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Factors affecting the mortality of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) by vehicle strike

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Abstract

Context. Vehicle strike is a major issue where wildlife habitat is intersected by busy roads. *Near Threatened* Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) is a large (5–10 kg) semi-arboreal mammal found in populated rural and forested areas of north-eastern Australia. Warning signs, rope bridges and underpasses have not prevented ~20 animals being killed on the road each year.

Aims. To identify factors influencing Lumholtz's tree-kangaroo vehicle strike to help inform mitigation options.

Methods. Citizen sightings (1998–2000) and 90 road-kills collected over 4.5 years on the Atherton Tablelands, Australia, were examined to determine the causes of vehicle strike in Lumholtz's tree-kangaroo. The spatial distributions of sightings and road-kills were characterised using nearest-neighbour analysis, and the relationship between them was determined using a Bayesian approach that accounted for spatial autocorrelation. Gender, age, weight, season, rainfall, road and verge characteristics, traffic volumes, speed limits and mitigation measures were recorded to assess their influence on road-kill risk. Adequacy of speed limits to prevent collisions along road sections with more than four road-kills per 8 km (hazard zones) was assessed from visibility and stopping distances.

Key results. Vehicle strikes mainly affected male tree-kangaroos (2–5 years, 5.5–8 kg), occurred where live animals were most frequently sighted and were most likely on roads with narrow verges, low visibility and medium traffic volumes. Speed limits at hazard zones were inadequate to prevent collisions. Few warning signs corresponded with these zones, and road mortalities persisted where they did.

Conclusions. Unpredictable dispersal of young males and vehicle speeds unsuited to road conditions drive road mortalities in Lumholtz's tree-kangaroo. Because tree-kangaroos do not appear to respond to existing mitigation measures, reducing traffic speeds, and increasing visibility, appear to be the most effective mitigation strategies for reducing tree-kangaroo road mortality.

Implications. Our findings suggest that tree-kangaroo road-kill can be reduced by reducing speed limits in line with government recommendations and increasing visibility by clearing road verges along sections of road with the highest tree-kangaroo mortality. Warning signage should be re-evaluated to determine whether its effectiveness can be improved.

Additional keywords: anthropogenic impacts, Bayesian modelling, density dependence, management strategies, spatial ecology, wildlife management.

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Introduction

Roads are a major cause of environmental degradation and biodiversity loss (Coffin 2007; Laurance *et al*. 2009; Rytwinski and Fahrig 2012), including through vehicle collisions with wildlife (Goosem 2007). Strategies to reduce this impact require knowledge of where road-kills occur and the contributing factors (Taylor and Goldingay 2010; Goosem 2015; Soanes and van der Ree 2015). Road-kill incidence may be influenced by species' densities, their movement corridors, timing of breeding, habitat heterogeneity, roadside conditions that limit driver visibility, and weather (Goosem 2007, 2008; Hobday and Minstrell 2008; Danks and Porter 2010; D'Amico *et al*. 2015; Dwyer *et al*. 2016).

Traffic volumes, vehicle speeds and vehicle size can also influence the probability of wildlife road-kill (Clevenger *et al*. 2003; Hobday and Minstrell 2008). Vehicle strike is an increasing issue in tropical regions because of escalating development causing fragmentation of tropical forests (Laurance *et al*. 2009).

In the wet tropical rainforests of north-eastern Australia, vehicle strike has been recorded as affecting over 100 vertebrate species (Goosem 1977). Mitigation strategies adopted in the region have either tried to influence driver behaviour through signage or reduced speed limits (Kofron and Chapman 2006), or have been informed by the biology of the target species, with rope-bridges being employed to reduce road-kill risk for small to medium arboreal mammals, such as fawn-footed melomys (*Melomys cervinipes*) and the Herbert River ringtail (*Pseudochirulus herbertensis*; Weston 2003; Weston *et al*. 2011), and underpasses for medium to small terrestrial mammals, such as the northern brown bandicoot (*Isoodon macrourus*) and red-legged pademelon (*Thylogale stigmatica*; Goosem 2003). However, neither option has reduced road mortality of *Near Threatened* Lumholtz's tree-kangaroos (*Dendrolagus lumholtzi*; Weston *et al*. 2011; Goosem 2012), whose low reproductive rate and large body size (Newell 1999*a*, 1999*c*; Kanowski *et al*. 2001; White and Ward 2010) make the species particularly vulnerable to vehicle strike (Rytwinski and Fahrig 2012). Despite feeding in the canopy, tree-kangaroos typically move between trees at ground level and readily cross large areas of open ground and roadways (Newell 1999*a*), and there is no convincing evidence that they use rope bridges linking canopies across the road (Weston 2003; Weston *et al*. 2011). Nor have underpasses reduced tree-kangaroo mortality, even though the species has sometimes been seen in them (Goosem 2012). Community concern over high road-kill incidence in this charismatic species (Newell 1999*a*; Kanowski *et al*. 2001; Tisdell *et al*. 2005) and the ineffectiveness of current mitigation measures make improved understanding of the patterns and causes of road mortality in Lumholtz's tree-kangaroo essential. In the present paper, we examine the patterns of Lumholtz's tree-kangaroo road-kill to determine the demographic profile (gender, age) of animals killed, seasonality of road-kill incidence, and the influence of road environmental characteristics, traffic volume and speed limits. We also identify hazard zones where road-kill incidence is currently high, and compare these with earlier identified black spots to determine whether warning signage has been effective at reducing mortality. We use this information to identify viable mitigation options for this large, *Near Threatened* semi-arboreal species.

Materials and methods

The species and study area

Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) is one of two species of tree-kangaroo found in Australia. It is widely distributed across the Wet Tropics World Heritage Area of north-eastern Australia (Fig. 1). Predominantly a rainforest species, it is also found in adjoining eucalypt open forests and woodlands (Kanowski *et al*. 2001; Heise-Pavlov and Gillanders 2016). Its habitat has been extensively cleared since the 1880s and is now dissected by several major roads linking towns on the Atherton Tablelands. Although tree-kangaroos are considered a marsupial analogue of leaf-eating monkeys (Newell 1999*b*), because they feed on leaves, flowers, fruits and seeds of rainforest trees and shrubs, they exhibit behaviours that set them apart from other arboreal folivores. Possibly having evolved from rock-wallabies (Martin 2005), their terrestrial macropod origins are exhibited in their readiness to come to ground to travel between trees, often for long distances (Newell 1999*a*), as well as to escape predators (Heise-Pavlov *et al*. 2013). In the wild, females mature sexually at ~3 years and males at 3–5 years (R. Martin, pers. comm., 13 March 2018). Animals can reach 14–17 years in captivity (Coombes 2005), but probably no more than 10 years in the wild (R. Martin, pers. comm., 13 March 2018). Population estimates for the species range between 8000 and 20 000 animals, with a density of 1.4–1.5 adults per hectare (Newell 1999*b*), and the species is listed as *Near Threatened* by both the IUCN and under *Queensland's Nature Conservation Act*, on the basis of its restricted range and assumed ongoing decline. Field observations have indicated that a number of adult female tree-kangaroos occupy small territories within the larger territory of a single adult male, that females, but not males, may remain close to their mothers and other adult females, and that much of the movement by young adult males is largely as a result of their expulsion from the mother's home range or to avoid conflict with older males, and so is both rapid and unpredictable (Procter-Gray 1985; Newell 1999*a*; R. Martin, pers. comm., 14 July 2018).

The study area covers the core distribution of Lumholtz's tree-kangaroo on the Atherton Tablelands (elevation 600–1000 m), defined by a concave hull drawn around all historical and recent records of tree-kangaroo sightings and road-kills used in the present paper, as described below. The study area almost entirely coincides with the Atherton province of the Wet Tropics bioregion, in which there has been minimal tree clearance since the mid-1990s (Queensland Department of Science Information Technology and Innovation 2017). The province has a humid subtropical climate (Stern *et al*. 2000). Annual average rainfall increases from ~1.4 m in the north to ~3.0 m in the south-east, with ~66–70% falling in the wet season (November–May). Temperatures range between ~10–22°C in the dry season (June–October) and ~18–30°C in the wet season (Bureau of Meteorology 2017).

Historical sightings and road-kills

The historical-sighting dataset consisted of a subset of location records of Lumholtz's tree-kangaroo collected by the Tree Kangaroo and Mammal Group (TKMG), a community organisation based on the Atherton Tablelands. These sightings were collected by volunteers between 1998 and 2000 and vetted by a panel of experts familiar with the region and species (Kanowski *et al*. 2001). Although biased towards roadside observations, they are considered representative of the entire distribution of the species. For the present study, we used only those records that had been assigned a spatial error of less than or equal to 150 m. This provided a spatial dataset with 1927 records, 190 of which were of road-killed animals. We limited our assessment of tree-kangaroo distribution to the TKMG dataset because records of the species from other

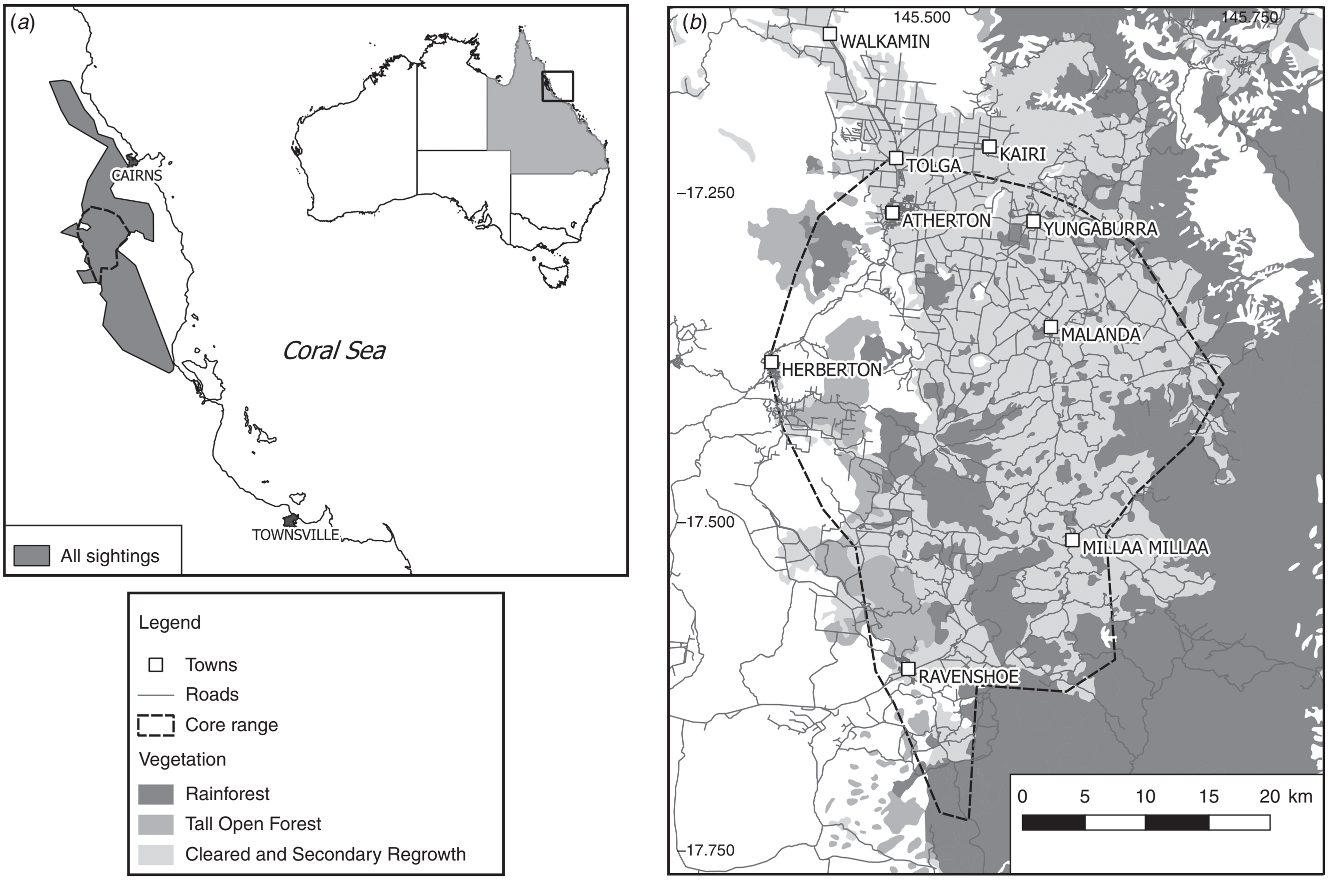

Fig. 1. Distribution of Lumholtz's tree-kangaroo on the basis of (*a*) all records, and (*b*) a concave hull drawn around Atherton Tablelands tree-kangaroo sightings and road-kill records, shown in relation to forest habitat, towns and road networks.

available databases (Atlas of Living Australia, www.ala.org.au and Queensland Government's WildNet database, https://environment.ehp.qld.gov.au/species-search/, accessed 21 March 2017) were far less numerous, although their distributions were broadly aligned with the TKMG sightings.

Recent road-kills

The recent road-kill dataset consisted of known locations of 90 road-kills recorded between September 2012 and January 2017, averaging 20 animals a year. These were obtained through an extensive campaign using the local wildlife care network, media and social media asking the public for notification of road-killed tree-kangaroos. Because of the high profile of this iconic species, we assumed that the majority of road-killed tree-kangaroos would be reported. Because road-kill records accrued during the course of the study, and condition of animals or lack of accurate locational information prevented some data being extracted for some analyses, each set of analyses has a unique sampling period and sample size.

As soon as possible after notification, the senior author visited each road-kill site, verified the species identity and the cause of death, recorded date of fatality and site coordinates, and collected and necropsied the dead animal, recording gender, weight and age on the basis of tooth wear (Coombes 2005; Damuth and Janis 2014). Of the first 53 road-killed animals necropsied up until December 2016, gender bias was assessed using an exact binomial test, seasonal variation (Australian spring, summer, autumn and winter) using Kruskal–Wallis test, and influence of seasonal rainfall (Bureau of Meteorology 2017) using Pearson correlation. Weight was recorded for 49 animals only, because the remaining animals were not intact.

Vehicle-strike clustering and density dependence

To establish whether vehicle strikes were clustered in certain areas or randomly dispersed, we conducted a nearest-neighbour analysis for the 1927 historical sightings, 190 historical road-kills and the 78 recent road-kills for which accurate locational information was available up until December 2016, by using QGIS (Quantum GIS Software 2017). Nearest-neighbour analysis compares the distances between each record in a distribution and the closest point to it with values that would be expected if the distribution were completely spatially random. To test whether cells containing sightings and road-kills were independently arranged (i.e. cells in close proximity were no more similar than cells further apart), which is a requirement of linear modelling, we conducted a Moran's I test and examined the shape of the Pearson's residuals in a sample variogram. This confirmed that, although our road-kills among neighbouring raster cells were not spatially autocorrelated ($I = 0.021$), the sightings were ($I = 0.211$).

Following Dwyer *et al.* (2016), a conditional auto-regressive (CAR) correlation structure was implemented into the model residuals so as to capture the small-scale spatially correlated patterns between adjoining cells. For this, we took a Bayesian approach, which allowed residual spatial correlation at each raster cell to be incorporated into our models as a function of the residual score at neighbouring cells (i.e. those sharing a common border). To account for the absence of prior information about our model parameters, we chose diffuse (non-informative) priors for all independent variables (given as a Gaussian distribution with a mean = 0 and standard deviation = 1000). Posterior distributions of model parameters were obtained using Markov-chain Monte Carlo (MCMC) methods. Three chains were used in the MCMC process, with 1 000 000 iterations each. A burn-in of 50 000 iterations was used and the remainder was thinned by 1 in 1000 draws to obtain 2850 observations for the posterior distributions. This led to an acceptable convergence for all structural parameters in our Bayesian models. Spatial tests and analysis were performed using the R programming language (R Core Team 2016). Bayesian models were executed using the WinBUGS software (version 1.4, Imperial College and MRC, Cambridge, UK) and implemented in the R2WinBUGS package (Sturtz *et al.* 2005) in R (R Core Team 2016). The CAR Poisson general linear model (GLM) is given by

$$\mathrm{Strikes}_i \sim \mathrm{Poisson}(\mu_i),$$

with a mean and variance as follows:

$$E(\mathrm{Strikes}_i) = \mathrm{var}(\mathrm{Strikes}_i) = \mu_i$$

The log-link function is given by

$$\log(\mu_i) = \eta_i$$

$$\eta_i = \beta_1 + \beta_2 \times \mathrm{Sightings}_i + \varepsilon_i,$$

where the number of traffic strikes ($\mathrm{Strikes}_i$) is assumed to follow a Poisson distribution with a mean and variance μ_i. The spatial correlation in the residual ε_i at cell Site i is modelled as a function of residuals at neighbouring cells, as follows:

$$E(\varepsilon_i) = \rho \times \sum_{j \neq i} c_{ij} \times \varepsilon_j,$$

where c_{ij} is a weighting function that depends on the distance between raster cells, and the parameter ρ measures the strength of the spatial autocorrelation (Zuur *et al.* 2012).

Road environment

To assess the influence of the road environment on road-kill probability, a set of 52 control sites was generated for comparison of the 52 road-kill reports for which there was accurate locational information up until December 2015. These were established at a random distance along the road corridor, beyond the line of sight of the road-kill site and in the same vegetation type (rainforest, open forest, cleared; assessed on the ground) and speed-limit and traffic-volume zones (as identified in subsequent sections of the methods). At each road-kill and control site, we recorded conditions that were likely to influence the probability of a tree-kangaroo and a driver being aware of an impending collision risk and capacity to avoid a collision occurring. These included width of the road (carriageway surfaced with bitumen, gravel or dirt) and visibility along the road corridor in each direction. For each side of the road, we recorded presence of a steep bank, drainage line or low metal guard rail, and characteristics of the verge (i.e. part of the road reserve between the road and the nearest treed vegetation). Verge characteristics recorded were width, presence and width of any mown strip, and presence and height of a steep roadside bank. Visibility was determined by sighting a Bushnell Sport 850 laser range finder (Overland Park, Missouri, USA) on a target held ~400 mm above the ground (approximate height of a tree-kangaroo's shoulders when standing on all fours). From these variables, minimum mown width, total mown width and minimum verge width were derived as continuous variables, and minimum visibility (line of sight: <50 m, 50–100 m, $\geq$100 m) and total verge width (<15 m, $\geq$ 15 m) as ordinal variables. Before analysing influences on road-kill incidence, inter-correlated variables were identified in R, using Pearson correlation to identify linear correlations, and Spearman correlation to identify non-linear correlations (R Core Team 2016). Model selection was based on combination variables that were not-significantly inter-correlated. To account for the effect of multiple comparisons, significance of the resultant *r*-values was adjusted using Holm's method. An Akaike information criterion (AIC)-based model-selection procedure was used to identify the logistic (binomial) regression that best explained the influence of the road environment on road-kill probability, using only combinations of independent variables or factors.

Traffic volumes

To investigate the relationship between traffic volume and the incidence of tree-kangaroo road-kills, all available road traffic data were obtained for the Atherton Tablelands. These data had been collected between 2012 and 2014 by using counters that were in place for at least 18 months, and were separated into average daily counts of light (<6 t) and heavy (>6 t) vehicles passing in A (northerly) and B (southerly) directions (Queensland Department of Main Roads, pers. comm., 9 February 2016; Tablelands Regional Council, pers. comm., 15 February 2016). Traffic volumes for each vehicle class were calculated for all stretches of road, assuming constant volumes between these counters, and combined to produce total daily traffic volumes. The roads for which traffic-volume data were available were then divided into 1-km segments, producing 66 road segments, 41 of which contained a total of 66 road-kill records. Each road segment was then allocated to low-, medium- and high-volume classes for each vehicle-size class; each volume class representing about one-third of the 66 road segments (light vehicle classes: $\leq$1350 vehicles per day ($n = 21$ road segments), 1350–1700 ($n = 23$) and >1700 ($n = 22$); heavy vehicle classes: $\leq$200 ($n = 21$), 200–270 ($n = 20$) and >270 ($n = 25$); total vehicle classes: $\leq$1500 ($n = 21$), 1500–1800 ($n = 23$), >1800 ($n = 22$). For each vehicle class, the relationship between road-kill incidence and volume class was assessed using a chi-square test.

Hazard zones

In January 2017, tree-kangaroo hazard zones were identified on the basis of the clustering of six or more road-kills from the recent road-kill dataset, which contained 90 animals over a 4.4-year period. These zones, ranging in length from 1.6 to 8 km, were compared with black spots identified from the historical road-kill dataset (Tree Kangaroo and Mammal Group 2000; Kanowski *et al*. 2001). We recorded the proximity of wildlife warning signs and underpasses in relation to hazard zones to assess the appropriateness of their placement; and determined the lowest speed limit at each road-kill site within the zones on the basis of the location of mandatory and advisory speed-limit signs. To assess collision risk for both heavy and light vehicles under each dry and wet conditions, we calculated the distance over which it would be possible to stop a vehicle (Queensland Government 2017), on the basis of the lowest speed limit at each site; and subtracted this distance from the visibility recorded at each road-kill site using the line-of-sight methods described previously. We concluded that a driver would be unable to stop in time to avoid collision with an animal on the road when stopping distance was greater than the visibility, and that a driver's capacity to stop would be marginal where the difference between visibility and stopping distance was <40 m.

Results

Demographic and seasonal patterns

An average of 19 tree-kangaroo road-kills were reported per year between September 2012 and December 2015. Among them, males significantly outnumbered females (probability of road-kill being a male = 0.66, exact binomial test: $n = 53$, $P = 0.027$). In total, 48% of road-killed animals were males between 3 and 6 years old (Fig. 2), so would be considered young adults. The majority of the 49 intact animals weighed were between 5.5 and 7.9 kg (min 3.0, max 9.8, mean 6.8). Highest road-kill incidence was in spring (2.2 animals per month) and lowest in winter (1.1 animals per month), although this pattern was not significant (Kruskal–Wallis $\chi^2_{\text{d.f. } 3} = 2.25$, $P = 0.522$), possibly because of the low sample sizes. Similarly, timing of road-kills was not significantly correlated with rainfall totals (Pearson $r = -0.039$, $n = 7$, $P = 0.883$).

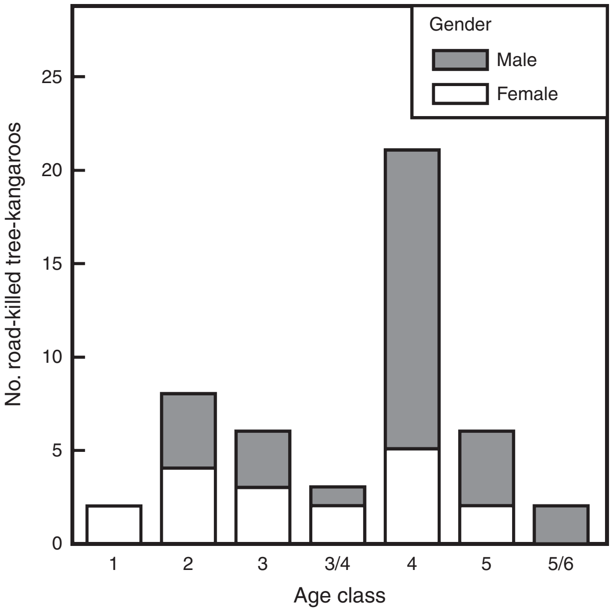

Fig. 2. Demographic profile of Lumholtz's tree-kangaroo road-kills. Age classes, on the basis of tooth wear, approximate years.

Spatial relationships

Nearest-neighbour analysis indicated that both sightings ($NNI = 0.170$, $z = -69.7$, $n = 1927$, $P < 0.001$***, Fig. 3*a*) and recent road-kill records ($NNI = 0.589$, $z = -6.95$, $n = 78$, $P < 0.001$***) were significantly clustered, as were road-kill records from the sighting database ($NNI = 0.415$, $z = -15.4$, $n = 190$, $P < 0.001$***, Fig. 3*b*). In our Poisson CAR GLM, the 2.5% and 97.5% percentiles (i.e. the 95% credible intervals) for Lumholtz tree-kangaroo sightings were given as (0.79, 1.24); indicating that there was at least a 95% chance that sightings were positively related to vehicle-strike frequency. The samples for the posterior of the spatial-correlation parameter had a mean of 0.93 and a 95% credible interval of 0.003 and 0.999. In all, 75 of the 78 tree-kangaroo road-kills occurred in cells that also contained live sightings. The remaining three were from cells adjacent to one or more cells containing live sightings. Two stretches of road with high levels of sightings but few road-kills were the Atherton–Yungaburra road and the Malanda end of the Atherton–Malanda road.

Road environment

Pearson *r* indicated significant within-group correlations between road-environment measures (i.e. visibility, mown width, verge width) and independence of road width (Table S1, available as Supplementary Material to this paper). In addition, moderate collinearity was also found between the variables associated with visibility and mown width. A significant non-linear correlation was found between total verge width and presence of a steep bank (Table S2).

Logistic regressions showed that visibility and total verge-width classes were the only non-inter-correlated variables or factors to influence road-kill probability independently, with total verge width having a larger effect (Table 1). As these variables were independent, they were suitable for combining in regression analysis. After accounting for total verge width, the size of the effect and the significance of minimum visibility increased (Fig. 4). A non-significant interaction indicated that the influence of the two variables was additive. Presence of a steep bank, drainage line or guard rail did not contribute significantly to any model.

Traffic volumes

Within the core distribution of tree-kangaroo, highest traffic volumes were on the Kennedy Highway between Walkamin and Atherton for both classes of vehicle (Fig. 3*c*). High volumes also travel from Atherton to and beyond Malanda and Yungaburra, or to Herberton. Lower levels of traffic travel between Yungaburra and Malanda, and least traffic is

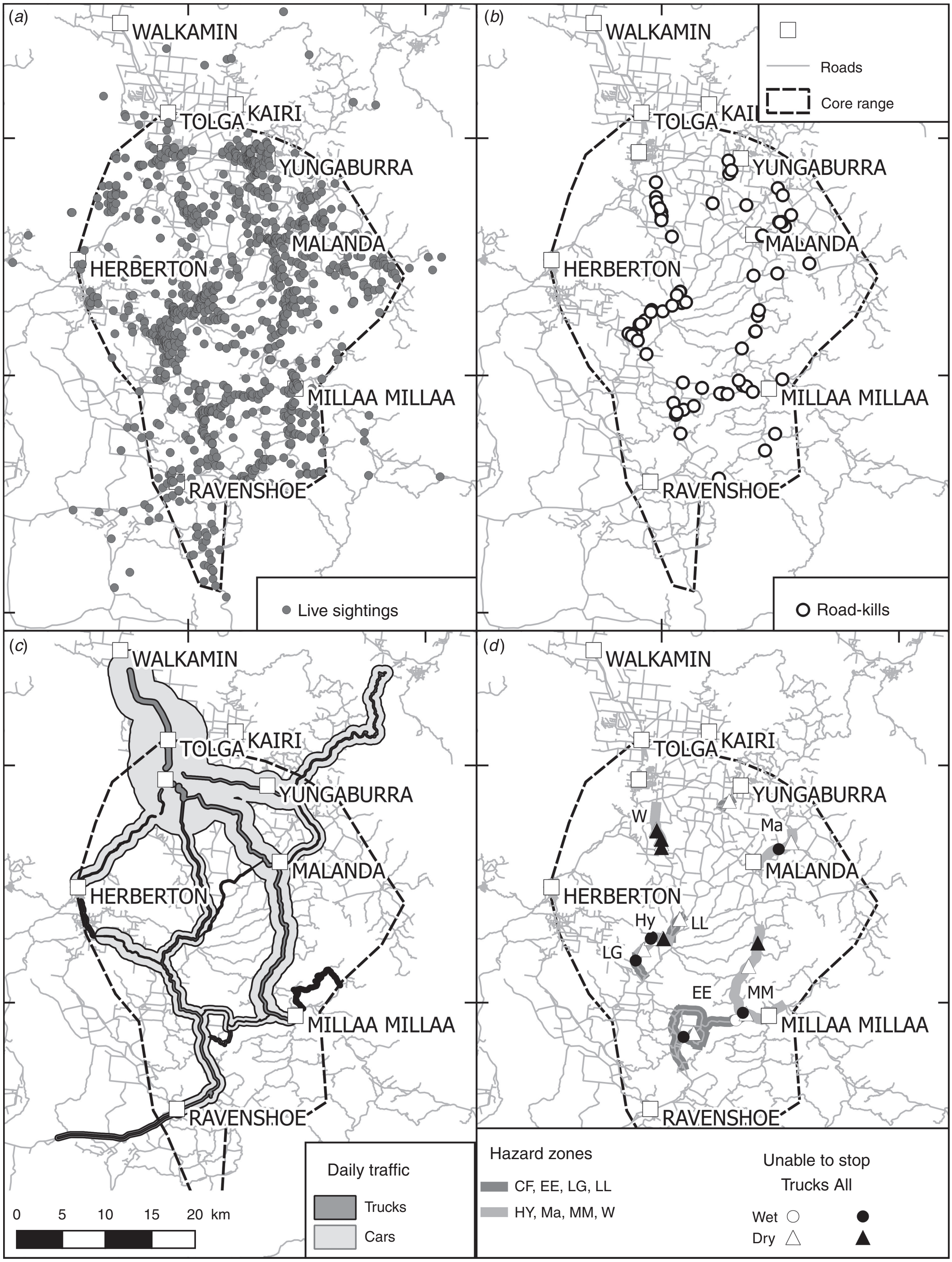

Fig. 3. Lumholtz's tree-kangaroo records and traffic conditions across the species' core habitat (dotted line): (*a*) live sightings from historical dataset; (*b*) recent road-kills; (*c*) daily average traffic volumes (linear scale, maximum heavy vehicles 674 and maximum light vehicles 8640); and (*d*) hazard zones.

Table 1. Comparison of binomial models used to assess factors affecting Lumholtz's tree-kangaroo road mortality on the basis of corrected Akaike information criteria (AICc)

Statistics for intercept (i) in null model apply to all other models in each group

Model rank	Model	Residual d.f.	χ^2 residual deviance	*P*	k	AICc	ΔAICc	Weight (%)
1	i + total verge width (<15 m, >15 m)	102	135.9	0.004	6	137.3	0.0	54.2
	+ minimum visibility (<50 m, 50–100 m, >100 m)	100	126.0	0.007				
	+ interaction	98	125.5	0.800				
2	i + total verge width (<15 m, >15 m)	102	135.9	0.004	2	138.0	0.7	38.6
3	i + minimum visibility (<50 m, 50–100 m, >100 m)	101	136.3	0.020	3	142.6	5.2	4.0
4	*Null model* – intercept (i)	103	144.2	n/a	1	146.2	8.9	0.6
5	i + min verge width (m)	102	142.2	0.161	2	146.3	9.0	0.6
6	i + total mown width (m)	102	143.0	0.271	2	147.1	9.7	0.4
7	i + steep bank (yes, no)	102	143.2	0.326	2	147.3	10.0	0.4
8	i + low rail (yes, no)	102	143.3	0.336	2	147.4	10.0	0.4
8	i + drainage line (yes, no)	102	143.5	0.403	2	147.6	10.3	0.3
7	i + minimum mown width (m)	102	143.8	0.537	2	147.9	10.6	0.3
8	i + road width (m)	102	143.8	0.550	2	147.9	10.6	0.3

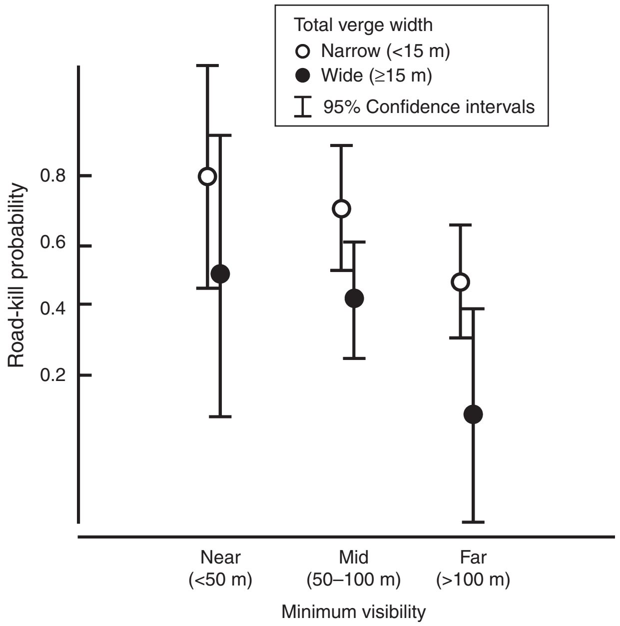

Fig. 4. Influence of total verge width and visibility classes on the probability of Lumholtz's tree-kangaroo road-kill.

found on the minor distributary roads. Road-kill incidence was significantly elevated along sections of road carrying medium volumes of traffic, regardless of vehicle class (light vehicles: $\chi^2_{\mathrm{d.f.}\ 2} = 6.63$, $P = 0.036$, $n = 66$; heavy vehicles: $\chi^2_{\mathrm{d.f.}\ 2} = 6.32$, $P = 0.043$, $n = 66$; total vehicles: $\chi^2_{\mathrm{d.f.}\ 2} = 6.63$, $P = 0.036$, $n = 66$).

Hazard zones

Seven hazard zones were identified with at least six recent road-kills within 8 km of roadway (Table 2, Fig. 3*d*). Of these, five had previously been identified as black spots, and two were newly identified. Since the previous study, the speed limit at the only previously identified black spot that was not identified as a hazard zone in this study had been reduced to 60 km h^{-1} or below and a tree-kangaroo warning sign had been erected at one end. Speed limits within other hazard zones varied between 40 and 80 km h^{-1}, and, in three cases, were up to 100 km h^{-1}. Each hazard zone contained sections through which a vehicle travelling at the mandatory or advisory speed-limit would be unable to stop in time to avoid striking a tree-kangaroo on the road (Fig. 3*d*), or where stopping distances were marginal (Table S3, Fig S1). For the 38 road-kill sites for which visibility data are available within these zones, all vehicles would be unable to stop at 18% of sites when the road is dry and 34% when the road is wet. For trucks, these values were 68% and 71%. Of nine tree-kangaroo warning signs found on Atherton Tableland roads during the study, only three were located within 1 km of a hazard zone (Longlands Gap and Lumholtz Lodge), leaving four hazard zones with no effective warning signs, and three with warning signs from one direction only. Three underpasses along East Evelyn road were located within the East Evelyn hazard zone. Two tree-kangaroo warning signs have since been erected on an upgraded stretch of East Barron Road, but neither is located at the start of or within an identified hazard zone. Between 50% and 75% of the tree-kangaroos killed in hazard zones were male.

Discussion

The present paper has shed new light on the reasons for road mortality among Lumholtz's tree-kangaroos. We showed that road-kill incidence is greatest for male and adult-sized animals, is density dependent and occurs at similar locations over time. We showed that speed limits in several hazard zones in which at least six animals had been killed over a 4.4-year period were inadequate to prevent such collisions. We also found that the only previously identified black spot that did not meet our hazard-zone criteria was where speed limits had been reduced to 60 km h^{-1} or below and a tree-kangaroo warning sign had been erected in the intervening period. We demonstrated, for the first time, how aspects of road design (i.e. narrow verges and poor visibility) increase road-kill risk for Lumholtz's tree-kangaroo and showed the ineffectiveness of existing road signage. We expand on these findings below and discuss their management implications.

Table 2. Lumholtz's tree-kangaroo road-kill hazard zones

Hazard-zone codes shown in parentheses. A, Tree Kangaroo and Mammal Group (2000); and B, Kanowski *et al.* (2001)

Road section	Hazard zone in this study	Number of road-kills	Male : female ratio	Distance from caution sign (km)	Speed limit range (km h^{-1})	Black spot in earlier studies	Comments
Hypipamee Crater (CF)	Yes	7	2.5	4.4, 5.4	40–80	A	Continuing problem, slight difference in defined area
Longlands (LG)	Yes	7	6.0	7.8, 1.0	40–80	B	Continuing problem, slight difference in defined area
Lumholtz Lodge (LL)	Yes	6	1.0	0.5, 7.6	60–80	–	Newly identified
East Evelyn (EE)	Yes	10	2.3	7.9, 4.1	40–80	A	Continuing problem, slight difference in defined area
Malanda–Millaa Millaa (MM)	Yes	12	2.0	6.3, 2.4	60–100	A, B	Continuing problem, slight difference in defined area
Malanda (Ma)	Yes	7	6.0	1.9, 10.1	40–100	A	Continuing problem, slight difference in defined area
Wongabel (W)	Yes	10	1.5	n.a., 20.5	100	–	Newly identified. An additional 6 road-kills recorded after the conclusion of this study (Apr. 2017 – Jan. 2018).
Curtain Fig (CF)	No	2	1.0	0.6, 15.5	40–60	A, B	Reduced problem. Speed limit reduction

Contributing factors

The strong association between road-kills and population distribution indicates that road-kills are density dependent, so animals are likely to be killed on the roads wherever the species occurs in large numbers. Similar patterns are seen in other large cryptic animals, such as the southern cassowary (*Casuarius casuarius johnsonii*; Dwyer *et al*. 2016). For both species, persistence of high levels of vehicle strike suggests a stable, rather than a declining, population. Predominance of young adult males among road-killed Lumholtz's tree-kangaroos is highly suggestive of a behavioural driver, supporting Newell's view that these animals are dispersing from the maternal home range (Newell 1999*a*). The unpredictable nature of such movements, and of subsequent efforts of young adult males to avoid conflict with older males (Procter-Gray 1985; R. Martin, pers. comm., 14 July 2018), does not support existence of regular movement corridors that might be managed using rope bridges or underpasses. Although dispersal of young males might be expected to produce seasonal road-kill patterns, this was not supported by our data, despite sightings of the species being elevated between August and November (Heise-Pavlov and Gillanders 2016). Nor were road-kills elevated at the wettest time of the year, despite the increased risk of collision (Queensland Government 2017). Larger datasets with assessment of rainfall at the time of collision may help establish any such relationships.

We also found that the road environment influences road-kill incidence, which increases as verge width and visibility decrease. Narrow verges limit the options for drivers and animals to avoid collisions. Low visibility reduces the time drivers and animals have to respond to a perceived collision risk. A significant peak in road-kill associated with moderate traffic flow is also likely to be an artefact of road design, because the high-volume routes in the region mostly have straight and wide road corridors. Although there is likely to be an interaction between traffic volumes and road environmental variables, it was not possible to assess this relationship in the present study, because the influence of environmental variables was assessed after controlling for traffic volumes.

Other studies have demonstrated that risk of collision is further increased where speed limits do not account for the time drivers need to react to animals on the road, and by any type of driver impairment or distraction (Petridou and Moustaki 2000). Whereas poor weather may also increase collision risk, wet road conditions may not (Andrey and Yagar 1993), which may explain the lack of seasonal patterns in our study. Calculation of stopping distances on the basis of line-of-sight alone does not take into account the visibility of the animal, which can be particularly poor at night. Night-time detectability of Lumholtz's tree-kangaroos is likely to be similar to that of the similarly coloured Tasmanian devils (*Sarcophilus harrisii*), i.e. 60 m on high beam and 34 m on low beam (Hobday 2010), regardless of the visibility along the road corridor. On the basis of this assessment, even on straight roads, driving speeds of 38–54 km h^{-1} would be required to avoid collision with a tree-kangaroo at night. Although the actual speed of vehicles involved in collisions with tree-kangaroos is unknown, 88% of the sites where road-kills occurred had speed limits higher than this. Therefore, we conclude that excessive speed is the ultimate cause of most road-kills for Lumholtz's tree-kangaroo.

Our results reaffirmed the location of most previously identified black spots for Lumholtz's tree-kangaroo (Kanowski *et al*. 2001), extending them into hazard zones, and identified two new hazard zones. Minimal tree clearance between the two periods suggests that these new zones are more likely to be the result of new information than of vegetation change. The only identified black spot not also classified as a hazard zone was where the speed limit had been reduced and a single tree-kangaroo warning sign had been erected at one end, suggesting that a combination of approaches may be needed to reduce mortality risks. High rates of tree-kangaroo road deaths continue to occur despite placement of at least eight other warning signs on the Atherton Tablelands, at least partly because of poor placement of six of them. Even so, in the two other cases where warning signs were positioned within 1 km of a hazard zone, high levels of road mortality have continued.

The newly identified hazard zone at Wongabel State Forest is within the 11th most dangerous section of highway in Queensland, on the basis of the number of human casualties per vehicle-kilometre travelled (Smith and Wikman 2007). It is typified by narrow verges, poor visibility, medium traffic volumes and high speed limits, all being significant risk factors for tree-kangaroos. The two stretches of road on which road-kills are lower than expected (Atherton–Yungaburra and Atherton–Malanda) have features that we found to characterise a low road-mortality risk, i.e. high traffic volumes, wide verges and good visibility. We observed that low guardrails along narrow, winding roads, which have often been cut into a steep slope, prevented animals moving off the roadway, although low numbers of such features in our study area precluded them having a significant influence at a population scale. However, any increase in their installation could become a future problem for the species. Other road-design features that influence the ability of an animal to move on or off the road (e.g. drainage line or steep bank) may affect casualties among some species (Goosem 2007), but were not significant in our study.

Mitigation measures

The present findings showed that options for mitigating tree-kangaroo road mortalities are extremely limited. Other studies have found wildlife warning signs to be of limited effectiveness (Bond and Jones 2013). Signs are even less likely to be effective when not strategically placed, as was the case for most signs in our study area. Nor have three underpasses constructed along the East Evelyn Road in 2001 (Goosem 2003) reduced the road-kill incidence of Lumholtz's tree-kangaroo. While the species has been recorded in one of these underpasses, we recorded 10 tree-kangaroo deaths along the section of road containing them. The unpredictable nature of young males fleeing conflict may explain why high mortalities continue where underpasses have been installed. Canopy connectivity and arboreal rope bridges that benefit 'gap-limited' species (Weston *et al*. 2011; Soanes and van der Ree 2015) are also likely to be of little benefit to tree-kangaroos. Indeed, our findings suggest that high canopy connectivity (associated with narrow roads, minimal verges and trees close to road edges) may actually increase tree-kangaroo road mortality, a conundrum identified by Laurance *et al*. (2009).

To be effective, mitigation measures must actually deter tree-kangaroos from crossing roads, improve visibility and escape options, and reduce the speed of vehicles. Fences, used effectively elsewhere, have yet to be used as a mitigation measure in the Wet Tropics (Goosem 2012). It is not known whether fences would be effective at preventing tree-kangaroos from crossing roads and studies would need to be conducted to determine whether fencing sections of roads is a viable option to reduce road deaths. Speed-limit reduction, traffic calming or effective fencing along either side of the road through the 2-km Wongabel hazard zone could prevent deaths of ~10 tree-kangaroos a year; and similar measures along 10 km of the Kennedy Hwy south of Lumholtz Lodge (17.41°S, 145.52°E) could reduce annual tree-kangaroo deaths by one-third (Fig S1). Improving visibility along road corridors and increasing the width of verges to at least 7.5 m on either side of the road are also likely to reduce deaths, because these measures provide both drivers and animals with more time to take evasive action and more space to avoid collisions. We recommend slashing of roadside vegetation wherever weeds and tall grasses have encroached on the road corridor. However, clearing native forest, and straightening or widening the road corridor, although likely to reduce tree-kangaroo deaths, are both expensive and likely to have adverse effects on other wildlife (Goosem 2001). This leaves reducing driver speeds, which are the ultimate cause of tree-kangaroo road deaths, as the cheapest and most effective mitigation option. To reduce accident risk to both tree-kangaroos and other road users (including cyclists), speed limits should be reduced wherever stopping distances are recognised as inadequate to prevent collision (Queensland Government 2017), particularly through the seven hazard zones identified in the present study (Table 2). Speed cameras, rumble strips and speed bumps, which have been effective elsewhere, are worthy of consideration (Mkanda and Chansa 2011; Gubbi *et al*. 2012). Although public education has limited or unproven value (Bond and Jones 2013), combined with these other measures, it may help enhance their effectiveness. Continued monitoring of the tree-kangaroo population and road-kills will be important for assessing the effectiveness of any mitigation measures.

Conclusions

The present study has highlighted the importance of understanding both species biology and road environments so as to develop effective strategies to reduce wildlife road-kill. Despite being a semi-arboreal species, Lumholtz's tree-kangaroo requires different solutions than those found to be effective for other canopy-dwelling species. Unpredictable dispersal patterns of young adult males that predominate in the road-killed population also precludes underpasses being an effective solution for this species. We conclude that excessive speed limits are the driving factor behind most road mortalities in places where road design provides few collision-escape options. We propose traffic calming and reducing speed limits, along with road-verge maintenance as the most effective mitigation strategies for reducing road mortality of Lumholtz's tree-kangaroo.

Conflicts of interest

The senior author is vice-president of the Tree Kangaroo and Mammal Group. Otherwise, the authors declare no conflict of interest in respect of this study.

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