KANGAROO-VEHICLE COLLISIONS IN AUSTRALIA'S SHEEP RANGELANDS, DURING AND FOLLOWING DROUGHT PERIODS

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The effects of roads on wildlife behaviour and ecological function are poorly known in arid Australia. The most obvious impact is roadkill from wildlife-vehicle collisions. Therefore we collected statistics on kangaroo-vehicle collisions, investigated the causal factors of these collisions, and related roadkill mortality to the population structure, size and distribution of four kangaroo species in two intensive six month studies during and following drought. The research was conducted along a 21.2 km sealed section of the Silver City Highway between Broken Hill and Tibooburra that passes through the University of New South Wales (NSW) Arid Zone Research Station at 'Fowlers Gap' in north-western NSW. The rate of roadkill was higher during drought (20.8 roadkills month^{-1}) than non-drought (2.6 roadkills month^{-1}). Affected species were red kangaroos (*Macropus rufus*), euros (*Macropus robustus erubescens*), western grey kangaroos (*Macropus fuliginosus*) and eastern grey kangaroos (*Macropus giganteus*). During drought, *M. fuliginosus* and *M. giganteus* were killed in lower proportions than their proportion in the source population, otherwise species were killed in proportion to their density along the road. There were no sex biases but male *M. r. erubescens* were much more likely to be beside the road than females and thus were killed more often during drought. The majority of roadkills were young individuals around 2 years old. Curves and stockraces along the road significantly increased the likelihood of roadkills. Likewise the frequency of roadkills was a function of the kangaroo population density along the road, night time traffic volume, low rainfall and higher vegetation cover and greenness along the road relative to surrounding areas. We evaluate the relationships between these causal factors and kangaroo-vehicle collisions, and discuss the possible effects of these collisions on kangaroo population structure under drought and post-drought conditions.

Key words: kangaroo-vehicle collisions, roadkill, mortality, demography, drought, road ecology, arid zone.

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ROADS present a difficult management problem for decision makers balancing the needs of creating an efficient transport network with the need to protect the environment and wildlife. Roads can have some positive outcomes for wildlife, acting as wildlife 'corridors' between previously fragmented areas (Bennett *et al.* 1994; Allem 1997; Fortin and Arnold 1997), but more often have negative consequences (Forman and Alexander 1998; Trombulak and Frissell 2000; Forman *et al.* 2003).

A significant detrimental effect of roads on wildlife is the high incidence of collisions between wildlife and motor vehicles. These usually cause the death of the animal, and the driver and/or passengers may suffer from stress, anxiety, injuries and the costs of motor vehicle damage. In many countries, research has been conducted on the causes and patterns of wildlife-vehicle collisions, the costs of collisions on humans and wildlife, and the effectiveness of various abatement technologies used to reduce the frequency of collisions (Drews 1995; Groot Bruinderink and Hazebroek 1996; Hubbard *et al.* 2000; Huijser and Bergers 2000; Clevenger *et al.* 2001) but few studies (Mumme *et al.* 2000; Hels and Buchwald 2001) have investigated the effects of roadkill mortality on the viability of wildlife populations.

In Australia, wildlife-vehicle collisions are known to be a major cause of mortality for many native animals (Brown *et al.* 1986; Pergolotti 1995; Newell 1999; Scott *et al.* 1999; Jones 2000; Kanowski *et al.* 2001; Koenig *et al.* 2002), and can incur considerable costs to humans when larger animals, such as kangaroos, are involved (ACT Kangaroo Advisory Committee 1997). Despite this, relatively little is known of the causes, patterns, and effects of wildlife-vehicle collisions on populations and their demography. This paucity of knowledge is compounded by the conflicting results obtained by past studies, particularly those focusing on kangaroos-vehicle collisions, which omitted key potential causal factors, such as traffic volume and speed, the structure of the roadside verge, and the surrounding population density from analysis, and were comprised of irregular sampling effort and small sample sizes (Coulson 1982, 1989, 1997; Lintermans and Cunningham 1997, Brown 2001). As a result, reducing the frequency of collisions through the use of mitigation measures has so far proven difficult and ineffectual (Lintermans 1997; Bender 2001).

Long-term investigations of wildlife-vehicle collisions in Australia have long been overdue. We focus on kangaroo-vehicle collisions in the sheep rangelands of southern Australia, an area which is subject to highly variable rainfall. We report on the spatio-temporal patterns and causes of kangaroo-vehicle collisions along a road representative of this area, and their potential effects on species populations and demography. We compared these patterns, causes and effects of roadkills during drought with a subsequent post-drought period to evaluate the relative impact of extremes in environmental conditions.

MATERIALS AND METHODS

Study area

The study was conducted at the University of New South Wales (NSW) Arid Zone Research Station, 'Fowlers Gap', (31° 05' S, 141° 43' E) in north-western NSW, Australia. 'Fowlers Gap' is located on the Silver City Highway approximately 110 km north of Broken Hill. The station is typical of Australia's southern sheep rangelands and covers an area of 39,200 ha. The climate at 'Fowlers Gap' is dry, mildly arid, with hot summers and mild winters. Mean annual rainfall (241 mm) is erratically distributed throughout the year; however, winter rains are generally more reliable than summer rains and have a greater impact on vegetation growth (Bell 1973). The topography is diverse as the western section of the station includes part of the Barrier Ranges (180 - 240 m), while the eastern section consists of alluvial floodplains (140 - 170 m) (Mabbutt 1973). The dominant vegetation in the areas of higher relief is low woody perennial shrubs (< 1 m), chiefly of the family Chenopodiaceae. The floodplains are dominated by various tussock grasses (~ 0.5 m) (Burrell 1973). Data on kangaroo-vehicle collisions were collected along a 21.2 km stretch of the Silver City Highway that traverses both the high and low terrain of the station.

Numbers, species, sex and age of roadkills

Data for roadkilled kangaroos were collected in two periods: drought – 24 weeks between January and June 2002, and post-drought – 20 weeks between February and June 2003. The 21.2 km highway section was checked every second day for roadkilled kangaroos from a motor vehicle travelling at low speed. For each roadkill, the date, location (Garmin GPS II), species and sex were recorded. When present and relatively undamaged, the heads of roadkilled kangaroos were collected for an estimation of age by molar progression (after Kirkpatrick 1965).

Spatial data

The road was divided into 200 m section and scored for features that included water sources (ephemeral creeks, water drainage channels, and natural and artificial water sources), man-made obstructions to kangaroo movement (stockraces and road cuttings), and areas of low driver visibility (curves, and dense shrubs lining the road). The frequency of roadkills occurring within each type of feature or the residual sections of the road was determined.

Temporal data

Population structure, distribution and density

Day (commencing at dawn) and night (2 h after sunset) counts of kangaroos were conducted weekly within 24 h of each other. Both counts were conducted along two transects: one along the road and the other along a parallel 7.3 km dirt track located approximately 500 m from the road (hinterland transect). Day counts most accurately estimated the size and composition (species and sex) of the source population. Night counts estimated the numbers and species of kangaroos within the driver's field of view and thus at immediate risk of a kangaroo-vehicle collision. To determine whether kangaroos aggregated along the road, the hinterland transect was compared to a parallel section of the road transect. Due to logistical/weather constraints, only counts for the last four months of both sampling periods were compared.

Population densities were estimated using a line or strip-transect method (Buckland *et al.* 2001). For the day counts, the angle and radial distance of each kangaroo or the centre of a group (cluster within 50 m of each other) from the transect were estimated. The data were truncated at a perpendicular distance of 185 m from the transect and a half-normal cosine function was fitted separately to the drought and post-drought data sets with post-stratification by week and species using Distance V4.0. For the night counts, the abundance of each kangaroo species within a fixed strip width of 20 m either side of the transect was estimated and density calculated from the area of the strip. Both day and night surveys were conducted by driving a standard vehicle (Nissan Navara 2.7 L diesel 4x4 utility) at about 25 km h^{-1} and scanning for kangaroos.

Traffic

In the drought sampling period, traffic along the highway was recorded using a time lapse video recorder (Panasonic AG-6040 at 72 h per VHS180 video tape) that received images of the road transmitted from a video camera (Monochrome M-202 Allthings P/L) viewing a section where vehicles slowed to negotiate a causeway across a usually dry creek. The video tapes were reviewed in low speed (0.25 playback), and the date and time of day were recorded for every vehicle type. For the post-drought sampling period, traffic data were logged using a traffic monitor (Metrocount Vehicle Classifier System 5600 series) that recorded the time, date and speed of vehicle passage, and classified the vehicles into 12 type/size classes. For both sampling periods, daytime traffic was defined as all traffic between two hours after sunrise and two hours before sunset, and night-time traffic was the residual (from two hours before sunset to two hours after sunrise).

Weather

Data on hourly temperature, humidity, wind speed and direction, barometric pressure and rainfall were collected via an automatic weather station (WM-918) located at the 'Fowlers Gap' homestead for both sampling periods.

Vegetation

At each roadkill site, the cover, height and greenness of roadside vegetation were estimated along replicated 30 m transects orientated perpendicular to the direction of the road. Plants were classified as grasses, forbs, copperburrs, round-leafed chenopods (bluebushes), or flat-leafed chenopods (saltbushes) as used in kangaroo dietary analyses (Ellis *et al.* 1977; Dawson and Ellis 1996). A 30 m tape was laid across the vegetation and for each plant type, % cover (proportion intersected by left edge of tape), height to the nearest 5 cm, and % greenness were recorded in each metre interval. The mean height and greenness within a metre were weighted by cover if more than one stand of a plant type was measured. Mean values across replicates were calculated to represent a site. Grasses, forbs, and copperburr were pooled into a single 'pasture' category for analysis.

Measurements of plant greenness and the number of replicates performed at each site differed slightly between the drought and post-drought sampling periods, with three categories of greenness (dry 0%, ≤ 50%, or > 50% green) used for drought periods compared with six categories of greenness (dry 0%, 1-20%, 21-40%, 41-60%, 61-80%, 81-100% green) for post-drought periods, and four replicate transects used during drought (two on each side of the road, 25 m apart) compared with two replicate transects during post-drought (one on each side of the road). The different methodologies were adopted to increase the precision of vegetation measurements in each sampling period (plant greenness was more variable during post-drought compared to drought, showing more stages of growth and senescence, and vegetation cover was lower during drought compared to post-drought, requiring more replicate transects to sample vegetation).

Statistical analyses

For the roadkill data, chi-square tests were used to compare the proportions of the species and sexes found with their respective proportions in the source population within sampling periods. Exact tests with 10,000 Monte Carlo simulations to account for the small post-drought sample size (SPSS for Windows 11.0) were used to compare the species, sex and age proportions of roadkilled kangaroos between sampling periods. For the analysis of the influence of road features on the frequency of collisions within sampling periods, chi-square tests were again used, with exact tests used for comparisons between sampling periods. For the vegetation data, Friedman tests were used to determine differences in cover, height and greenness between metre intervals within sampling periods, with Dunn's Test used to reveal where differences lay. Only differences between the first metre interval to the other metres were considered. Comparisons of vegetation between sampling periods were made with *t*-tests, using the mean values of the vegetation variables calculated over entire transect lengths. Comparisons between sampling periods for vehicle types and traffic volume were made using a chi-square test and *t*-test respectively. Comparisons of kangaroo population densities within and between sampling periods were made by examining overlap in their upper and lower confidence intervals (95%) estimated by Distance 4.0.

The relative influences of temporal factors – average weekly maximum temperatures, days since last rain, cumulative rainfall in the last 30 days, average weekly daytime and night-time kangaroo densities along the road, and average weekly night-time traffic volume – on the weekly frequencies of roadkills during drought were modelled using a stepwise multiple regression. The daily probability of a roadkill during drought was estimated from daily traffic using logistic regression (the road kill data was converted to binary data, where 1 = one or more kills and 0 = no kills for each day). Due to the small post-drought roadkill sample size, the influences of temporal factors on roadkill frequencies could not be independently modelled. Therefore the fit of the observed weekly post-drought roadkill frequencies with those expected from the drought model was tested using chi-square analysis. To obtain expected daily roadkill frequencies from the logistic model, the probabilities of a roadkill occurring were first calculated using median values in 33 defined traffic categories (0-5 vehicles, 6-10 vehicles, …….. 161-165 vehicles per day) and these probabilities were used to calculate expected frequencies. New models encompassing both sampling periods were constructed to include the effects of broader environmental conditions on roadkill frequencies.

RESULTS

Rainfall

The drought sampling period followed a 3-year period of below average rainfall (UNSW 2002). Eleven rainfall events, totalling 35.8 mm of rain, occurred in the drought period. This amount was below the 5th percentile of the 36 year record indicative of severe drought as categorised by the Australian Bureau of Meteorology. Of the rainfall events, only one (24 mm on 22nd January 2002) was significant enough to induce plant germination and growth. Throughout the remainder of the year, 26 mm of rain fell, bringing the total rainfall for 2002 to 61.8 mm. There were also 11 rainfall events during the post-drought sampling period but the total of 115 mm was in the 70th percentile of the previous 36 year record. Most events had an effect on vegetation growth with three measuring over 20 mm (26 mm on the 21st February, 25 mm on the 22nd February, and 24 mm on the 13th May).

Kangaroos in the source population

The average daytime kangaroo density along the road during the drought was around 10-fold that of the post-drought period (Fig. 1). This was consistent with aerial surveys of the Broken Hill kangaroo management block where red (*Macropus rufus*) and grey (*Macropus giganteus* and *M. fuliginosus*) kangaroo densities dropped by 48% and 73% respectively between June 2002 and June 2003 (NSW National Parks and Wildlife Service). Species composition was similar between sampling periods, with *M. giganteus* and *M. fuliginosus* forming more of the kangaroo population (50.3% in drought and 66.5% in post-drought) than *M. rufus* (41.8% in drought and 39.2% in post-drought) or euros (*Macropus robustus erubescens*) (10.5% in drought and 1.8% in post-drought). Sex was reliably determined for *M. rufus* and *M. r. erubescens*. Females were the predominant sex amongst *M. rufus* in both sampling periods (72.5% in drought and 60% in post-drought) whereas males were the predominant sex in *M. r. erubescens* during drought (94.6% males).

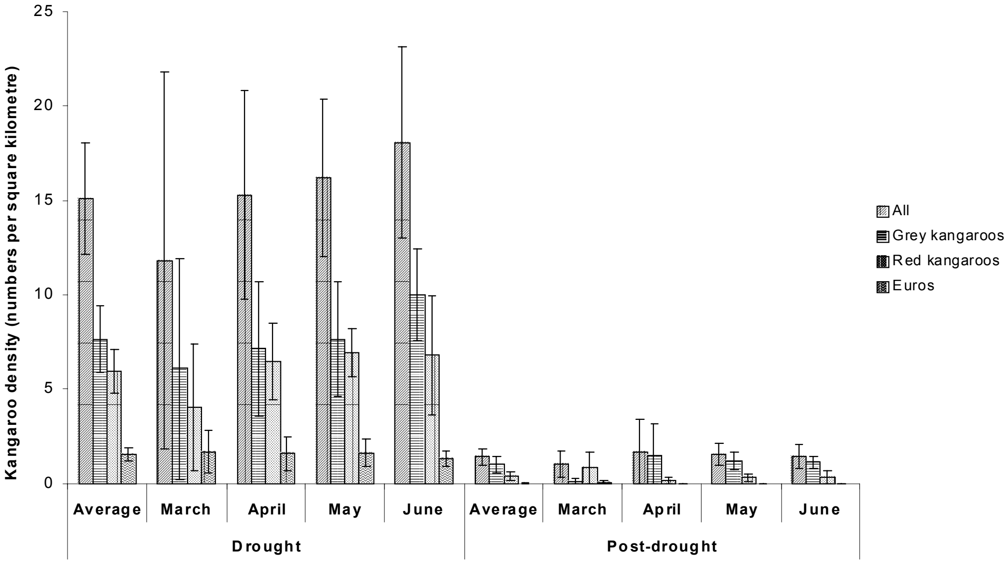

Fig. 1. Mean daytime total kangaroo and individual species densities along the road over time during drought and post-drought periods. Error bars symbolise upper and lower 95% confidence limits.

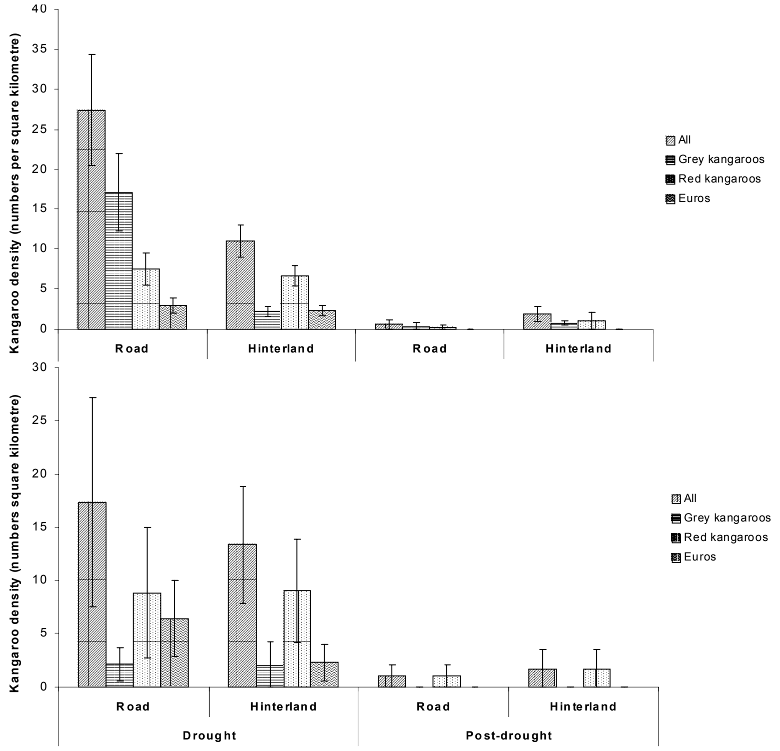

Fig. 2. Mean daytime (a) and night-time (b) total kangaroo and individual species densities along the road and hinterland during drought and post-drought periods. Error bars symbolise upper and lower 95% confidence limits.

Like the daytime estimates, average night-time kangaroo densities along the road were significantly higher during drought (mean ± 95% CI, 14.1 ± 5.9 kangaroos km^{-2}) compared to post-drought (0.8 ± 0.5 kangaroos km^{-2}). The night-time estimates were not significantly different to those estimated during the day in either sampling period (Wilcoxon signed ranks test: $Z = -0.17$, $n = 17$, $p = 0.88$ for drought, $Z = -1.73$, $n = 18$, $p = 0.08$ for post-drought). However, *M. rufus* were proportionally more numerous at night than the day (drought 58.5% vs 41.8%; post-drought 91.7% vs 39.2%), as were *M. r. erubescens* in drought (33.6% vs 10.5%) but not post-drought (0% vs 1.8%). Grey kangaroos formed a small proportion of the night-time population relative to daytime (drought 7.8% vs 50.3%; post-drought 8.3% vs 66.5%).

Distribution of kangaroos

The daytime density of kangaroos was significantly higher on the road than the hinterland track during drought, mainly due to the higher numbers of grey kangaroos present along the road (Fig. 2a). In contrast the daytime kangaroo density during the post-drought period did not differ significantly between the road and hinterland track but tended to be higher along the latter (Fig 2a). There were no significant differences in kangaroo densities between the transects in either sampling period at night (Fig. 2b), except for *M. r. erubescens,* which had a significantly higher density along the road than the hinterland during drought (Fig. 2b).

Traffic

The average daily traffic was not significantly different between the sampling periods (mean ± SE, 62.5 ± 2.7 vehicles day^{-1}, range = 32 - 152 in drought; 56.8 ± 2.2, range = 26 - 165 in post-drought) ($t_{113} = 1.62$, $p = 0.11$). Light vehicles (sedans, utilities, four-wheel drives) predominated (73.9% drought; 85.0% post-drought) over medium and heavy vehicles (e.g., trucks and semi-trailers). There was a trend for proportionally higher numbers of medium and heavy vehicles during the drought period ($\chi^2 = 3.749$, $df = 1$, $p = 0.08$) which was probably related to livestock and feed movements. There was also a trend for higher vehicle movements at night in drought than post-drought (28.5 ± 2.0 vs 23.5 ± 1.6 vehicles night^{-1}; $t_{176} = 1.91$, $p = 0.06$).

Vegetation

During drought, pasture cover and greenness were significantly higher at the road edge compared to most metre intervals out to 30 m from the road

(Friedman $_{(1,29)}$ = 35.66, $p < 0.001$ and Friedman $_{(1,29)}$ = 16.79, $p < 0.001$, respectively; mean ranks compared with Dunn's test). Pasture height did not change significantly with increasing distance from the road in drought and neither cover, greenness or height differed significantly with distance from the road post-drought. However, along the entire 30 m transect mean pasture cover and greenness were significantly higher and height significantly lower in the post-drought than the drought period (mean % cover = 38.5 ± 0.8 vs 7.0 ± 0.3, t_{29} = -33.6, $p < 0.001$; mean % greenness = 55.5 ± 1.3 vs 44.8 ± 1.2, t_{29} = -6.5, $p < 0.001$; mean height = 0.75 ± 0.0 cm vs 0.95 ± 0.045 cm, t_{29} = 3.8, $p = 0.001$).

Numbers, species, sex and age of roadkills

A total of 125 roadkilled kangaroos were found during the drought sampling period which averaged about 20.8 kangaroos killed per month. The majority were *M. rufus* (Table 1). In contrast, only 13 roadkills were found during the post-drought sampling period (2.6 roadkills per month), and the majority were grey kangaroos (Table 1). The frequency distribution of species killed differed significantly between periods (exact test: $\chi^2 = 60.8$, $df = 2$, $p < 0.001$). Likewise the post-drought period showed a significantly greater female bias compared to drought (drought: females = 53%, males = 47%, post-drought: females = 73%, males = 27%; exact test: $\chi^2 = 8.66$, $df = 1$, $p = 0.005$).

In the drought, the proportions of species killed differed significantly from their source proportions as estimated from day counts along the road ($\chi^2 = 50.9$, $df = 2$, $p < 0.001$), where *M. rufus* and *M. r. erubescens* were killed in higher numbers than expected (*M. rufus*: observed: 74, expected: 49, and *M. r. erubescens*: observed: 37, expected: 13) and grey kangaroos killed in lower numbers than expected (observed: 14, expected: 63). However, no significant difference was found if compared with the night-time densities along the road ($\chi^2 = 0.54$, $df = 2$, $p > 0.5$). No sex biases were found for *M. rufus* or *M. r. erubescens* when compared to the respective proportions of males and females in the source population during drought. During post-drought, no species or sex bias (*M. rufus*) was found when compared to their respective proportions in the source population.

Roadkilled kangaroos during drought were aged between one and 16 years (median = 3, mode = 2, Fig. 3). Over half of the kills consisted of young kangaroos, with one, two and three year olds making up 11.5%, 34.6% and 15.4% of kills respectively. During the post-drought sampling period, individuals were aged between two and five years (median = 3, mode = 2), with one, two and three year olds making up 0%, 45% and 18% of kills. No significant differences in the ages of roadkilled kangaroos were found between sampling periods (exact test: χ^2 = 10.74, $df = 11$, $p = 0.51$).

Species	Total		Females*		Males*	
	Drought (n = 125)	Post-drought (n = 13)	Drought (n = 58)	Post-drought (n = 8)	Drought (n = 51)	Post-drought (n = 3)
M. rufus	59	23	66	100	34	0
M. giganteus/fuliginosus	11	62	64	75	36	25
M. r. erubescens	30	15	26	0	74	100

Table 1. Percentage of species and sex of roadkills during drought and post-drought. * Excludes individuals where sex was indeterminate due to condition of carcass (16 in drought and two in post-drought).

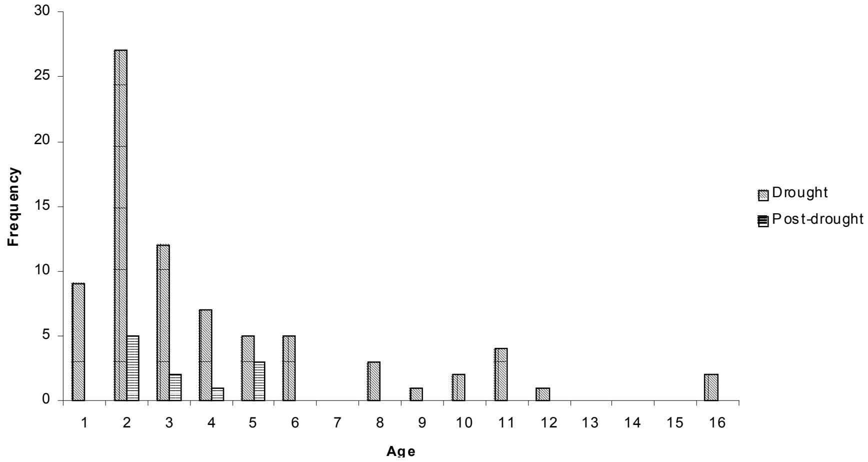

Fig. 3. Age distribution of roadkilled kangaroos during drought and post-drought periods.

Spatial patterns of roadkills

Significantly higher proportions of kills were associated with curves (32% and 15.4%), creeks (3.2% and 0%), drainage areas (12% and 7.7%), cuttings (14.4% and 7.7%), stockraces (5.6% and 7.7%) and artificial water sources (4.6% and 0%), and lower proportions associated with areas of dense shrub (4.8% and 23.1%) during drought compared to post-drought (exact test: $\chi^2 = 31.048$, $df = 6$, $p < 0.001$). During drought, significantly higher numbers of roadkills were associated with curves than expected ($\chi^2 = 12.13$, $df = 1$, $p < 0.001$) and there was a trend for higher numbers of roadkills in stockraces ($\chi^2 = 3.59$, $df = 1$, $p = 0.06$). While no road features were significantly associated with roadkills during post-drought, some trends were consistent with the larger drought sample (e.g., stockraces: observed = 7.7%, expected = 2.8%).

Temporal patterns of roadkills

During drought, the frequency of roadkills per week was positively associated with average weekly night-time traffic volume ($R^2 = 0.88$, $\beta = 0.94$, $F_{1,11} = 79.1$, $p < 0.001$). The equation ($y = 0.245x$) was used to predict the frequency of roadkills in the post-drought period. The relationship with average night-time traffic volume in drought significantly over-estimated the frequency of roadkills post-drought ($\chi^2 = 23.61$, $df = 15$, $p = 0.05$). The new model of the relationship between weekly roadkill frequency and average night time traffic incorporating both environmental conditions (Fig 4) confirmed a significant positive relationship ($\beta = 0.41$, $F_{1,16} = 5.12$, $p = 0.03$, regression equation: $y = 0.122x$) but explained less of the variance ($R^2 = 0.17$) than the drought model. High rainfall (> 20 mm) in the previous 30 days significantly reduced roadkill in drought ($\beta = -0.81$, $p = 0.01$) relative to low rainfall (< 10 mm) but no such trend was found in post-drought conditions (Fig. 5).

Logistic regression was used to model the probability of a roadkill during drought as a function of daily traffic volume (Classification percentage = 65.2; traffic variable: Wald = 10.8, $df = 1$, $p = 0.001$, exp (B) = 1.06, constant: Wald = 12.7, $df = 1$, $p << 0.001$, exp (B) = 0.04). The resulting equation $P(\text{roadkill}) = 1/(1 + e^{3.3\text{-}0.06*\text{Traffic volume}})$ was used to predict the frequency of roadkill in 33 traffic categories in post-drought. The drought model significantly overestimated roadkill frequencies ($\chi^2 = 36.79$, $df = 31$, $p = 0.007$). A new model combining data sets (Fig. 6), gave a significant fit (traffic variable: Wald = 5.2, $df = 1$, $p = 0.022$, exp (B) = 1.017, constant: Wald = 21.9, $df = 1$, $p < 0.001$, exp (B) = 0.113), but was not as good a predictor of roadkill as the original drought model (original model: $R_L^2 = 0.12$ and $R = 0.27$, model for both sampling periods: $R_L^2 = 0.024$ and $R = 0.12$). Broadening the range of environmental conditions resulted in a lower probability of a roadkill for a given traffic volume with an asymptote well above the maximum traffic volume recorded in either drought or post-drought samples.

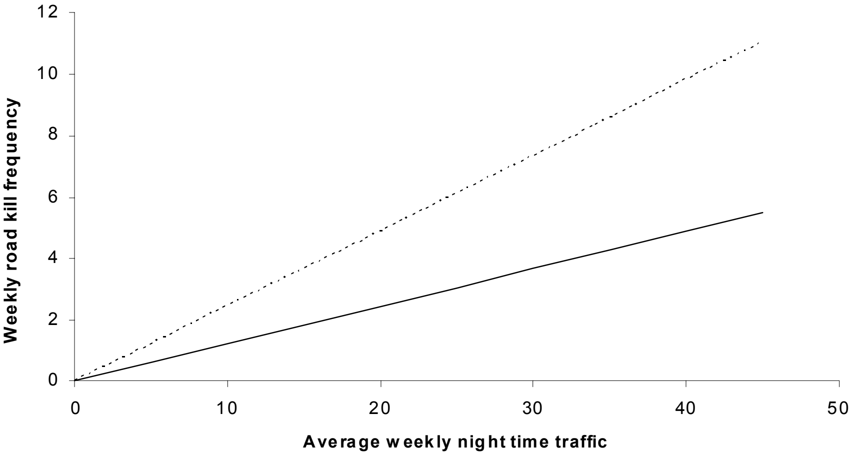

Fig. 4. Weekly roadkill frequency versus night time traffic (all traffic between two hours before sunset and two hours after sunrise) during drought (drought model) and over both environmental conditions (model for both sampling periods). Regression equations: drought model: $y = 0.245\,x$, model for both sampling periods: $y = 0.122x$. …… = Drought model, _____ = Model for both sampling periods.

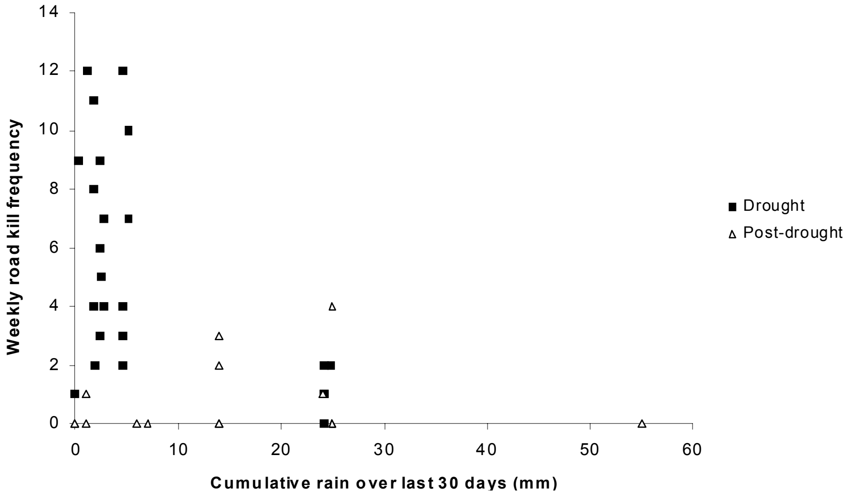

Fig. 5. Plot of weekly roadkill frequency versus cumulative rainfall over the last 30 days during drought and post-drought periods.

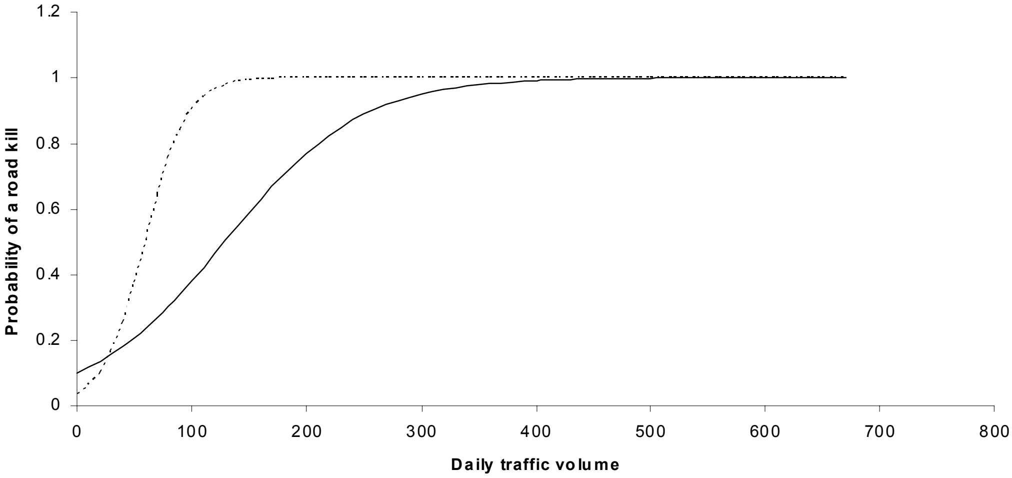

Fig. 6. Probability of a roadkill occurring against traffic volume during drought (drought model) and over both environmental conditions (model for both sampling periods). Regression equations: drought model: $y = 1/(1 + e^{3.3-5.1*x})$, model for both sampling periods: $y = 1/(1 + e^{2.2-0.02*x})$. …… = Drought model, ____ = Model for both sampling periods.

DISCUSSION

This study shows that environmental conditions play a key role in determining the patterns and frequencies of kangaroo-vehicle collisions. Understanding the relative influences of the various causal factors on collisions and how these factors change in different environmental conditions is therefore vital for future mitigation attempts. This is especially important in Australia where extreme and unpredictable weather conditions are the norm, fluctuating between cycles of drought and non-drought.

Our study showed that *M. rufus* and *M. r. erubescens* were more susceptible to being killed than grey kangaroos during drought, but that this was not the case directly following drought. These results may be attributed to both different diets and behaviour of the species, which would place them at different levels of risk relative to one another. *M. rufus* and *M. r. erubescens* are known to have extremely selective diets, taking in high proportions of grasses and forbs even when these plant types are limited (Dawson and Ellis 1994, 1996). At times of extreme food shortage, these species will move outside of their core habitats in search of forage, returning again when conditions improve (Clancy and Croft 1992; Dawson 1998). In contrast, grey kangaroos, particularly *M. fuliginosus*, are more generalist in their diets. They are able to take in browse in addition to pasture (Barker 1987; Norbury 1987), and are relatively sedentary, even when conditions are poor (Jarman and Taylor 1983; Arnold *et al.* 1992). During drought, the higher pasture cover and greenness along the road edge relative to areas further from the edge may have attracted higher numbers of *M. rufus* and *M. r. erubescens* to the road compared to grey kangaroos during their active foraging periods, placing them at higher risk of being involved in collisions. Another possible reason for the lower proportion of grey kangaroos killed may be due to these species' flight response behaviours towards approaching vehicles, as reported by Brown (2001), and towards risks in general (Jarman and Wright 1993). Early flight away from the road would reduce their susceptibility of being involved in a collision with an approaching vehicle. With the return of favourable conditions during post-drought, *M. rufus* and *M. r. erubescens* may have retreated to their core habitats, reducing their already low overall densities in this period along the road. Kangaroo species would then have been killed in similar proportion to their densities along the road.

We found no sex bias in roadkilled *M. rufus* or *M. r. erubescens* in either sampling period when compared to their proportions in the source population. This is consistent with Coulson (1997) who found no bias towards either sex in roadkilled *M. rufus*, with higher numbers of female kangaroos reflecting the predominance of females in the population. However, a strong male bias was found in *M. fuliginosus, M. giganteus* and swamp wallabies (*Wallabia bicolor*) in Coulson's (1997) study and in eastern grey kangaroos in Lintermans and Cunningham's (1997) study. The male biases were attributed to both the larger movement patterns of males, and the risky behaviour of male kangaroos relative to females. Male *M. r. erubescens* also have wider movement patterns than females (Clancy and Croft 1992) and as males dominated the *M. r. erubescens* population along the road during drought, they were killed much more frequently than the generally absent females.

The selective deaths of *M. rufus* and male *M. r. erubescens* during drought may have significant impacts on both the species composition of the area and on the population demographics of *M. r. erubescens*. Grey kangaroo populations have the potential of becoming more numerous in relation to other kangaroo species during and following drought periods, as these species may be at lower risk of being killed in a collision with vehicles by being relatively less common along the road at night. Grey kangaroos became proportionally more common in the roadside population post-drought. Selective male mortality in *M. r. erubescens* populations may reduce genetic variation and reproductive success if there are fewer males but there are likely to be 'surplus' breeding males in the population (Clancy and Croft 1992).

The pyramidal age distributions of kangaroo populations (Russell 1971; Norbury *et al.* 1994) were reflected in the age distributions of roadkilled kangaroos, indicating no bias towards any age class. Young individuals are more numerous but may be at proportionally greater risk due to the naivety of younger animals towards danger. The lack of one-year olds in the post-drought sampling period was most likely the result of the prolonged drought, which caused female kangaroos of all species to postpone reproduction.

The higher numbers of roadkills within curves is likely due to driver behaviour (less opportunity to swerve) in combination with reduced visibility in these areas. The similar trend for higher numbers of roadkills than expected within stockraces may be attributed to the fence along the road verge obstructing kangaroo movement away from the road and oncoming vehicles.

The volume of night time traffic was a strong predictor of the frequency of roadkills in drought but the relationship failed to accurately predict roadkill in the post-drought period. Likewise daily traffic volume was a better predictor of the probability of a roadkill in drought than post-drought. While there was a trend for higher mean night time traffic volumes during drought and for higher proportions of medium and heavy vehicles during drought compared to post-drought, these small differences were unlikely to explain the higher amount of variation in roadkill explained by traffic volume during drought compared to post-drought. More likely the density of kangaroos along the roadside plays a role (high in drought, low post-drought) but variation within either sampling period was insufficient to detect this.

The aggregation of kangaroos along the roadside in drought was most likely a function of the high cover of green pasture at the verge. This in turn was probably a function of rainfall (Noy-Meir 1973) as the frequency of roadkill significantly reduced with rainfalls of > 20 mm in the preceding 30 days. Under the latter conditions, green pasture was likely available in the hinterland. This relationship disappeared under the higher and more regular rainfall of the post-drought period. As we did not measure pasture characteristics in the hinterland further research will be necessary to support this hypothesis. Even so other studies suggest an aggregation at the roadside in drought. Coulson (1989) found roadkill frequencies of *M. giganteus* and *W. bicolor* were higher in drought and suggested that higher quality forage on the road verge relative to surrounding areas attracted high numbers of kangaroos to the road edge. Similarly, Newmark *et al.* (1996) found higher numbers of roadkills during dry periods in Tanzania.

Conclusions

Roadkills are an undisputable source of mortality for kangaroos, with *M. rufus* and *M. r. erubescens* more susceptible to being killed than grey kangaroos at our site. Thus mortality from collisions with vehicles may have community level effects amongst sympatric kangaroo species. Furthermore the behaviour that the arid-adapted species have evolved to cope with drought enhances their 'predation risk' from inattentive drivers. The demographics of *M. rufus* populations are unlikely to be affected by roadkills as no bias towards any particular sex or age class was found; however the demographics of *M. r. erubescens* populations may be disproportionately skewed by roadkills as the behaviour of males may place them at greater risks of collisions than females. The viability of kangaroo populations may be more vulnerable during periods directly following severe droughts compared to during droughts as the impacts of mortality such as roadkill are likely to be proportionally greater on smaller populations. However, individuals may disperse away from the road with higher and more regular rainfall and thus risk is lessened. Efforts to reduce the frequency of roadkills should concentrate on road design, especially targeting the higher risks associated with curves, the trapping effect of stockraces and pasture conditions along road verges. The generality of any relationships between road ecology and roadkill needs to be tested under a range of environmental conditions. We have clearly shown that models constructed during a high incidence of roadkill in drought are poor predictors of post-drought roadkill frequencies.

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