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Frequency and causes of kangaroo–vehicle collisions on an Australian outback highway

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Abstract. Kangaroo–vehicle collisions are frequent on Australian highways. Despite high economic costs, detrimental effects on animal welfare, and potential impacts on population viability, little research has been done to investigate the impact of road mortality on kangaroo populations, where and why accidents occur, and how the collisions can be mitigated. We therefore collected data on species (*Macropus rufus*, *M. giganteus*, *M. fuliginosus*, *M. robustus)*, sex and age of kangaroos killed on a 21.2-km bitumenised section of outback highway over 6 months in far western New South Wales, Australia. The spatial and temporal distribution of road-killed kangaroos was investigated in relation to the cover and quality of road-side vegetation, road characteristics, the density of kangaroos along the road, climatic variables and traffic volume. A total of 125 kangaroos were found killed on the road at a rate of 0.03 deaths km^{-1} day^{-1}. Grey kangaroos of two species (*M. giganteus*, *M. fuliginosus*) were under-represented in the road-kill sample in comparison with their proportion in the source population estimated during the day. No bias towards either sex was found. The age structure of road-killed kangaroos was similar to age structures typical of source kangaroo populations. Road-kills mainly occurred in open plains country. In road sections with curves or stock races, road-kill frequencies were higher than expected. Greater cover and greenness of roadside vegetation at the verge probably attracted kangaroos to the road and variation in this vegetation affected the spatial distribution of road-kills. The temporal distribution of road-kills was positively correlated with the volume of night-time traffic. The probability of a kangaroo–vehicle collision increased exponentially with traffic volume. Results are discussed in relation to the potential for mitigation of kangaroo–vehicle collisions.

Introduction

In rural Australia the most prominent victims of the numerous animals killed each year in collisions with motor vehicles are the members of the Macropodoidea (kangaroos, wallabies and rat-kangaroos), especially the large kangaroos in the genus *Macropus*. Collisions with vehicles take a substantial toll on kangaroo populations but this has been inadequately investigated and quantified. Human costs (distress, injury or death) are also high (Abu-Zidan *et al*. 2002) and vehicles are likely to carry some damage if not heavily armoured against such impacts. The probability of secondary accidents with scavengers (foxes, wedge-tailed eagles, ravens and crows, and feral pigs) is high but not quantified. The cost of collisions from impacts with medium-to-large mammals, most of them kangaroos, reaches tens of millions of dollar each year (NRMA Insurance 2002; SGIC 2003), adding to vehicle insurance premiums. Vehicle armoury, such as roo- or bull-bars, adds further costs as they increase vehicle weight, increase air resistance and thus decrease fuel efficiency. Such armoury also prevents the optimal deployment of vehicle safety features such as crumple zones and air bags, and they increase the chance of serious injuries if pedestrians are hit. Further costs accrue in road maintenance in order to remove carcasses. There is also a potential loss in economic benefits from tourism, as many visitors to regional Australia find outback highways littered with kangaroo carcasses repugnant.

In the USA, Canada, and Europe similar issues arise with large species of ungulates, such as deer, elk and moose. There has been a lot of research concerning the problem and many attempts to mitigate accidents (see Chapter 6 in Forman *et al*. 2003). Despite the obvious importance of the issue, only a handful of published research papers addressing the subject of road kills of macropodoids in Australia exists (e.g. Coulson 1982, 1989, 1997; Osawa 1989). In these the survey effort was often opportunistic and conclusions were drawn without data on the demographics of the source population or traffic volume. Research on ways of mitigating kangaroo–vehicle collisions has also been limited. Studies have suffered from poor replication and have generally been inconclusive (reviewed by Lintermans 1997).

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There are numerous counter-measures (whistles and noisemakers, driver education, diversionary feeding areas, warning signs, fences, underpasses or overpasses, wildlife reflectors, population reduction, odour repellents) that can be taken to reduce the frequency and severity of wildlife–vehicle collisions (Groot Bruinderink and Hazebroek 1996; Bender 2005). Most of the measures, if they are effective, are useful and/or affordable only when they are applied in relatively small areas or over restricted periods. Hence, knowledge of both the spatial and temporal distribution of animal–vehicle collisions is important to effectively target counter-measures.

The lack of quantitative information on the numbers of kangaroos hit on outback highways, which species and age/sex classes are involved, where and why they are hit, and how these incidences can be mitigated demands further investigation. In this context, we report the results of a small-scale but intensive study with the following aims:

(1) quantification of the number, species, sex and age of kangaroos killed along a segment of outback highway relative to the source population along the road and in the hinterland;
(2) analysis of spatial patterns of road kills in order to identify the characteristics of road-kill hotspots and causal factors that may in the future be targeted by abatement technologies; and
(3) identification of temporal patterns in the frequency of road kills and description of the relationships of animal density, road traffic and environmental conditions with the likelihood of kangaroo–vehicle collisions.

Materials and methods

Study area

The study was conducted at the University of New South Wales Arid Zone Research Station, Fowlers Gap (31°05′S, 141°43′E) in north-western New South Wales, Australia. The station covers ~39 000 ha of saltbush steppe within the sheep rangelands (Caughley 1987), which typically support a high density of kangaroos (*Macropus rufus*, *M. robustus erubescens*, *M. giganteus* and *M. fuliginosus*). The climate is dry, mildly arid, with hot summers and mild winters (Bell 1973). The station is traversed for 21.2 km by a bitumenised section of the Silver City Highway from Broken Hill to Tibooburra (Fig. 1). The southern 10 km of the highway is hilly, with ridges of 180–240 m above sea level. The vegetation consists of shrub (mainly Chenopodiaceae) ~1 m high. Further north the terrain is flatter (140–170 m above sea level). Here the vegetation is dominated by tussock grasses (especially *Astrebla lappacea*), with a height of ~0.5 m. Several features that might attract kangaroos to the vicinity of the road (ephemeral creeks, smaller water-drainage channels, natural and artificial water sources) or hinder their flight movements (road cuttings, fences) are found along this section of the road.

During the study period (January–June 2002), the station was dry, with rainfall in this period and the prior 6 months totalling 117 mm against a long-term annual average of 241 mm; the area in which the station is located was drought declared. June had a serious rainfall deficiency (<10 percentile of long-term average) by the Australian Bureau of Meteorology's criterion.

Kangaroo population surveys

Daylight and night-time counts of kangaroos along the road were conducted to estimate the size and composition (species and sex) of the source population for road-kills along the road and to monitor possible population fluctuations. Complementary counts were conducted along a 7.3-km-long graded earthen track in the hinterland (Fig. 1) at a distance of ~500 m from the road to estimate any aggregation of kangaroos at the road relative to the hinterland. Counts were conducted once per week for both the road and hinterland track. Paired night and day counts were done within a 24-h period.

Daylight counts were performed from sunrise when kangaroos were active and easily seen and completed within 3 h. Counts were conducted from a driver's perspective in a standard vehicle (Nissan Navara 4 WD utility) driven at 25 km h^{-1}. A strip 200 m to either side of the road/track was scanned for kangaroos. When sighted the vehicle was briefly stopped and for every individual or group (defined after Croft 1981) of kangaroos the angle (to the nearest 10°) and distance (to the nearest 10 m) from the observer were estimated. The number of kangaroos per group and the species and the sex of each individual were determined. The population density during the day for the combined species of kangaroos was estimated using the line-transect method and the program Distance 4.0 (Buckland *et al*. 2001). The data were truncated at a perpendicular distance of 185 m from the transect in order to improve the precision of the estimate. A half-normal cosine function was fitted based on minimisation of Akaike's Information Criterion with post-stratification by week.

Night-time counts were conducted in the evenings, starting about 2 h after sunset, and were usually completed in less than 2 h. The vehicle was driven at 25 km h^{-1} in the middle of the road/track and all kangaroos within the range of the high-beam (a distance of 20 m either side of the vehicle) were recorded. When a kangaroo was seen, the vehicle was briefly stopped, the location (odometer reading) recorded and the species and sex identified (assisted if necessary by using a spotlight). The population density during the night was calculated as the number of kangaroos seen in the width of the strip sampled.

Road-kill data sampling

The highway was checked for road-killed kangaroos over 24 weeks from January to June 2002 by driving along in a vehicle at low speed every second day. For each road-kill the date, location (200 m section of road from the southern boundary of Fowlers Gap), species and sex were recorded. When intact, skulls were collected for age estimation using molar progression (Kirkpatrick 1964). Chi-square tests were used to compare the proportion of species and sexes of road-kills with their respective proportions in the population.

The spatial distribution of road-kills was analysed by dividing the road into 200-m sections. For each section, road features (road cuttings, stock races, curves, drainage channels/creeks crossing the highway), road-side features (tall vegetation ≥2 m that may hinder a driver's view, watering points – stock troughs/filled water holes – within 500 m of the road) and the number of road kills were recorded. A watering point (trough) beside the road (Fig. 1) had a broader catchment of kangaroos travelling to or from it than other features and so this feature was assigned to five 200-m sections centred on the section adjacent to the watering point. A contingency table analysis was used to detect any significant clustering of road-kills in association with a road or road-side feature.

Roadside vegetation structure and composition

Vegetation surveys were conducted at road-kill locations and 25 randomly chosen locations where no road kills were found. For each location four replicates were done, two on each side of the road, about 25 m apart. Vegetation categories followed those used to describe kangaroo diets (summarised in Dawson 1995) and so plants were assigned to one of five plant categories (grass, forb, round-leafed chenopod, flat-leafed chenopod and copperburr). For each transect, a 30-m-long measuring-tape was unrolled from the edge of the bitumen perpendicular to the road. Every plant found below the tape was assigned to one of the plant categories, and then the width (to the nearest millimetre) of the plant lying under the tape, its height (in 5-cm intervals) and its greenness (dry 0%, ≤50% or >50% green) were recorded. Cover was calculated as the percentage of a metre interval occupied by a plant type. Grass, forb and copperburr were pooled into a single ‘pasture’ category (cf. Short 1987) for further analysis.

Mean cover values per metre interval were calculated from the four replicates at each site and then sites were used as replicates in a Friedman test to assess differences in cover, height and greenness between metre intervals. If a significant difference was found then a multiple range test (Dunn’s Test, after Conover 1980) was applied to determine which metre intervals were significantly different from the first metre interval at the road verge. Results were plotted as mean ranks per metre as this smoothed out data and highlighted real effects. This analysis was done separately for road-kill and non-road-kill locations. The distances from the road at which significant changes in cover, height and relative greenness occurred were compared between road-kill and non-road-kill sites. A more quantitative comparison compared the means per metre interval for both datasets in a paired *t*-test.

Traffic volume

Passing traffic in both directions was recorded continuously for the duration of the study by setting up a video camera (Monochrome M-202 Allthings P/L, WA), camouflaged underneath a road sign. The video signal was discretely transmitted at 1.6 GHz to a satellite TV receiver 500 m away in a Station building. Here the images were recorded with a time-lapse video recorder (Panasonic AG-6040) at 72 h per VHS180 tape. The tapes were reviewed at low speed (0.25× play-back) and the date, time of the day and type were recorded for every vehicle passing the camera. For subsequent analysis, the 24-h period was divided into day-time traffic (sunrise + 2 h to sunset – 2 h) and night-time traffic (sunset – 2 h to sunrise + 2 h).

General linear modelling was used to determine any relationships between the temporal distribution of road kills and the average weekly temperature, day-time and night-time kangaroo density along the road, night-time traffic, days since last rain and cumulative rainfall in the last 30 days. Weather data were obtained daily from a weather station located at the Fowlers Gap homestead.

Results

Kangaroo population along the highway

The average kangaroo density along the highway was estimated as 13.3 kangaroos km^{-2} (c.v. = 0.11) from day-time counts. The kangaroo population consisted of 47.6% of grey kangaroos (combined *M. giganteus* and *M. fuliginosus*), 38.8% red kangaroos (*M. rufus*) and 13.5% euros (*M. robustus erubescens*). Red kangaroos had a female bias amongst those present along the road (73% females and 23% males), whereas euros had a strong male bias (92.7% males, 7.3% females). Sex could not be reliably determined across all size classes of grey kangaroos and so a potential sex bias in the road-kill sample was not investigated.

The night-time density of kangaroos along the roadside (mean = 14.1 kangaroos km^{-2}) was similar to day-time (*t*-test: $t_{16} = 0.337$, $P = 0.74$). However, density was more variable than during day-time (c.v. = 0.89 for night, 0.11 for day). The species most frequently counted at night were red kangaroos (53.1%). followed by euros (39%) and grey kangaroos (7.8%). A reliable sex determination at night was not possible. Thus grey kangaroos were most likely to be seen in the early morning but least likely in the evening when red kangaroos dominated. The proportion of euros seen more than doubled in the evening.

Species, sex and age of road killed kangaroos

A total of 125 road-killed kangaroos were found. This was a rate of 0.3 deaths km^{-1} day^{-1}. The majority were red kangaroos (59%), with 30% euros and 11% grey kangaroos

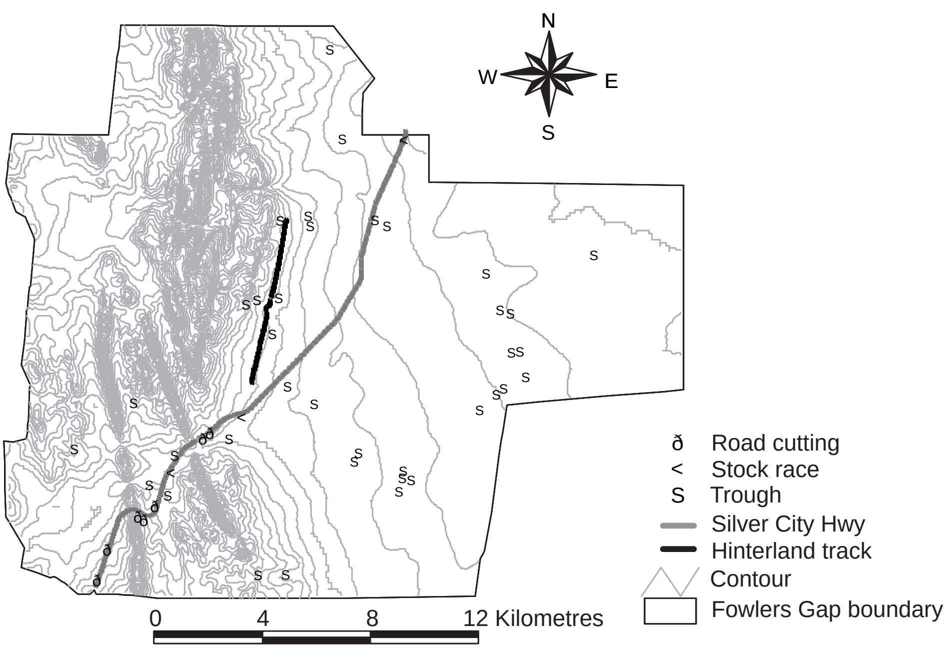

Fig. 1. The location of the Silver City Highway and the hinterland on Fowlers Gap Research Station and the position of selected road and roadside features.

Table 1. Percentage of red kangaroos, euros and grey kangaroos (eastern and western) and their sex amongst road-killed kangaroos

Species	Sample size	% total	% females	% males
Red kangaroo	74	59	66	34
Euro	37	30	26	74
Grey kangaroos	14	11	64	36

making up the balance (Table 1). The relative frequency of species in the road-kill sample significantly deviated from the species composition of day-time densities along the road ($\chi^2 = 71.52$, d.f. = 2, $P < 0.001$) but not night-time densities ($\chi^2 = 3.87$, d.f. = 2, $P = 0.5$). The day-time bias was towards red kangaroos and euros being killed in higher numbers than expected (red kangaroos: counted: 74.0, expected: 48.5; euros: counted: 37.0, expected: 17.0) and grey kangaroos being killed in much lower numbers than expected (counted: 14.0, expected: 59.5).

The sexes of red kangaroos were killed in proportion to their respective densities estimated from the day-time population surveys ($\chi^2 = 0.18$, d.f. = 1, $P = 0.18$). Euro females were killed more than expected (observed: 9, expected: 2.4) relative to males (observed: 25, expected: 31.6) ($\chi^2 = 19.8$, d.f. = 1, $P << 0.001$).

Road-killed kangaroos were aged 1–16 years (Fig. 2) and typically were less than 6 years. The median age for most species–sex classes was 2–3 years (red kangaroo female = 2, red kangaroo male = 3; euro female = 2; grey kangaroos = 2). The exception was male euros with a median age of 6 years.

Risk and hazard factors

The mean density of kangaroos was higher along the road than along the hinterland transect but the difference was significant only during the day-time counts (Fig. 3). Road-side vegetation was the potential attractor.

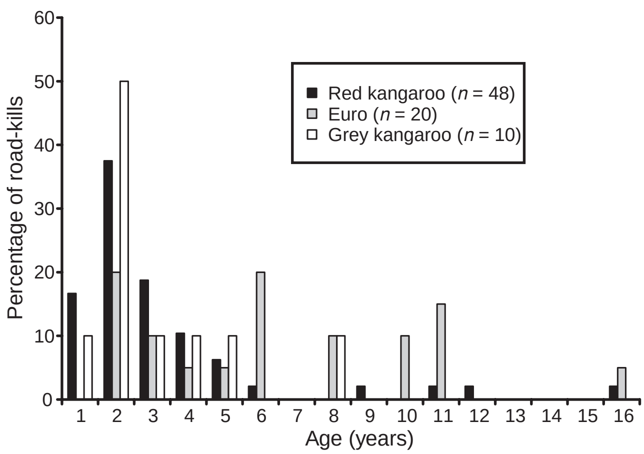

Fig. 2. Age distribution (in years) of road-killed red kangaroos, euros and grey kangaroos (eastern and western) estimated from molar progression.

Pasture cover and relative greenness decreased significantly with increasing distance from the road verge out to the 30-m limit sampled ($F_{1,29} = 35.66$, $P < 0.001$; $F_{1,29} = 16.79$, $P << 0.001$; respectively). A relatively broad 16-m band next to the road had pasture cover similar to the 1-m verge but thereafter cover was significantly lower (Fig. 4*a*). However, pasture greenness significantly declined within 2 m of the road edge (Fig. 4*b*). Pasture height did not significantly change between the first and the remaining 1-m intervals over the 30-m transect from the road edge. Mean pasture cover, relative height and relative greenness were significantly higher at road-kill locations than at non-road-kill locations (paired $t_{29} = -7.87$, $P << 0.001$; paired $t_{29} = 3.69$, $P = 0.001$; paired $t_{29} = -7.92$, $P = << 0.001$; respectively).

Road-kills occurred along the entire length of road surveyed but kangaroos were killed significantly more frequently on road stretches in the open plains than on those leading through hilly terrain ($\chi^2 = 3.76$, d.f. = 1, $P = 0.05$). Higher than expected numbers of road-kills occurred on curves, where 32% of all kills occurred ($\chi^2 = 12.13$, d.f. = 1, $P << 0.001$). Stock races are 40–50-m sections of 5-wire livestock fence offset ~1–2 m from the road edge and running either side and parallel to it. These showed a trend for higher than expected road-kill numbers ($\chi^2 = 3.59$, d.f. = 1, $P = 0.06$). Drainage channels, road cuttings, creek beds, tall vegetation and watering points in the vicinity of the road did not account for significantly more or fewer road kills than were expected (Table 2).

Temporal variation in the frequency of road-kills was best explained by the average night-time traffic volume ($\beta = 0.94$, $R^2 = 0.88$, $F_{1,11} = 79.06$, $P << 0.001$), with the regression line forced through the origin since the intercept explained no significant variation (Fig. 5). The average (±s.e.) night-time traffic was 22.5 ± 1.4 vehicles, with a minimum of 2 and a maximum of 124 vehicles per night. Night-time traffic made up ~40% of the average (±s.e.) daily traffic volume of 52.7 ± 2.0 vehicles.

Cumulative rainfall over the previous 30 days was also relatively highly negatively correlated with the frequency of

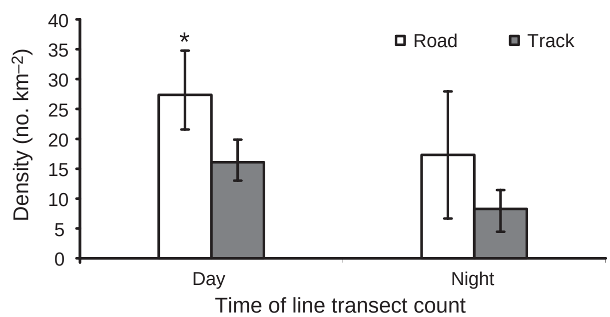

Fig. 3. Mean (±95% confidence interval) density of kangaroos along the Silver City Highway on Fowlers Gap Research Station and a 7-km parallel hinterland track estimated during the night and day. An asterisk indicates a significant difference at the $P = 0.05$ level.

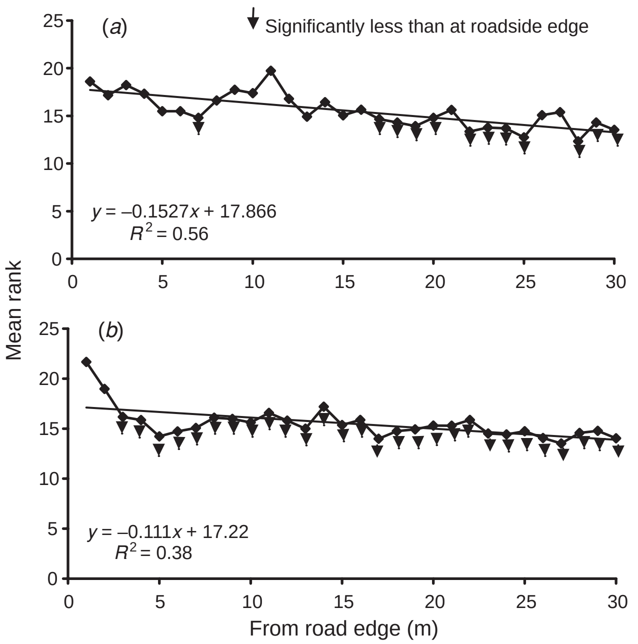

Fig. 4. Mean rank, from a sample of 125 road-killed kangaroo sites, of (*a*) pasture cover and (*b*) relative pasture greenness for each metre interval from 1 to 30 m perpendicular to the road (Silver City Highway) on Fowlers Gap Research Station. A trend line with equation and variance explained (R^2) is shown on the figure. Down arrows indicate significantly lower mean ranks (calculated from Friedman test) than the first metre interval, as assessed by Dunn's *post hoc* test (Conover 1980).

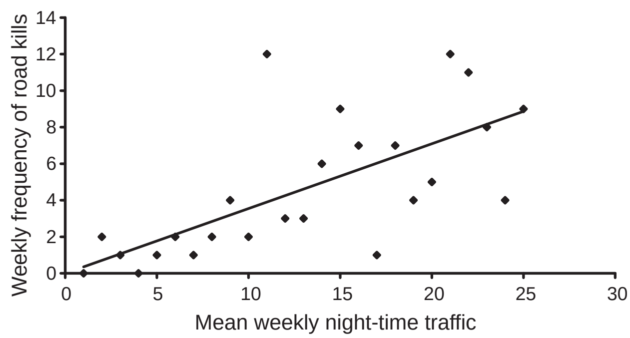

Fig. 5. The relationship between weekly frequency of road-killed kangaroos and night-time traffic along the Silver City Highway through Fowlers Gap Research Station. Regression equation: $y = 0.245x$; $R^2 = 0.88$.

road-kills (Table 3) but as the data were clumped the relationship was more representative of a threshold effect or stepped function. Weeks with low cumulative rainfall (≤20 mm) typically had many more road-kills than weeks with rainfall of above 20 mm. Average weekly minimum and maximum temperature, average weekly day-time and night-time kangaroo density along the road and the number of days since last rain were not significantly correlated with the frequency of road kills (Table 3). To estimate the probability of a kangaroo–vehicle accident the records of the daily number of road kills were converted to binary data (1 = one or more kills, 0 = no kills). A logistic regression with daily traffic volume gave a significant fit (overall classification percentage 65.2%, traffic variable: Wald = 10.83, d.f. = 1, $P = 0.001$, exp(B) = 1.057, constant: Wald = 12.71, d.f. = 1, $P << 0.001$, exp(B) = 0.039). The probability of a road-kill (Y) increased exponentially with increasing traffic volume (X) according to the formula

$$Y = 1/(1 + e^{3.3 - 0.06X}).$$

Thus, for the average daily traffic volume of 52.7 vehicles the probability of having at least one road kill was 0.41 along the 21.2 km of highway.

Discussion

The results of this study indicate that despite a high density of grey kangaroos along the roadside in the early mornings they were killed in relatively low proportions. Thus the impact of road mortality on this stretch of highway is different for the various kangaroo species and, through selective death, may play a role in the changes in the kangaroo species composition in the area. Despite some bias in the detectability of grey kangaroos during the night owing to their dark colouration they were less frequently observed close to the road than the other species, which indicates a different use of the road verge. As the risk of a collision is relative to the use of the road side at night (main activity time of kangaroos and

Table 2. The effects of road or roadside features on a disproportionate increase or decrease in the frequency of road-killed kangaroos

Road/roadside feature	Impact on road-kill frequency	% road-kills	χ^2	*P*
Curve	Increase	29.6	12.13	<<0.001
Drainage channel	None	10.6	1.04	0.31
Road cutting	None	13.6	0.02	0.90
Creek	None	4.0	0.07	0.79
Area with tall vegetation	None	5.6	0.15	0.69
Watering point	None	34.2	0.31	0.58
Stock race	Increase	5.6	3.59	0.06

Table 3. Summary of results of stepwise multiple regression of variables that may affect the frequency of road-killed kangaroos

Variable	Standardised coefficient	*P*
Day-time kangaroo density	0.12	0.66
Night-time kangaroo density	0.08	0.29
Maximum temperature	–0.35	0.30
Minimum temperature	–0.24	0.59
Cumulative rainfall in previous 30 days	–0.81	0.01
Days since last rainfall	–0.37	0.14
Night-time traffic	0.94	<<0.001

low visibility for drivers), grey kangaroos suffered less risk than the other species. A possible explanation for lesser use of the road verge by grey kangaroos is their diet. Grey kangaroos, especially western grey kangaroos, are more generalist herbivores than the other species, taking more browse in their diet, and thus they may be less attracted to short pastures along roadsides. Additionally, shorter grazing times of western grey kangaroos compared with red kangaroos (Baker 1987) may reduce the time that grey kangaroos spend at the road verge and are exposed to the potential risk of a collision.

A bias towards males in the road-kill sample was expected as males of all the large kangaroo species tend to have larger home-range sizes (Moss 1995) and show higher mobility in their search for oestrous females (Jaremovic and Croft 1991; Edwards *et al*. 1994; Norbury *et al*. 1994). The larger size of males demands a higher dietary intake in order to maintain their bulk (Dawson 1989). This requirement may attract them to the road verge with its greener pasture and higher pasture cover. Male red and western grey kangaroos graze about 1 h longer than females (Priddel 1986), which leaves them exposed longer to the threat of road mortality. Coulson (1997) reported a strong bias in road kills towards males in all species, except for red kangaroos. In the absence of data on the structure of the source population, Coulson compared the ratio of males and females in the road-kill sample to parity, despite the fact that most kangaroo populations are female biased (Quin 1989; Arnold *et al*. 1991; Jaremovic and Croft 1991; Witte 2002). Thus Coulson overestimated the proportion of males in the population and still found a bias towards males in road kills. The actual bias was therefore even stronger. However, his sampling effort was inconsistent and so the high number of males he recorded could be due to the fact that males are larger, take longer to decompose and are therefore visible on the road for longer. Males are also easier to identify with certainty, even from rather decomposed carcasses, than females.

In this study, where the sampling effort was high and information on the source population available, no bias towards either sex was found for red kangaroos. In euros there appeared to be a strong trend towards female road-kills, which was unexpected. This was most probably not due to any real bias but rather to an under-representation of female euros in the roadside population. Core habitat of euros, especially females, is hilly terrain and all road-kills of female euros occurred along the 'hill' section of the highway. Owing to the topography and the small size of female euros they were more difficult to detect than males during population counts. The habitat utilisation of males was much broader, including drainage channels and watering points on the plains where they were easily seen. Thus female euros were likely to be underestimated in the population count along the road. The number of road-killed grey kangaroos (7 females and 4 males) did not suggest any sex bias but numbers were too low to validate a statistical analysis.

There were no contemporary data on the age structure of the kangaroo populations on Fowlers Gap. However, Russell and Richardson (1971) found a pyramidal age distribution for euros on Fowlers Gap. The same pyramidal distribution was found elsewhere for western grey kangaroos (Norbury *et al*. 1988) and grey kangaroos when the two species were undifferentiated (Wilson 1975). The age structure of road kills in this study was similar to these results. A large proportion of the kangaroos killed were immature, with fewer and fewer individuals represented in the older age classes. Kangaroos younger than one year were expected to be more numerous, but young kangaroos of that age are usually still in the pouch of their mothers and because of their small size could have been easily carried away by scavengers after their mother had been hit and so probably eluded the count. Also, conditions before and during the study were very dry, which led many females to cease reproduction. Two-year-old kangaroos were the age class most frequently encountered as road kills. Kangaroos of that age have just become independent of their mothers and their inexperience might explain their high proportion in the road-kill sample. The lack of seven-year-olds amongst road-kills is most probably due to a low recruitment in 1995 as a result of a severe drought in autumn 1994 (Witte 2002). Missing age cohorts in a red kangaroo population correlated with severe drought have been identified in central Australian populations (Newsome 1977).

The two subdivisions of the road, the southern 9 km and the northern 12.2 km, pass through topographically and botanically different areas. The northern subdivision is flat and open and the vegetation is dominated by tussock grass. These open grass plains are the preferred habitat of red and grey kangaroos and, accordingly, they occurred in relatively high numbers there. The significant trend for the frequency of kills to be higher in the flat part of the road was in accord with a higher overall density of kangaroos in that area according to the frequency of sightings during the day-count surveys. Driver behaviour may also have contributed to the higher number of road-kills in the plains section. The northern flat-road section is mainly straight and even, allowing high travelling speeds, whereas the numerous curves and dips in the southern section demand slower and more careful driving.

Curves in the road, whether the frequent ones in the southern section or the long sweeping ones in the northern section, increased the frequency of road-kills (32% of all such accidents). Similarly, 35% of all wildlife collisions in Nordrhein-Westfalen (Germany) took place in areas with reduced visibility and slopes (Hartwig 1993). The greater number of road kills in the vicinity of curves is probably a result of the driver's shortened sight in curves and subsequent reduced reaction time to avoid a collision. Furthermore, drivers are less likely to take evasive action in a tight curve owing to a high risk of vehicle roll-over. At night, when most kangaroo accidents happen, the situation is worse as the distance along the roadway that is illuminated by the headlights when driving through a curve is shortened. The effect of curves extends for some distance after leaving the actual curve as vehicles tend to speed up when coming out of a curve and kangaroos on the straight follow-up section of road may be detected too late. Stock races tended to increase the frequency of road kills despite their short length of ~50 m, and were associated with 5% of all kills. A stock race with its parallel fences within 1–2 m of the road pavement impedes any kangaroo feeding on the road verge or passing through the stock race from retreating from oncoming vehicles into the hinterland: they get trapped between the fences bounding both sides of the road, which may cause them to criss-cross the pavement several times in panic, enhancing the chance of an accident. Short livestock grids (1–2 m) are more benign but much more expensive to install across the road pavement.

All other road or roadside features (watering points, road cuttings, creeks, drainage channels and areas of tall vegetation) did not disproportionately increase or decrease the probability of an accident. Steep road cuttings could potentially entrap kangaroos like a stock race but the barrier is usually >10 m from the verge, unlike the latter. Dips associated with drainage channels and tall roadside vegetation (sparse in arid landscapes) may impair a driver's vision like curves but apparently did not exacerbate vehicle–kangaroo collisions.

Vegetation

The other important factor that likely influenced the frequency and location of road-kills was the road-side vegetation. The road edge differed significantly in pasture cover and relative greenness from the vegetation further away from the road. Overall pasture cover and greenness decreased significantly over the 30 m perpendicular to the road. The pattern observed in all characteristics (cover, relative height and relative greenness) was a peak at the immediate road edge, a trough at ~6 m and another peak at 11 m from the road edge, before remaining on a more even level.

These findings are likely related to the road construction and maintenance procedures of the Road and Traffic Authority in New South Wales. Along this section of highway a strip of ~10 m to either side of the road was graded in construction and again during the 2002 drought. This grading ensured that the ground slopes away from the road surface, which prevents rainwater from pooling on the road. Also higher vegetation on the road verge that might hinder the driver's view is removed from time to time by mowing or grading. In the grading process the removed soil is pushed to the side and creates a small 'soil hill' (table drain) at ~10 m from the road. When it rains most of the water that runs off the road soaks the immediate road edge. Any excess water then flows down the slope, picks up seeds and soil before collecting in front of the soil hill before the ground evens out. This provides plants at the road edge with more water and enables them to grow rapidly, creating higher cover, greater greenness, and taller plants, explaining the typical maxima for these vegetation characteristics right next to the bitumen (road pavement). In the sloped area where the water mainly runs off pasture cover, relative height and greenness decreased. Adjacent to the subsequent soil hill where the water pools, top soil and seeds congregate (either carried there by water or wind), and so another peak in pasture cover, greenness and height occurred, which was greater than at the immediate road edge since it was less often disturbed by mowing or grading.

The dry conditions experienced during this study probably made the differences between immediate road edge and areas further away more obvious. The showers that occurred during this study brought little rain and did not generally affect the vegetation but, owing to the run off from the road, allowed plants on the road edge to grow better. As kangaroos preferentially eat green vegetation, often shoots and young plants of low height (Chippendale 1968; Denny 1982), road verges with higher cover, higher relative greenness and shorter vegetation relative to the surroundings have the potential to attract kangaroos to feed. This enhances the likelihood of them being involved in a collision with a vehicle. A certain degree of grazing may enhance plant growth (McNaughton 1979, 1983) so preferential grazing by kangaroos along the road may potentially further increase the attractiveness of road-side vegetation. However, rain not only enhances vegetation growth alongside the road but also provides drinking water. On numerous occasions kangaroos were observed both feeding on the road edge and licking up water pooled on the road pavement or in the table drain after rain.

The evidence that the road or the road edge attracted kangaroos was dependent on the time that observations were made. During the day, kangaroo numbers were significantly higher along the road than along the hinterland track. However, no significant difference in total kangaroo population between the road and the hinterland track was found at night, when most accidents occurred, but kangaroo densities along the road did tend to be higher. The difference between night and day may have simply been a function of the greater strip width used for density counts in the day. Further study of the behaviour of kangaroos along the roadside independent of the potentially disturbing effect of a vehicle approaching and passing at low speed (in order for an observer to count them) is warranted. The individuals at risk of collision with a vehicle are likely those that feed often along the road and/or cross it frequently. That behaviour might be resolved with radio-tracking at a high spatial and temporal resolution (e.g. GPS receiver collars on a short duty cycle).

The comparison of road-kill and non-road-kill locations revealed significantly better pasture at the former. Road-kill locations had higher vegetation cover, higher relative greenness and higher relative height. Thus roadside vegetation characteristics may not only attract kangaroos to move into the vicinity of the road, but they may also influence the distribution of road kills along the road. The non-road-kill locations also had a broader edge; i.e. the vegetation band that was not significantly different from the road edge, extended further away from the road. As a result, kangaroos might feed a little further away from the bitumen, still profiting from the edge effect but reducing their risk of being run over. There was no obvious reason why the edge was broader as there was no indication that these locations were not maintained in the same manner as road-kill locations, nor did they look topographically different. Thus further study on variation in soil chemistry and patterns of infiltration along the roadside may reveal causes of heterogeneity in pasture quality and width along the verge.

Other studies have found relationships between road-kill frequency and vegetation, but this has been the effect of vegetation in reducing animal visibility to the driver (Bashore *et al*. 1985; Hubbard *et al*. 2000) rather than the attractiveness of roadside forage to large herbivores. We found no relationship between the sparse patches of tall vegetation and road-kill frequency in our arid landscape (see above). Vegetation along the road edge was rarely higher than 50 cm and the density of taller plants was low. Thus the vegetation was not likely to hide an animal as large as a kangaroo. Clearing of vegetation along roadsides in arid low shrubland and grassland to improve driver visibility is likely unnecessary. The consequence may be to stimulate pasture growth, attracting kangaroos to the verge and through a higher risk of a kangaroo–vehicle collision the safety of drivers is reduced, not improved.

Temporal distribution

We did not isolate the time of the day when road-kills occurred because the road was checked only once in the mornings. However, few accidents were expected to happen between late morning and early afternoon when kangaroos usually rested (Watson and Dawson 1993).

Kangaroos in arid and semi-arid regions do not have particular breeding times but generally breed throughout the year (Newsome 1965; Russell and Richardson 1971; Norbury *et al*. 1988; Cairns *et al*. 1991). Hence seasonal breeding activity or dispersal of juveniles cannot explain seasonal differences in the frequency of road-kills in kangaroos, unlike in other fauna such as deer (Allen and McCullough 1976; Hubbard *et al*. 2000), ungulates in general (Groot Bruinderink and Hazebroek 1996), prairie nesting ducks (Sargeant 1981), and the European badger (Davies *et al*. 1987). A high percentage of the variation in the weekly frequency of road-kills of kangaroos in this study was explained by changes in traffic volume. Traffic volume has also been a significant positive predictor of road-kill frequency in numerous studies on road-kill of various other fauna (Fahrig *et al*. 1995; Inbar and Mayer 1999). Hence times with especially high traffic volume, such as school holidays, can be expected to show peaks in road-kill numbers. We expected that the frequency of collisions would likewise be correlated with kangaroo densities. However, kangaroo density, whether estimated in the day or night, was not significantly correlated with the road-kill frequency. Thus kangaroo numbers within the range of densities estimated in our study may be less relevant to the risk of a vehicle–kangaroo collision than the behaviour of the kangaroos if dependent on traffic volume, as discussed below.

Very few rainfall events occurred during the study period and even though rainfall in the last 30 days was highly correlated with the frequency of road-kills, the form of the relationship could not be accurately estimated. In the absence of intermediate rainfalls, a stepped function was found so that relatively high rainfall in the last 30 days resulted in low road-kill numbers whereas low rainfall resulted in variable but higher road-kill numbers. The reason for this is that high rainfall induces widespread vegetation growth, whereas low rainfall, which is too low to affect the vegetation in general, still induces plant growth on the road verge owing to rainwater runoff from the road. As a consequence, low rainfall attracts kangaroos to the road whereas higher rainfall distributes them over a larger area and away from the road. Thus the factor increasing risk is likely to be not how many kangaroos are near the road but how close to the roadside edge they forage.

Temperature was predicted to have an impact on road-kill numbers, as temperature regulates the diurnal and seasonal activity patterns of kangaroos. Grazing commences later and ceases earlier in spring and summer than during autumn and winter and so the activity span for kangaroos is much shorter and more concentrated in summer (Priddel 1986; Clarke *et al*. 1989; Watson and Dawson 1993). In winter low temperatures allow kangaroos to be active over a longer period so they are exposed to a possible road death for longer. Also, as days are short, people are more likely to drive in twilight or hours of darkness (an increase in night-time traffic). Hence traffic overlaps more with kangaroo activity times in winter than in summer, which in consequence puts more kangaroos at risk of being hit. However, temperature in this study was not significantly correlated with the road-kill frequency.

The probability of an accident did not increase linearly but exponentially with traffic volume. The probability of a kangaroo–vehicle collision was 100% if the daily traffic volume was 290 vehicles; however, a traffic volume that high was never recorded. During this study, with an average traffic volume of 53 vehicles per day, the probability of an accident was about 41%. The behavioural response of kangaroos to vehicles or a disturbance in general may be the reason for the exponential and not linear form of the model. At low traffic volumes vehicles are perceived as a threat and the kangaroos flee. With a certain frequency of passing vehicles they are possibly more habituated to traffic and reduce the flight distance. They may not have enough time to settle and return undisturbed to the road edge to continue grazing and the next vehicle may catch them on their return. Also the higher vehicle numbers could make them more alert, jumpier and flightier, resulting in scattered and undirected flights.

Conclusions

Grey kangaroos were under-represented in the road-kill sample whereas red kangaroos and euros were over-represented relative to their densities near the road in the early mornings. However, at night an estimate of species densities within the field of view of a typical vehicle's headlights revealed no such bias. Kangaroo road-kills were not biased towards a sex or a certain age class and therefore mortality arising from collisions with vehicles is not likely to alter the population structure.

Efforts to mitigate kangaroo–vehicle collisions should be concentrated on flat open country, especially targeting curves. Replacement of stock races with grids or alternative deterrents to livestock using the road to cross between paddocks will reduce road-kill. By analogy, fences close to the road should be avoided. Mitigation technologies, or trials thereof, should be in place or run especially in times of high traffic volume (e.g. school holidays or on roads with high traffic volume).

Road-side vegetation has the potential to attract kangaroos towards the road, increasing their risk of being involved in an accident. Thus a change in the road-side management and alteration of the road-side vegetation to make it less attractive for foraging will likely reduce the number of kangaroo–vehicle collisions. However, there seem to be differences between the species in their use of the road verge, which may be due to differences in their diet or possibly in their behaviour towards vehicles. To establish whether the behaviour in reaction to oncoming vehicles may explain any bias in the species or sexes, an investigation into the response of the species and the sexes to oncoming vehicles is needed.

Finally, the conditions during this study were very dry and so generalisation of the results to periods of more normal rainfall is not possible. The species composition of vegetation along the road verge may change under better conditions with higher overall vegetation cover (cf. Angold 1997). Any period when grass growth and abundance on road verges is promoted could attract kangaroos as specialised grass eaters (Dawson and Ellis 1994, 1996).

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