

# Demographic and functional responses of wild dogs to poison baiting

By Lee R. Allen

**Summary** Lethal control of wild dogs – that is Dingo (*Canis lupus dingo*) and Dingo/Dog (*Canis lupus familiaris*) hybrids – to reduce livestock predation in Australian rangelands is claimed to cause continental-scale impacts on biodiversity. Although top predator populations may recover numerically after baiting, they are predicted to be functionally different and incapable of fulfilling critical ecological roles. This study reports the impact of baiting programmes on wild dog abundance, age structures and the prey of wild dogs during large-scale manipulative experiments. Wild dog relative abundance almost always decreased after baiting, but reductions were variable and short-lived unless the prior baiting programme was particularly effective or there were follow-up baiting programmes within a few months. However, age structures of wild dogs in baited and nil-treatment areas were demonstrably different, and prey populations did diverge relative to nil-treatment areas. Re-analysed observations of wild dogs preying on kangaroos from a separate study show that successful chases that result in attacks of kangaroos by wild dogs occurred when mean wild dog ages were higher and mean group size was larger. It is likely that the impact of lethal control on wild dog numbers, group sizes and age structures compromise their ability to handle large difficult-to-catch prey. Under certain circumstances, these changes sometimes lead to increased calf loss (*Bos indicus*/*B. taurus* genotypes) and kangaroo numbers. Rangeland beef producers could consider controlling wild dogs in high-risk periods when predation is more likely and avoid baiting at other times.

**Key words:** biodiversity, kangaroo, livestock, predation, predator control, trophic cascade.

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## Introduction

Many large predators (e.g. Lion *Panthera leo*, Tiger *P. tigris*, Leopard *P. pardus*, Bear *Ursus arctos* and various canids such as Wolf *Canis lupus* and Jackal *C. aureus*, *C. adustus* and *C. mesomelas*) are managed on almost every continent because they attack livestock and threaten the viability of producers and sometimes the safety of humans (Saberwal *et al.* 1994; Kusak *et al.* 2005; Wang & Macdonald 2006; Nyahongo & Røskoft 2011; Schuette *et al.* 2013). As well as being iconic 'native' species on their respective continents, large predators can also be important keystone species that regulate prey populations on lower trophic levels (Estes *et al.* 2011), making the preservation of large predators critical to maintaining biodiversity and healthy ecosystem function (Johnson *et al.* 2007; Sergio *et al.* 2008; Prugh *et al.* 2009; Levi & Wilmers 2012). Conflict between biodiversity conservation and agricultural production is almost inevitable and often polarised.

The Dingo and other Dog/Dingo hybrids (collectively referred to here as wild dogs) are the largest mammalian predators on mainland Australia. They were declared pests in most places by the late 1800s because of the substantial livestock losses they inflicted, primarily on sheep (*Ovis aries*) (Allen & West 2013). Today, many tonnes of fluoroacetate (1080) poisoned meat bait are laid on public and private agricultural land to reduce the impact or spread of wild dogs (APVMA 2008). Where undertaken, conventional wild dog management on beef cattle properties in northern Australia is to bait in late autumn after the first round muster, at a time when wild dogs are mating and are very active (Fleming *et al.* 2001). A second baiting, if conducted at all, generally occurs in late spring after the second round muster prior to summer calving. Government agencies and grazer organisations encourage and facilitate the coordination of baiting programmes at these times so that large tracts of land are treated simultaneously (McKenzie *et al.* 2014).

Wild dogs are a well-known and serious threat to Australia's sheep industry (Allen & Fleming 2004; Allen & West 2013), but the attitudes of beef cattle producers to wild dogs have long been ambivalent (Allen & Sparkes 2001). Evidence of calf predation is mostly anecdotal or indirect, but estimated livestock losses can be substantial [\$23 million in direct cattle losses in Queensland alone (Hewitt 2009)] with costs of control making up a significant proportion of the economic losses [an additional \$11 million (Hewitt 2009)]. Diet studies generally show a low incidence of cattle remains in wild dog's diets (typically <5%) unless cattle carcasses are being scavenged [up to 23% (Corbett 2001)] or there are few alternative prey to eat, that is central Australia 6–42% [Allen & Leung 2014]. Veterinary investigations into the causes of calf loss rarely find evidence that predation was the cause of death (mortality factors reviewed in Burns *et al.* (2010). Manipulative experiments (Eldridge *et al.* 2002; Fleming *et al.* 2012; Allen 2014) comparing calf loss between pregnancy diagnosis and

weaning, in treatment areas or properties with and without annual or biannual wild dog baiting, generally show that wild dogs infrequently kill detectable numbers of calves yet some properties, some years can experience severe losses. Allen (2014) reported counter-intuitive results from central-south and north Queensland showing that calf loss occurred more frequently and with greater losses where wild dogs were controlled compared to paired nil-treatment areas where they were not controlled. In that study, below-average rainfall was a significant factor associated with calf loss but only where wild dogs were controlled. This finding suggests that baited and/or recolonised wild dog populations might be functionally different to those in unbaited populations.

This paper investigates whether demographic differences exist between wild dog populations in baited and nil-treatment areas. It investigates how these differences might affect prey selection in order to explain why baiting-induced calf loss was found to occur during drought subsequent to baiting, but not in nearby nil-treatment areas. Demographic differences between wild dog populations in baited and nil-treatment areas were investigated by (i) measuring the impact of baiting programmes on wild dog relative abundance, (ii) by measuring how long population reductions caused by baiting lasted before abundance returned to pre-control levels and (iii) by investigating whether changes in population age structures occurred following baiting programmes. To gain insight into how baiting may affect functional relationships, data from a separate study were re-analysed to see how group size and the age of wild dogs affect their efficiency in capturing large prey. Trends in prey populations in baited and nil-treatment areas were compared to detect whether divergences occurred indicating functional differences in the way wild dogs in baited areas interacted with their prey.

## General Methods

A large-scale manipulative experiment was conducted between 1994 and 1998 com-

paring calf loss and wild dog and other wildlife population trends in paired baited and nil-treatment areas on two extensive beef cattle properties located in central-south and north Queensland (Mt Owen and Strathmore station, respectively). The abundance of wild dogs (dingo phenotypes) and their prey was monitored from spoor, detected on tracking stations, constructed across unformed vehicle tracks [i.e. the Passive Tracking Index or PTI method reviewed in Engeman and Allen (2000)]. Relative abundance was calculated as the cumulative mean of daily mean number of tracks per tracking station per day. Precision of each PTI value was calculated using the variance method described in Engeman (2005). Further descriptions of the two study sites, the management practices, vegetation and rainfall, details of the methods of monitoring calf loss, wildlife abundance and wild dog diets are reported elsewhere in Allen *et al.* (2012, 2014) and Allen (2014).

At each study site, wild dog populations on a randomly selected portion of the cattle properties were routinely baited once or twice annually with 100–450 kg of 1080-poisoned meat bait. Baited treatment areas were ~40 000 and ~200 000 ha on Mt Owen and Strathmore, respectively. The remaining portion of each property (of equal or greater size than the baited area) was left unbaited and became the nil-treatment area. The two treatments were separated by a buffer zone of at least 10 km [i.e. approximately the diameter of one or more wild dog territories (Allen 2009)] at the closest point to provide independence between treatments at each survey.

## Demographic Impacts of Baiting

### Wild dog relative abundance

The impact of baiting programmes on the demography of wild dog populations was calculated as the percentage reduction in the cumulative mean number of wild dog intrusions across tracking stations per day surveyed immediately before and after baiting programmes in the baited area. As demonstrated in Allen *et al.* (1996) and

Allen and Engeman (2014), this method is very sensitive at detecting changes in wild dog abundance caused by baiting. The spoor of other wildlife detected on tracking stations was also identified and recorded.

On Mt Owen, 19 PTI surveys were conducted before and after seven wild dog baiting programmes where 50 tracking stations per treatment area were monitored for an average of 4.5 days per survey. Nine PTI surveys were conducted around five baiting programmes on Strathmore where 50 tracking stations per treatment area were monitored for an average of 5.8 days per survey. Surveys were conducted on average 38.9 ( $\pm 8.2$ ) days before baiting and 36.7 ( $\pm 6.8$ ) days after baiting [see Fig. 1 in Allen (2014)].

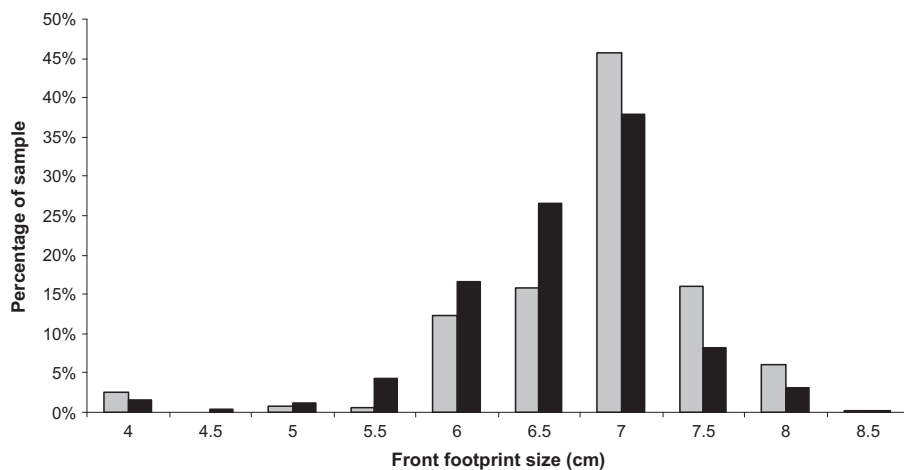
### Duration of baiting effect

The number of months between baiting programmes and the next survey that showed that PTI values had returned to within 10% of prebaiting PTI values was calculated to find out how long wild dog populations remain low after baiting. 'Within 10%' allowed for variability in the calculation of the PTI. In addition, the time of year when PTI values recovered to prebaiting levels was considered in relation to peak calving times September to November (Bortolussi *et al.* 2005) and when predation risk to cattle might be considered greatest.

### Impact of baiting on wild dog age structures

The length of the front footprint (to the nearest 0.5 cm excluding toe nails) of 1415 wild dog tracks was recorded from tracking stations located in both baited and nil-treatment areas (496 and 919 footprints, respectively) on Mt Owen and Strathmore during 14 PTI surveys.

Footprint data from both study sites and all surveys were summed within 0.5 cm footprint length categories. The proportion of the sample assigned to each footprint length category was analysed using the nonparametric, Kolmogorov–Smirnov two-sample test. This test is sensitive to differences in the shape of cumulative distributions of the two (footprint size) samples and is used to identify



**Figure 1.** Distribution of mean front footprint lengths of wild dog populations measured in baited and nil-treatment (solid black columns) areas.

whether the footprint size cumulative distributions are different and where maximum deviation occurs.

To calibrate footprint length with age, the front footprint length of 33 dingoes kept in zoological gardens and sanctuaries were also measured. The age of these dingoes was calculated from birth records, and their individual footprint lengths were similarly measured from tracking stations constructed in their pens.

In a second analysis, the percentage of wild dog tracks in each footprint length category was calculated for each treatment area, pre- and postbaiting, for two consecutive baiting programmes at Mt Owen (where more frequent survey data were available). By plotting the frequency of prints in each footprint length category from survey to survey, cohorts of pups and juveniles (4–6 cm footprints) could be monitored from their first appearance on PTI tracking stations until, as yearlings >9 months, (Thomson 1992a), the length of their footprints became indistinguishable from the footprints of adult dogs (6.5–7.0 cm prints).

## Results

Omitting data from stations rendered unreadable by rain, cattle or vehicles, 4124 wild dog tracks were recorded in 8739 station-nights of monitoring at Mt Owen. At Strathmore 4252 station-nights of tracking accumulated 800 wild dog

tracks. Consistent with standard baiting practices in these areas (Allen & Fleming 2004), a total of 2200 kg of 1080-poisoned bait was distributed in 'baited' treatment areas during the study. Variance calculations produced 95% confidence intervals that range from 2.3% to 22.1% (median of 6.5%) of wild dog PTI values. One control programme (Mt Owen, December 1995) was not resurveyed until 5 months (171 days) postbaiting by which time wild dog PTI values had increased six- to eight-fold in both treatments areas. This programme is omitted from the analysis.

### Impact of baiting programmes on wild dog abundance

Eleven of 12 baiting programmes (92%) resulted in reduced wild dog PTI values postbaiting where 95% confidence intervals did not overlap and  $P$ -values were <0.05. Wild dog PTI values were reduced by >50% in nine (75%) of these baiting programmes [see Fig. 1 in Allen (2014)], but on average a 54% reduction was achieved (range 9.1% increase in wild dog PTI values postbaiting to 100% decrease).

Baiting programmes conducted soon after the first round cattle muster between mid-May to early August and surveyed for wild dog activity between mid-June and late August ( $n = 6$ ) produced a mean reduction in PTI values of 51.9 ( $\pm 18.3$ )%. In contrast, wild dog PTI values in nil-

treatment areas during this same period varied significantly yet on average increased by 54.4 ( $\pm 49.4$ )%. Baiting programmes conducted in late winter and spring (months during which pup rearing is occurring) which were resurveyed between mid-September and mid-November produced mean PTI reduction of 57.5 ( $\pm 7.3$ )%, ( $n = 6$ ). At this same time, reductions in PTI values also occurred in nil-treatment areas [42.0 ( $\pm 20.2$ )%, ( $n = 4$ )].

### Duration of control effect

Wild dog PTI values in baited areas generally returned to precontrol levels within 1–12 months following baiting. In most instances, recolonisation of wild dogs to precontrol levels occurred between spring and autumn concurrent with calving and weaning. One of 11 (9%) baiting programmes reduced and maintained wild dog PTI values below precontrol levels for over 12 months. Without follow-up baiting programmes intervening, 75% or six of eight baiting programmes resulted in wild dog PTI values returning to prebaiting levels in <8 months. Where lethal control completely eliminated wild dog activity (e.g. Strathmore, July 1997) or was followed by a subsequent baiting programme within a few months (e.g. Mt Owen, 1994 and 1996), wild dog PTI values took longer to return to prebaiting levels.

### Impacts of baiting on age structures

Analysis of front footprint length measurements between Strathmore and Mt Owen show that there was no difference in the distribution of footprint lengths between locations ( $F = 2.12_{1,415,9}$ ,  $P = 0.14$ ). Wild dogs in nil-treatment areas had a mean front footprint length of 6.63 ( $\pm 0.02$ ) cm, while those in baited areas had a mean of 6.83 ( $\pm 0.03$ ) cm. The difference is statistically significant ( $t = 3.37$ ,  $df = 341$ ,  $P < 0.01$ ). Wild dogs in baited areas had a greater proportion of footprint length measurements in the larger footprint categories with the K-S test on cumulative proportions showing a maximum deviation occurs at a footprint

length of 6.5 cm ( $D = 0.18$ , the asymptotic  $K-S = 3.29$ ,  $P < 0.00$ ) (Fig. 1).

The distribution of footprint length categories in baited and nil-treatment areas in September 1996 (Fig. 2a) shows that few

juveniles (footprint lengths categories 4–6 cm) occur in the baited area 3 months after baiting. The baited treatment area was baited again in late September 1996. Pups born in June–July 1996 were

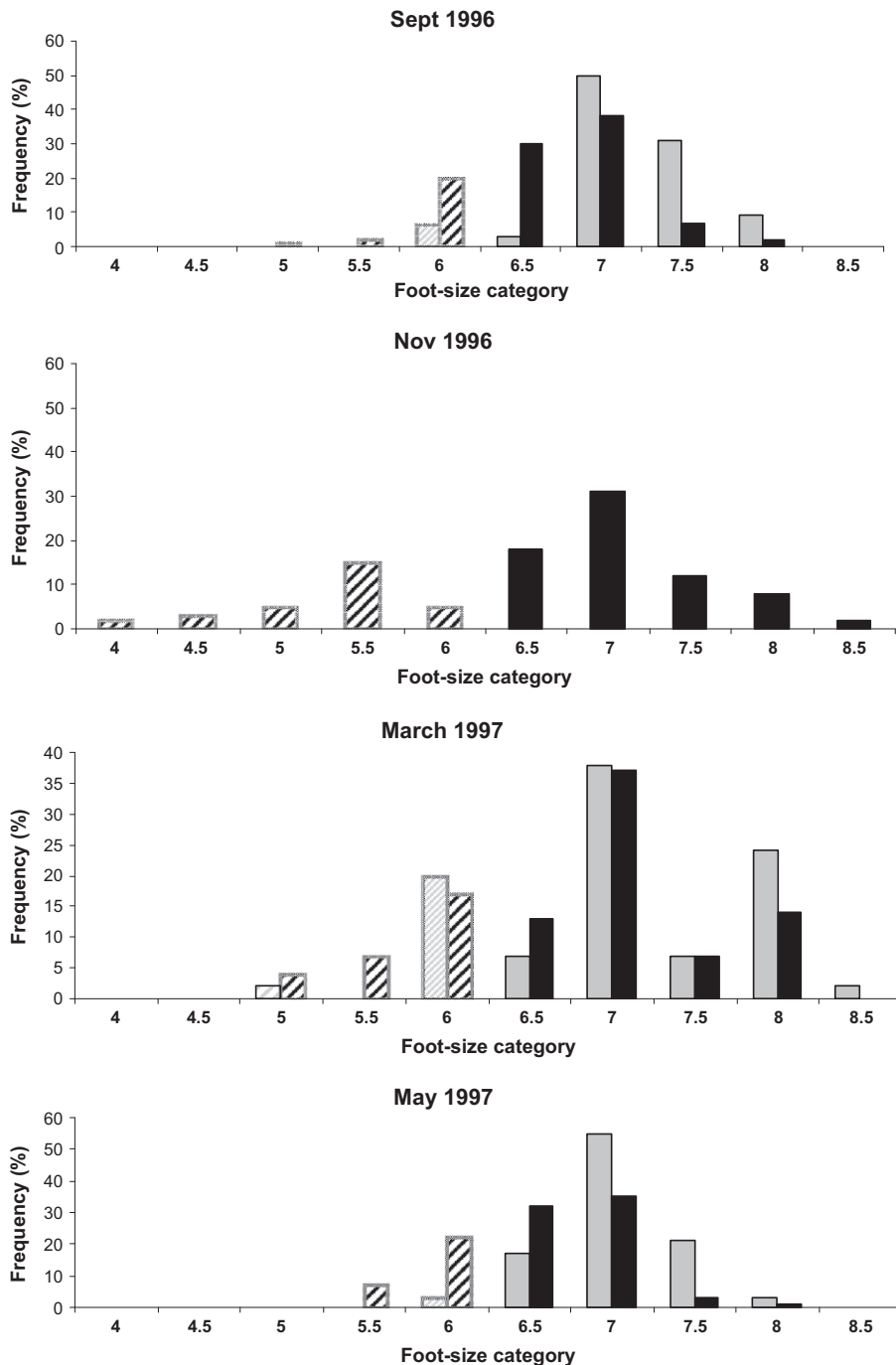
detected in the nil-treatment area in the November 1996 survey, while few wild dogs (three tracks of 5.0–5.5 cm) could be found in the baited area postbaiting (Fig. 2b). By March 1997, the PTI data suggest that the wild dog population in the baited area had numerically recovered to precontrol levels (prebaiting PTI value of 0.12 in September 1996 and 0.42 in April 1997). Because November to March is the nonbreeding/dispersal season for wild dogs (Corbett 2001), such a large increase in wild dog activity in March from near absence in November, strongly indicates immigration. The distribution of footprint length categories in March 1997 (Fig. 2c) suggests that at least 20% of the immigrants were 1996-born wild dogs (i.e. front footprint lengths of 6 and 6.5 cm), along with some relatively large adults ( $>8$  cm). By May 1997, the distribution of prints in footprint length categories shows little difference between baited and nil-treatment areas as the 1996-born pups were now approximately 10 months old and their footprints became indistinguishable from adult wild dogs (Fig. 2d).

## Baiting Effects on Wild Dog Functional Relationships

If baiting reduces population size (at least temporarily) and changes the size and age structures of wild dog groups, how might this affect predator-prey relationships?

### Methods

To investigate how changes to population size and age structure of wild dog groups produced by baiting (as shown in this paper) might affect the ability of wild dogs to handle large prey, the field records of Thomson (1992b) were re-examined. Thomson observed and recorded 272 interactions between collared wild dogs (and their companions) and kangaroos (Red Kangaroo *Macropus rufus* and Common Wallaroo *M. robustus*) in the Fortescue River area of Western Australia. The mean age of the known-age members of wild dog groups observed from an aircraft and identified by their collar transmitter frequencies (primarily), territories and pack associations, chasing or attacking kangaroos, were calculated from 205 wild



**Figure 2.** Proportion of the wild dog population in footprint length categories showing temporal changes in front footprint lengths of wild dogs measured in baited and nil-treated (black columns) areas in September 1996 (3 months after baiting), November 1996 (7 weeks after a subsequent baiting), March 1997 (6 months after baiting) and May 1997 (8 months after baiting). Juvenile footprint lengths (4–6 cm, hatched columns) eventually become indistinguishable from adults as they approach 12 months of age.

dogs captured and aged during the study of Thomson (1992a). Wild dogs, first captured as pups ( $n = 23$ ) or juveniles ( $n = 26$ ), were assumed born mid-year in the previous breeding season [wild dogs are monoestrous (Corbett 2001)]. Adults were aged from pulp cavity-tooth width ratios from X-ray images of their canine teeth ( $n = 88$ ) [method described in Thomson and Rose (1992) and further evaluated in Kershaw *et al.* (2005)] or, where they were not recovered at death, their age at first capture was based on tooth wear and general physical characteristics ( $n = 67$ ).

Mean group size of the wild dogs observed 'chasing' (pursuing kangaroos) or 'attacking' kangaroos was calculated from Thomson's (1992b) recorded observations, 37 of which resulted in attacks. Attacks were defined as an aggressive physical encounter and/or killing of the prey. Descriptive statistics and *t*-tests were used to compare mean group size and mean age characteristics of dingoes successfully or unsuccessfully chasing kangaroos.

## Results

The mean group size of wild dogs successfully chasing kangaroos that resulted in the kangaroo being attacked was 3.3 ( $\pm 0.2$ ) wild dogs (range 2–6). This contrasts ( $t = 6.31$ ,  $df = 240$ ,  $P < 0.00$ ) with a mean group size of 1.8 ( $\pm 0.1$ ) dingoes (range 1–10) for unsuccessful chases that did not result in the kangaroo being attacked. The mean age of the known-age dingoes observed attacking kangaroos was also significantly greater than the mean age of the dingoes observed chasing, but not attacking kangaroos [attacks: 3.0 ( $\pm 0.3$ ) years, range 1–7; chases: 1.9 ( $\pm 0.1$ ) years, range 1–11 years;  $t = 3.79$ ,  $df = 259$ ,  $P < 0.00$ ].

## Evidence of Functional Change in Baited Wild Dogs

This analysis investigated whether prey populations within baited and nil-treatment areas were comparable and remained so (i.e. responded similar to changes in seasonal conditions independent of baiting) or whether they diverged

over time indicating the predator–prey relationship had changed. Divergence alone does not indicate a functional change unless associated with a change in prey selection.

## Methods

Macropods (mostly Eastern Grey Kangaroo *Macropus giganteus* and Red-necked Wallaby *M. rufogriseus*) and Brush-tailed Possum (*Trichosurus vulpecula*) made up, respectively, 29% and 57% of the prey remains discovered in 653 wild dog scats collected on Mt Owen between 1994 and 1998 [details reported in Allen *et al.* (2012)]. Catling *et al.* (1997) compared alternative survey techniques and recommended track counts for detecting macropods and possums. PTI values for possums and macropods and their associated 95% confidence intervals were plotted against time, and a paired *t*-test was used to compare mean PTI values between treatments. Because there were fewer PTI surveys conducted at Strathmore and for fewer years and because there was different preferred prey species in wild dog diets, the data from Strathmore were not included in this analysis.

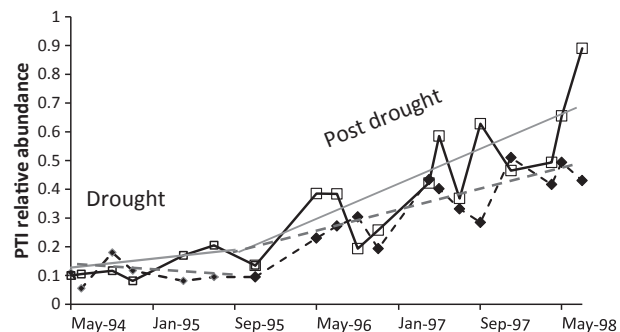
Multiple regression analyses comparing the slopes of linear relationships between PTI values (dependent variable) and date, treatment and season (independent variables) and their interactions were examined. Because time series data can potentially be confounded by positive autocorrelation (i.e. the PTI/population size at one survey point is potentially dependent on the PTI/population size at the previous survey), the Durbin–Watson

test of independence was applied to the residuals (Marques *et al.* 2013). Season, that is drought (May 1994 to November 1995 surveys) and postdrought when above-average rainfall was recorded (November 1995 to July 1998 surveys), was included to examine the effects of a substantial change in rainfall conditions and population trends.

## Results

Macropod and possum PTI data were not auto-correlated (D-W statistic of 2.28 and 2.17, respectively). Baited and nil-treatment area macropod PTI values were nearly identical when surveys first commenced in 1994 and remained similar during drought (near zero slope and mean PTIs not significantly different) but increased and diverged postdrought (Fig. 3) increasing substantially more in baited areas compared to nil-treatment areas. Mean PTIs were significantly different postdrought and over time between treatments, but not during the drought period, and multiple regression showed significant time, season, treatment and time\*season and time\*treatment effects (Table 1).

Possum PTI values were always higher in the nil-treatment area compared to the baited area (Fig. 4), and *t*-tests of mean PTI values and multiple regression analyses reflected this difference independent of season (Table 1). Linear trend lines fitted to possum PTI values (Fig. 4) were more or less parallel (with near zero slopes) during drought and postdrought periods between treatment areas and were not significantly different (i.e. not



**Figure 3.** PTI values and linear trend lines for macropods in baited (□ symbols) and nil-treatment (♦ symbols) areas during drought and postdrought.

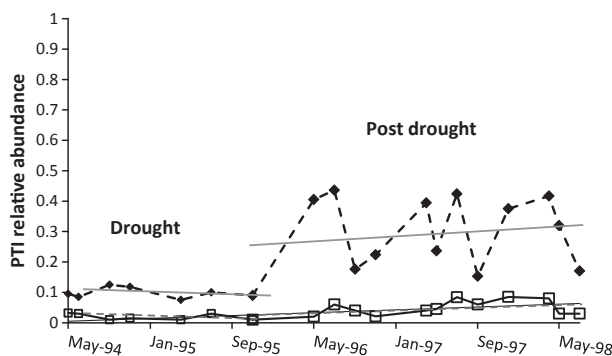
**Table 1.** Results of t-tests of PTI means and multiple regression analyses**Macropods**

<i>Two-tailed t-test of PTI means</i>					
	Mean	SE	<i>t</i> =	df	<i>P</i> =
All surveys					
Baited	0.35	0.05	−2.66	18	0.008
Nil-treatment	0.26	0.03			
Drought					
Baited	0.13	0.02	−1.05	6	0.166
Nil-treatment	0.10	0.01			
Postdrought					
Baited	0.48	0.05	−2.57	11	0.013
Nil-treatment	0.36	0.03			
<i>Multiple regression ANOVA</i>					
Source	<i>R</i> <sup>2</sup> =	df=	<i>F</i> =	<i>P</i> =	
Regression	83.25%	5	31.81	<0.001	
Season		1	6.79	0.014	
Time		1	22.41	<0.001	
Treatment		1	5.16	0.030	
Time*season		1	6.80	0.014	
Time*treatment		1	5.35	0.027	

**Possums**

<i>Two-tailed t-test of PTI means</i>					
	Mean	SE	<i>t</i> =	df	<i>P</i> =
All surveys					
Baited	0.04	0.01	−6.93	18	<0.001
Nil-treatment	0.23	0.03			
Drought					
Baited	0.02	0.00	10.05	6	<0.001
Nil-treatment	0.10	0.01			
Postdrought					
Baited	0.05	0.01	7.96	11	<0.001
Nil-treatment	0.31	0.03			
<i>Multiple Regression ANOVA</i>					
Source	<i>R</i> <sup>2</sup> =	df=	<i>F</i> =	<i>P</i> =	
Regression	75.77%	5	20.01	<0.001	
Season		1	0	0.992	
Time		1	0.78	0.385	
Treatment		1	8.06	0.008	
Time*season		1	0	0.965	
Time*treatment		1	8.73	0.006	

Time = date of survey; treatment = baited versus nil-treatment areas; season = surveys conducted during drought versus postdrought; and interactions between these variables.

**Figure 4.** PTI values and linear trend lines for possums in baited (□ symbols) and nil-treatment areas (♦ symbols) during drought and postdrought.

diverging). However, possum PTI values increased quickly in the nil-treatment area but not the baited area immediately post-drought yet remained relatively stable thereafter in both baited and nil-treatment areas.

**Discussion**

These data confirm that demographic differences in wild dog populations do occur as a result of baiting, as expected when some individuals are culled. Baiting programmes indeed reduce wild dog relative abundance, and although wild dog PTI values generally recover quickly after baiting, their age structures are different (Figs 1,2). Diverging trends in preferred prey PTIs subsequent to baiting (Figs 3,4) and correlation with greater calf losses where baiting has occurred (Allen 2014); (McGowan *et al.* 2014) suggest that these social changes and demographic differences can affect the way wild dogs interact with prey. Thomson's data show that larger and more mature wild dog groups are required to efficiently handle large prey. Wild dog populations postbaiting could therefore be less efficient at preying on large, difficult-to-catch species like kangaroos and are more dependent on easy-to-catch species like possums [see discussion of this in Allen *et al.* (2014)]. When preferred prey populations decline during a drought and large adult kangaroos are the alternative, wild dog groups comprised of fewer, younger and less experienced individuals would probably be forced to select less preferred prey. This could explain why in the study of Allen (2014), calf loss correlated with drought in baited areas but not in adjacent nil-treatment areas and why McGowan *et al.* (2014) found a significantly higher mean lactation failure on properties whose owners considered wild dogs impacted on their livestock and baited compared to those owners who did not consider wild dogs to be a problem and did nothing to control them (11.81% and 6.29%, respectively).

There is little difference in size between adult sheep, kangaroos and newborn calves (body weights of ~50, 45–60 and 34–40 kg, respectively). Prey behaviour and the degree of risk each prey spe-

cies represents to the predator are important factors affecting prey selection (Mech 1988). The panicky fleeing behaviour of sheep (Allen & Fleming 2004) and kangaroos elicits a chase and attack response by wild dogs. Domestic sheep have no antipredatory defences of any consequence against wild dogs but kangaroos use size (Shepherd 1981), speed and stamina to avoid predation. When in water (Corbett & Newsome 1987; Purcell 2010) or backed against structures that prevent wild dogs from attacking from behind (Thomson 1992b), adult kangaroos will use their claws and powerful hind feet to defend themselves and will sometimes kill wild dog attackers. Cattle also have a variety of antipredatory behaviours that dissuade wild dogs from attacking calves. Adult cattle protect calves by aggressively charging at wild dogs and by keeping calves in nursery groups in the care of adult minders while their mothers are away (Allen 2014).

These data show that recolonised wild dog populations generally have adult-sized footprints (Fig. 2c) and, based on calibrations with known-age dingoes, they are mostly comprised of animals over 9 months of age with adult-sized footprints. Other studies show that dispersing wild dogs are mostly yearling females and yearling to 3-year-old males that disperse singularly or as small subgroups from fractured packs (Thomson *et al.* 1992; Fleming *et al.* 2001). 'Yearling' also corresponds to an age when domestic dogs display excessive activity and are naturally inclined to problem behaviours (Wells & Hepper 2000). Given that recolonised wild dog populations are mostly from this age group [(Thomson *et al.* 1992) and this study] and assuming they exhibit similar activity levels to domestic dogs at this age, a combination of unrestrained activity, inexperience at group hunting and necessity (hunger) probably increases the likelihood of wild dogs harassing calves. Torn ears and tails on calves [i.e. 'bitten cattle', reported by Hewitt (2009) to make up 10% of the economic loss caused by wild dogs] indicate that many calf attacks are unsuccessful.

Switching between prey species is thought to increase stability of population

fluctuations and attenuate the impact that predators have on lower trophic levels (Choquenot & Forsyth 2013; Allen *et al.* 2014). These empirical results support the model predictions of Choquenot and Forsyth (2013) that kangaroo populations would primarily be limited by bottom-up factors during drought and top-down effects (i.e. predation) in flush (post-drought) seasons and that baiting wild dogs would theoretically decouple the top-down effects in flush seasons potentially leading to over-abundant kangaroo populations (Fig. 3 postdrought).

### Implication for Future Management

Wild dogs are likely to regulate (Pople *et al.* 2000) or limit kangaroo populations (Caughley *et al.* 1980), species that are major contributors to total grazing pressure and at times over-grazing (Wilson 1991). The role that wild dogs could play in biodiversity conservation and sustainable pasture management for rangeland livestock production is recognised but has received little attention and should be investigated further (Freudenberger *et al.* 1999; Johnson *et al.* 2007; Wicks & Allen 2012).

Assuming a linear or strong positive relationship between wild dog numbers and their impact on calves (which underlies why some beef producers control wild dogs), one could conclude that wild dog baiting programmes were generally effective if short-term reductions in wild dog numbers (i.e. spoor or PTI values) were the sole criteria for measuring 'efficacy'. Measured against reductions in impact (predation loss of calves), however, baiting is seldom effective because:

- 1 Predation loss infrequently occurs in rangeland beef cattle when more preferred prey are available (Eldridge *et al.* 2002); (Burns *et al.* 2010); (Allen 2014).
- 2 Ordinarily, wild dog populations have numerically recovered from baiting programmes before calving commences or, wild dog populations recover over summer when most calves are small and vulnerable [this paper and Bortolussi *et al.* (2005)] and,

- 3 Baiting appears to change the age structure and group size of recolonised wild dog populations making them more likely to be less efficient hunters of difficult-to-catch prey and more prone to harass calves [Allen (2014) and this paper].

Large-scale coordinated baiting of areas much greater than 200 000 ha [the area baited in the study of Allen (2014) that had the greatest and most frequent predation loss], biannual baiting or baiting at the commencement of calving could theoretically address the issue of recolonisation during calving. However, these approaches do not change the more general findings that baiting can change the functional role of wild dogs; wild dogs could be key to limiting kangaroo numbers; and predation of calves occurs infrequently. Changing the timing of control programmes to those months when calving predominantly occurs and when predation is likely may reduce wild dog numbers and calf loss during critical (drought) periods. Otherwise, the potential indirect benefits of wild dogs to pasture productivity and biodiversity conservation through their impact on kangaroo populations could likely outweigh the infrequent negative impacts unmanaged wild dogs can have on rangeland beef cattle.

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