and 1996 (ANOVA  $F_{3,41} = 3.61$ ,  $P < 0.03$ ).

## Population sampling and age structure

In 1997, 236 foxes were recovered from the control site and 63 from the treatment site during the comprehensive final sampling (Fig. 2). In the control site, 85% of foxes were cyanide baited, 14% were trapped and 1% were shot. In the treatment site, 63% were cyanide baited, 29% were trapped and 8% were shot. In 1995 and 1996, 205 and 151 foxes, respectively, were obtained from the additional sites using cyanide baiting (Fig. 2).

There were no significant differences between the age structures of the fox populations from any of the sites. The proportion of yearling recruits in the treatment (24%) and control sites (17%) in 1997 was not significantly different ( $\chi^2 = 2.21$ , d.f. = 1,  $P > 0.05$ ).

The rates of increase for the fox populations in the treatment and control sites could not be calculated because no reliable, non-destructive census methods which enabled consecutive density estimates to be made were available. However, the relative estimates obtained from the additional sites in 1995 and 1996 and from the control site in 1997 indicated that fox density in unbaited areas was stable (Thomson et al. 2000).

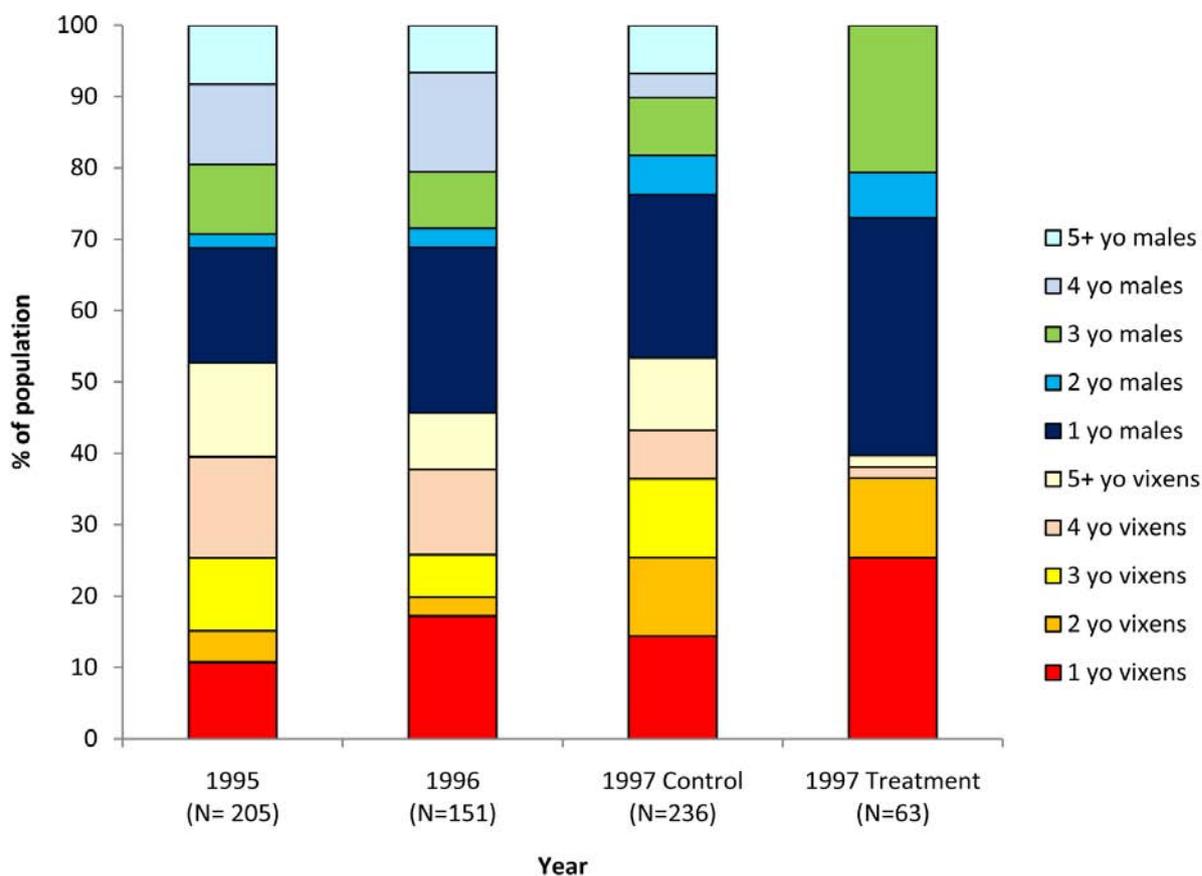


Figure 2. The age structures of fox populations sampled in the additional sites in 1995 and 1996 and in the control and treatment sites in 1997.

## Reproduction

The ovulation rate in the treatment site was significantly higher than those for the control site in 1997 and the additional sites in 1995 and 1996 (ANOVA  $F_{3,275} = 29.8$ ,  $P < 0.001$ ; Table 1). Similarly, the number of implantations per vixen and the mean observed litter size in the treatment site in 1997 were significantly larger than those from the control site in 1997 and the additional sites in 1995 and 1996 ( $F_{3,275} = 15.03$ ,  $P < 0.001$  and  $F_{3,275} = 11.06$ ,  $P < 0.001$  for implantation rate and litter

size respectively; Table 1). There were no significant differences between sites in the resorption rate (ANOVA  $F_{3,275} = 1.77$ ,  $P = 0.15$ ), the proportion of non-breeders ( $\chi^2 = 6.5$ , d.f. = 3,  $P > 0.05$ ) or the sex ratio ( $\chi^2 = 5.7$ , d.f. = 3,  $P > 0.05$ ; Table 1). The sex ratio of in-utero cubs was not significantly different from 1:1 in any site. The timing of conception ranged from mid-June to mid-July (Table 2).

There was no significant difference in the number of deduced-viable cubs produced by vixens of different ages in the control site in 1997 or in the additional sites in 1995 and 1996 (ANOVA  $F_{5,249} = 1.45$ ,  $P > 0.20$ ; Table 1).

**Table 1**

Reproductive data for foxes sampled at sites near Carnarvon. Sex ratios were derived from data shown in Fig. 2. Ovulation rate is shown as the number of corpora lutea per vixen, implantation rate as number of scars/embryos per vixen, resorption rate as number of resorptions per total implantations, litter size as the number of full-term cubs per vixen. Non-breeding is shown as the proportion of vixens failing to produce live cubs (see Methods for further explanation). 'All vixens' excludes those sampled too early in the breeding season in 1995 to make valid comparisons of reproductive data;  $n$  for all vixens also represents the sample size for the other reproductive data. Means are shown  $\pm$  SE.

	1995	1996	1997 Control	1997 Treatment
Sex ratio (M:F)	1:1.11	1:0.84	1:1.15	1:0.66
Ovulation rate (n) per age class (yr)				
1	4.3 $\pm$ 0.7 (10)	5.2 $\pm$ 0.7 (26)	4.4 $\pm$ 1.4 (37)	7.1 $\pm$ 1.7 (17)
2	5.3 $\pm$ 1.4 (7)	4.8 $\pm$ 1.7 (4)	4.8 $\pm$ 1.2 (26)	5.8 $\pm$ 3.6 (6)
3	4.5 $\pm$ 1.6 (11)	4.8 $\pm$ 1.3 (11)	4.5 $\pm$ 1.7 (25)	No data (0)
4	4.5 $\pm$ 1.0 (19)	5.1 $\pm$ 2.0 (16)	4.9 $\pm$ 0.9 (14)	7.0 $\pm$ 0.0 (1)
5	3.7 $\pm$ 1.3 (13)	4.7 $\pm$ 2.6 (12)	4.9 $\pm$ 1.1 (25)	10.0 $\pm$ 0.0 (1)
Mean	4.4 $\pm$ 1.3 (60)	5.0 $\pm$ 0.2 (69)	4.7 $\pm$ 1.1 (127)	7.2 $\pm$ 0.3 (25)
Range	0–8	0–9	0–8	0–10
Implantation rate per age class (yr)				
1	3.5 $\pm$ 0.4	3.7 $\pm$ 0.4	3.1 $\pm$ 0.3	5.8 $\pm$ 0.7
2	4.4 $\pm$ 0.4	3.3 $\pm$ 1.2	4.0 $\pm$ 0.3	6.8 $\pm$ 0.7
3	4.4 $\pm$ 0.6	4.2 $\pm$ 0.6	4.4 $\pm$ 0.37	No data
4	4.2 $\pm$ 0.3	3.2 $\pm$ 0.6	4.2 $\pm$ 0.35	8.0 $\pm$ 0.0
5	4.1 $\pm$ 0.3	4.3 $\pm$ 0.6	4.3 $\pm$ 0.21	6.0 $\pm$ 0.0
Mean	4.1 $\pm$ 0.2	3.7 $\pm$ 0.3	3.9 $\pm$ 0.15	6.1 $\pm$ 0.5
Range	0–6	0–7	0–7	0–10
Resorption rate per age class (yr)				
1	0.2 $\pm$ 0.1	0.5 $\pm$ 0.2	0.6 $\pm$ 0.14	1.0 $\pm$ 0.5
2	0.1 $\pm$ 0.1	1.3 $\pm$ 0.9	0.9 $\pm$ 0.20	0.2 $\pm$ 0.2
3	0.5 $\pm$ 0.4	0.9 $\pm$ 0.3	0.4 $\pm$ 0.12	No data
4	0.5 $\pm$ 0.2	0.2 $\pm$ 0.1	0.6 $\pm$ 0.23	0.0 $\pm$ 0.0
5	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1	0.9 $\pm$ 0.27	1.0 $\pm$ 0.0
Mean	0.4 $\pm$ 0.1	0.5 $\pm$ 0.1	0.7 $\pm$ 0.09	0.8 $\pm$ 0.4
% resorbed	8.9	12.9	16.7	12.4
Litter size per age class (yr)				
1	3.3 $\pm$ 0.4	3.1 $\pm$ 0.4	2.6 $\pm$ 0.3	4.8 $\pm$ 0.8
2	4.3 $\pm$ 0.5	2.0 $\pm$ 1.1	3.1 $\pm$ 0.37	6.7 $\pm$ 0.6
3	3.8 $\pm$ 0.6	3.3 $\pm$ 0.6	3.9 $\pm$ 0.36	No data
4	3.7 $\pm$ 0.4	3.0 $\pm$ 0.6	3.6 $\pm$ 0.46	8.0 $\pm$ 0.0
5	3.8 $\pm$ 0.3	4.2 $\pm$ 0.6	3.4 $\pm$ 0.26	5.0 $\pm$ 0.0
Mean	3.8 $\pm$ 0.2	3.2 $\pm$ 0.3	3.2 $\pm$ 0.15	5.4 $\pm$ 0.6
Range	0–8	0–6	0–7	0–10
% non-breeding yearlings (n)				
	0 (10)	15.4 (26)	15.1 (33)	31.3 (16)
% non-breeding all vixens (n)				
	5.0 (60)	18.8 (69)	11.1 (127)	20.0 (25)

Also, the proportion of yearling vixens deduced to be non-breeders did not differ significantly between sites ( $\chi^2 = 4.6$ , d.f. = 3,  $P > 0.05$ ; Table 1).

Vixens in the additional sites in 1995 were significantly heavier than those collected at all other sites including the treatment site (ANOVA  $F_{3,270} = 8.39$ ,  $P < 0.001$ ; Table 2) but no other significant differences in the weight of foxes between sites were observed. The greater weight of the vixens sampled in 1995 appeared to be due to the timing of breeding, with those vixens being in later stages of pregnancy compared with those from other years (see below). The suggestion that normal body weight did not differ substantially between sites is consistent with the fact that the proportion of foxes scored with abundant subcutaneous fat did not vary significantly between sites ( $\chi^2 = 2.1$ , d.f. = 3,  $P > 0.05$ ; Table 2). A significantly higher proportion of vixens in all sites had abundant fat scores when compared to males, ( $\chi^2 = 107.8$ , d.f. = 1,  $P < 0.001$ ; Table 2).

The incidence of mange did not differ significantly between sites ( $\chi^2 = 6.61$ , d.f. = 3,  $P > 0.05$ ; Table 2). However, male foxes had significantly higher levels of severe mange than vixens ( $\chi^2 = 12.2$ , d.f. = 1,  $P < 0.001$ ; Table 2).

## DISCUSSION

The abundance of foxes in the control site in 1997 and in the additional sites sampled in 1995 and 1996 was similar and this indicates that the density of foxes in the Carnarvon region was relatively uniform, not only spatially, but also temporally. This conclusion lends support to the notion that any differences detected in reproductive parameters between the control and treatment sites in 1997 are likely to have resulted from the imposed reduction in fox population density.

The reproductive output of the fox population in the treatment site in 1997 appears to have increased as a response to density reduction. The ovulation rate at the treatment site was significantly higher than in the control and additional sites and was also higher than reported for foxes elsewhere in Australia (Table 3). A similar high ovulation rate was observed in an area of high food availability in Sweden (7 ova/vixen for a sample of 15 non-yearling foxes; Englund 1970) and these results indicate that foxes are capable of producing more ova than are usually recorded.

The higher ovulation rate observed in the treatment site was accompanied by a significantly higher

**Table 2**

Condition and conception dates of foxes at the sampling sites. M = male, F = female and T = total. As in Table 1, the data for 1995 exclude females that were sampled too early in the season for valid comparisons to be made. Mean weights are shown  $\pm$  SE.

		1995	<i>n</i>	1996	<i>n</i>	1997 Control	<i>n</i>	1997 Treatment	<i>n</i>
Weight (kg)	M	5.0 $\pm$ 0.1	51	4.9 $\pm$ 0.1	82	5.1 $\pm$ 0.1	110	5.0 $\pm$ 0.1	38
	F	4.9 $\pm$ 0.1	60	4.5 $\pm$ 0.1	69	4.5 $\pm$ 0.0	126	4.4 $\pm$ 0.2	25
	T	4.9 $\pm$ 0.1	111	4.7 $\pm$ 0.1	151	4.9 $\pm$ 0.0	236	4.7 $\pm$ 0.1	63
Abundant fat (% incidence)	M	1.9	51	12.7	82	17.3	110	10.2	38
	F	53.3	60	48.0	69	63.8	126	51.4	25
	T	27.7	111	36.5	151	33.8	236	25.8	63
Severe mange (% incidence)	M	19.6	51	13.8	82	11.8	110	2.8	38
	F	3.3	60	5.9	69	4.7	126	0.0	25
	T	10.8	111	10.0	151	8.0	236	1.4	63
Conception		29/6–14/7		10/6–17/6		24/6–4/7		24/6–4/7	

**Table 3**

Reproductive data on wild foxes from published Australian studies. Data are shown as means. Litter size refers to embryonic litter size.

Area	Ovulation rate	Implantation rate	Litter size	Source
ACT	5.0	3.9	4.3	McIntosh (1963)
NSW	4.5	4.2	3.8	Ryan (1976)
NSW <sup>A</sup>	4.6	3.6	3.2	McIlroy et al. (2001)
WA	–	–	3.7	Marlow et al. (2000)
WA unbaited	4.7	3.9	3.2	This study
WA baited	7.2	6.1	5.4	This study

<sup>A</sup> Non-ovulating vixens were excluded from the data; drought conditions prevailed for some of the sampling.

implantation rate of 6.1 embryos/vixen. This rate is higher than those observed in the control site in 1997, the additional sampling sites in 1995 and 1996, and the mean implantation rate for Australian foxes generally (3.6–4.2 embryos; McIntosh 1963; Ryan 1976; McIlroy et al. 2001). The higher implantation rate in the treatment site in 1997 appears to have resulted from a higher ovulation rate, rather than from an increase in the per-ova implantation rate, because there was no difference in the ratios of implantation rates to ovulation rates between the treatment and control sites in 1997 (0.85 and 0.83, respectively). The increased implantation rate did not result in increased resorptions and there was a relatively low resorption rate across all our sites (8.6–16.7%). This is consistent with the resorption rates observed in other Australian fox populations (e.g. 'rare', McIntosh 1963; 8%, Ryan 1976; 13.1%, McIlroy et al. 2001).

The higher ovulation and implantation rates in the treatment site in 1997 resulted in a significantly larger average litter size (5.4 cubs) than in the control site (3.2 cubs). This litter size was also significantly larger than the average litter size in the two additional sites of 1995 and 1996 (3.8 and 3.2 cubs respectively) and for foxes sampled elsewhere in Australia (see Table 3). This observation suggests that the per-capita increase in resources available to foxes in the treatment site resulted in an increase in fecundity. A similar increase in litter size in response to increases in resource availability has been observed by other authors (e.g. Layne & McKeon 1956; Englund 1970; Voigt & Macdonald 1984; McIlroy et al. 2001) and is pronounced in harvested fox populations (i.e. 4.1–10, Pils & Martin 1978; and 6.7, Storm et al. 1976). An inverse relationship between litter size and density has also been reported for coyotes (Knowlton 1972).

The observed larger litter sizes in the fox population at the treatment site provide support to previous conclusions that social suppression of breeding is unlikely to have occurred at Carnarvon where fox densities were relatively low and a mated-pair system was likely to prevail (Marlow et al. 2000). The proportions of non-breeding vixens observed in the various sites during our study (5.0–20.2%) were within the range reported elsewhere for red foxes (2.1–24.5%, derived from McIlroy et al. 2001) and were relatively low. The capacity for the Carnarvon fox population to respond to artificial population reduction through substantial increases in the proportion of vixens breeding was therefore limited. In contrast, if social regulation of breeding was influencing reproductive success, changes in the number of cubs produced by the population would have resulted from differences in the number of vixens breeding successfully rather than being due to a change in litter size per se (see Macdonald 1983; Lindström 1988; Newsome 1995).

There was no clear relationship between a vixen's age and her litter size, and this is consistent with the observations of Voigt and Macdonald (1984) and from an earlier Carnarvon study (Marlow et al. 2000). In contrast,

other studies have demonstrated a general increase in fecundity of vixens with age (e.g. Englund 1970; Allen 1984; McIlroy et al. 2001). Our result further supports the conclusion that reproduction in the Carnarvon populations was not socially regulated because yearling vixens are usually less fecund in populations where this occurs (e.g. Harris 1979). It is interesting to note that the foxes in the treatment site were generally younger than those in the control and additional sites and this is consistent with an increased level of immigration into the treatment site by predominately young foxes at the beginning of the experiment. However, the higher prevalence of young foxes did not appear to influence their capacity to produce larger litters of cubs.

The sex ratios of the populations sampled in the Carnarvon area were broadly consistent with the 1:1 ratio recorded for other fox populations in Australia (McIntosh 1963; Marlow et al. 2000). The population at the treatment site had the highest ratio of adult males to vixens (1:0.66) but the reproductive capabilities of the population clearly were not adversely affected. This result contrasts with those of Allen (1984) who found that ovulation rates and litter sizes tended to be lower in populations with higher proportions of male foxes.

The estimated timing of parturition varied slightly between years but was generally consistent with the June to October timing of pregnancies indicated in other Australian studies (McIntosh 1963; Ryan 1976; McIlroy et al. 2001). Nevertheless, the breeding season of foxes in Carnarvon appears to be several weeks earlier compared with the more southern study areas of McIlroy et al. (2001). A latitudinal gradient in the timing of breeding may exist for Australian foxes, as suggested for dingoes *Canis lupus dingo* (Corbett 1995).

There was a lower incidence of severe mange at the treatment site, especially for male foxes. This result is consistent with the reduced degree of contact likely to occur between foxes at lower density (Ross & Fairley 1969). However, the incidence of mange at the time of ovulation was not quantified and whether this influenced the reproductive performance of foxes in our study is unknown.

## Management implications

The observed increase in litter size in the treatment site would hasten that population's return to its original density. Similar responses to decreased density by red fox populations have been observed (e.g. 64–76% reduction during an annual fox harvest) and it was calculated that those populations could potentially achieve a full recovery within one year (Layne & McKeon 1956). This capacity of fox populations to compensate for decreases in density has implications for fox baiting programs and adds to the challenge of successfully controlling foxes and protecting vulnerable prey species. Baiting needs to be repeated frequently to maintain fox densities at low levels. The actual frequency required will depend upon the vulnerability of the prey species to fox predation, the area of the site in which

control is to be undertaken, and the area to perimeter ratio of the site (de Tores & Marlow 2012). Larger areas do not need to be baited as frequently due to reduced encroachment by foxes residing in adjoining areas, and in large forested areas the optimum frequency of baiting is six times per year (de Tores & Marlow 2012). In smaller areas with high perimeter to area ratios, such as the wheatbelt reserve of Dryandra Woodland, the delivery of baits 12 times per year is necessary to protect vulnerable fauna from fox predation (Marlow et al. 2015). The foxes' apparent capacity to compensate for substantial population reduction, and their capacity to recolonise depopulated areas, means that frequent baiting will need to be maintained into the foreseeable future in areas where conservation and agricultural assets need to be protected from fox predation.

## ACKNOWLEDGEMENTS

We would like to thank Glenn Edwards and an anonymous referee who made constructive comments on this manuscript. We gratefully acknowledge the support of the landholders who allowed us to use their properties. Their help and generosity throughout this study is greatly appreciated. We would also like to thank Laurie Twigg and Andrew Woolnough for commenting on an earlier draft of this manuscript. This study was partly funded by the former Vertebrate Biocontrol CRC (now Invasive Animals CRC) and Environment Australia. Trial procedures were approved by the Western Australian Department of Conservation and Land Management (now Department of Parks and Wildlife) Animal Experimentation Ethics Committee (number 1/92/96).

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