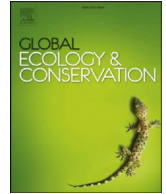




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Where wildlife and traffic collide: Roadkill rates change through time in a wildlife-tourism hotspot



Anthony R. Rendall^{a,*}, Vicki Webb^a, Duncan R. Sutherland^b, John G. White^a,
Leanne Renwick^b, Raylene Cooke^a

^a Deakin University, Geelong, Australia. School of Life and Environmental Sciences, Faculty of Science, Engineering and the Built Environment, 221 Burwood Hwy, Burwood 3125, Victoria, Australia

^b Conservation Department, Phillip Island Nature Parks, Cowes 3922, Victoria, Australia

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ABSTRACT

Understanding when and where roadkill is most likely to occur is vital to reducing wildlife-vehicle collisions. However, little is known about how roadkill rates change through time and whether or not the key influences on roadkill also change. Understanding changes in roadkill will facilitate the best implementation of mitigation measures. We aimed to determine how roadkill rates have changed between two distinct time periods and assess whether the spatial and temporal drivers of roadkill rates may have changed: with a view to informing taxon-specific mitigation strategies. We assess the spatial and temporal factors that influence road mortalities in two periods (1998–1999 and 2014) at the same site for multiple taxa. Bi-weekly surveys were undertaken from February to May 1998 and 1999 and again from February to June 2014. In total 2479 individual roadkill were recorded throughout the surveys, with 1.59 roadkill per km per month in the 1990s, increasing to 2.39 per km per month in 2014. Roadkill rates increased primarily with road speed limit with mortalities peaking at moderate (60–80 km/h) speeds, however, the structural complexity of roadside vegetation influenced roadkill rates for some taxa but not others. We show that roadkill rates have changed through time with shifts in both the temporal and spatial influences on these roadkill rates. These changes are likely associated with changes in the abundance of taxa and increased vehicle traffic. The spatial and temporal drivers of roadkill rates were found to be taxon specific, and although mitigation measures exist, assessment of their efficacy remains a priority.

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1. Introduction

There is a considerable body of research globally focusing on the negative impact of roads on wildlife (Coffin, 2007; Taylor and Goldingay, 2010), however uncertainty remains for many taxa about whether roadkill rates and patterns change through time. Studies investigating the long-term patterns of roadkill often report that roadkill populations may fluctuate in response to shifts in species abundances (Brockie et al., 2009; Canova and Balestrieri, 2019; Gehrt and Clark, 2003), change in response to possible behavioural adaptation to roads (Brown and Brown, 2013) or in response to management efforts and landscape changes (Madden and Perkins, 2017). Understanding how roadkill rates change through time is critical, particularly in the

* Corresponding author.

E-mail address: a.rendall@deakin.edu.au (A.R. Rendall).

context of developing successful mitigation strategies. Implementing mitigation measures is complex (Eberhardt et al., 2013; Zimmermann Teixeira et al., 2017) and understanding both the spatial and temporal patterns of roadkill is vital for effective management (Ramp et al., 2005). This is particularly true in the case of successful conservation programs where wildlife populations are increasing, and hence the nature of wildlife-vehicle collisions is likely to change (Canova and Balestrieri, 2019).

Understanding the factors influencing roadkill rates is a focus within the scientific literature, although many studies are short-term (months to a few years). These studies highlight the capacity for roads to impact the viability of populations (Barbosa et al., 2020; Ramp and Ben-Ami, 2006), and restrict (Ashman et al., 2020; Wattles et al., 2018; Yokochi et al., 2015) or increase the movement of species populations around roads (Carthew et al., 2013; Planillo et al., 2018); yet few consider the long-term implications of these spatial influences of roads on wildlife. These processes could reduce or remove the prevalence of roadkill if populations are incapable of persisting, or shift the prevalence of roadkill to smaller roads where mitigation measures may not be prioritised (Zimmermann Teixeira et al., 2017); conversely shifts in the species community through removal of apex predators (Ritchie and Johnson, 2009) or conservation actions to reintroduce threatened species could increase or alter the composition of roadkill.

Conservation areas play a critical role in biodiversity conservation efforts, and their subsequent attraction to tourists make them an ideal location to consider potential changes in roadkill patterns. Traffic volume is known to be a significant contributor to roadkill rates (Taylor and Goldingay, 2010), with the timing of traffic an important additional consideration (Visintin et al., 2018). Tourism can have great financial benefits for local communities (Driml and Common, 1995), however, with increasing benefit there may also be an increased likelihood of wildlife-vehicle collisions (Garriga et al., 2012). This increased likelihood will impact species in different ways; in Europe species with higher population densities, smaller body sizes and that reach maturity earlier were at greatest risk (Grilo et al., 2020). Increased traffic volume may therefore have known implications for wildlife; yet further research is needed to understand how this may influence the spatial patterns of roadkill through time. It is therefore imperative that conservation landscapes adequately plan and implement mitigation measures that target species most at risk with a consideration of the potential changes in roadkill patterns; to do so, an understanding of long-term trends in roadkill rates is required.

Phillip Island, located in Victoria, Australia, provides an ideal case study to investigate how roadkill rates have changed through time. There are two factors that may have influenced changes in roadkill rates between 1998–1999 and 2014; increased visitation through ecotourism; and shifted wildlife abundances due to the successful suppression of an invasive predator. Phillip Island attracts over 1.85 million visitors annually, and this figure is expected to exceed 4 million visitors annually by 2035 (Tourism Victoria, 2014). The successful suppression of the red fox (*Vulpes vulpes*) may also have increased local wildlife abundances (Kirkwood et al., 2014) as well as on-going revegetation efforts. Little is known about the factors influencing wildlife mortality rates across the island's road network; or how changes in visitor numbers (and hence traffic volume) may influence wildlife populations. We use two datasets, one collected from 1998 to 1999 - with lower vehicle traffic and limited fox suppression; and another collected in 2014 with a substantial increase in vehicle traffic and effective fox suppression to investigate how roadkill rates may have shifted due to these landscape-level changes. More specifically we:

- 1) Compare how the species composition of roadkill between 1998–1999 and 2014 has changed. Predicting that species roadkill rates would increase due to a range of landscape-level changes.
- 2) Identify how roadkill rates are influenced by spatial and temporal factors for all roadkill in the 1998–1999 data and compare this with those influences identified for all roadkill in the 2014 data. We predicted these influences would remain constant through time, with the impact of these variables possibly being enhanced with increased roadkill.
- 3) Determine whether spatial and temporal influences of roadkill rates are taxon-specific for the 2014 data with a view to providing taxon-specific mitigation recommendations. We predicted taxa would show differing responses to spatial and temporal influences supporting the need to develop taxon-specific mitigations.

2. Methods

2.1. Study area

Phillip Island (38°29'S, 145°13'E) is located 120 km SSE of Melbourne, Victoria, Australia. The island is approximately 10,000 ha in size with 60% of land used for agriculture and 20% associated with urban developments. The remaining 20% of the landscape is a series of nature reserves managed for wildlife conservation (Fig. S1). There are more than 10,000 permanent residents on Phillip Island, a population which has doubled over the past two decades (Australian Bureau of Statistics, 2018), and is predicted to increase by a further 30% over the next 20 years likely resulting in further developments. In addition, over 1.85 million people visit the island each year (Tourism Victoria, 2014), an increase from an average of 644,000 between 1998 and 1999 (Phillip Island Nature Parks, 1999). The majority of visitors (93%) to the island are self-drive tourists, contributing to increased road traffic volumes (Street, 2012).

2.2. Roadkill data

We surveyed for wildlife killed by vehicles in two time periods (1) from 1st February to 31st May in 1998 and 1999 (1998: N = 56 days of sampling; 1999: N = 54) and (2) from 17th February to 1st June 2014 (N = 30). A circuit of six roads totalling 45 km

were surveyed from 1998 to 1999. In 2014, three additional roads were added, increasing the total route to 57 km. All pre-existing roadkill was removed prior to the commencement of each sampling period. Surveys commenced at 7:30 am and were undertaken by vehicles travelling less than 50 km/h. We extracted data collected during the 1990s that matched the sampling period of the 2014 data. Data collection during this period was conducted at least bi-weekly, although the day of survey varied. In 2014, surveys were conducted on Fridays (representing weekday roadkill) and Mondays (representing weekend roadkill), Phillip Island is one of the largest tourism attractions in Victoria with traffic and attendance to the island peaking over weekends. Vertebrate carcasses of all taxa were identified to species level with the date and location of each mortality recorded. All carcasses were marked and cleared from the road to avoid duplicate recordings. Wildlife rescuers were notified of this research and any carcasses encountered by them were left conspicuous for the surveyor.

2.3. Temporal covariates

The potential temporal factors influencing roadkill rates included climatic variables, weekdays versus weekends, and traffic volume. Traffic volume and weekday versus weekend were only available for the 2014 data. Climatic variables included maximum daily temperature and rainfall (averaged across the days between surveys) obtained from the Bureau of Meteorology (Bureau of Meteorology, 2016). These data were then averaged across three weather stations (Phillip Island Penguin Reserve, Rhyll and Ventnor) to generate island-wide estimates for each survey. Temperature and rainfall are both known to influence roadkill rates (Carvalho et al., 2017; D'Amico et al., 2016); with these effects species-specific – for example amphibian roadkill are often associated with lower temperatures, and reptile, bird and mammals at higher temperatures (D'Amico et al., 2016; da Rosa and Bager, 2012; Garriga et al., 2017). The wet season is often identified as a period with higher roadkill, although not necessarily due to increased precipitation (Braz and França, 2016). We include rainfall as its response is variable (i.e. D'Amico et al., 2016) and for its possible impact on driver visibility. For the 2014 data, the timing of the survey was included as weekday or weekend to quantify the impact of different traffic patterns throughout the week. Traffic volume was inferred from visitation rates to the 'Penguin Parade' the most visited tourist attraction on the island. The 'Penguin Parade' is situated on the opposite side of the island to the bridge which connects Phillip Island to the mainland meaning this metric represents visitors who have travelled across the island. No island-wide statistics on traffic volume were available.

2.4. Spatial covariates

To investigate the spatial influences of roadkill, each road was divided into 250 m segments (N = 230). Where short segments at the end of roads existed; segment lengths were adjusted comparably to ensure the entire road length was represented (mean segment length = 247 m; median = 249 m). For each road segment we calculated the speed limit, distance to nearest crest, bend, or freshwater body (rivers, farm dams, ponds or lakes), surrounding land use (urban or non-urban), and the amount of roadside vegetation (as measured by the mean height of vegetation within 10 m of the edge of the road for the length of the segment). Vegetation structural complexity was only calculated for the 2014 data and therefore not used in comparisons between time periods. Speed limits were treated as a continuous variable in all models. Distance to nearest crest or bend was included to account for reduced visibility caused by either horizontal (i.e. bend) or vertical (i.e. crest) road curvatures (Grilo et al., 2009). Distance to water was included as this is likely to be a limiting resource for many species and may influence road-crossing frequency (Fischer, 2018). All distance measures were calculated from the midpoint of each segment. Surrounding land use was classified as either urban (residential, commercial or car park regions) or non-urban (farmland and remnant habitat patches) as surrounding land uses can influence roadkill rates (Garriga et al., 2012). The level of structural complexity of vegetation adjacent to the road was included to quantify its potential to reduce visibility or provide habitat for wildlife (Finder et al., 1999; Taylor and Goldingay, 2010). Habitat structural complexity was calculated from LiDAR point cloud data collected in 2008. A digital elevation model (DEM) and a digital surface model (DSM) were generated representing the ground/topography and the highest point above ground (i.e. tree canopy) respectively. The DSM was subtracted from the DEM to produce a layer of habitat structure at a 1 m² vertical resolution. Each road segment was buffered by 15 m (representing 10 m of habitat either side of the road) with the mean vegetation height (hereafter 'vegetation structural complexity') for each segment. To quantify how roadkill rates related to species' density, the relative density of the swamp wallaby, the most frequently detected roadkill species was estimated (see Appendix 2).

2.5. Data analysis

All taxa were considered in our models; however, short-tailed shearwaters (*Ardenna tenuirostris*) were only included in the roadkill composition comparison. This species contributed to outliers within the historical data, when a considerable number of fledglings (~four months old) were killed along individual road segments around Cape Woolamai at the eastern end of the island (Rodríguez et al., 2017). In the 2014 dataset this species recorded very low mortality rates of fledglings attributable to near complete breeding failure of the species in 2014 (Sutherland unpublished data).

Generalised Additive Models (GAMs) were used to identify the drivers of roadkill across Phillip Island. For the 1998–1999 data, models were run for all roadkill combined and considered both daily and spatial influences on roadkill rates (2014 data was subset to the same road segments used in 1998–1999 for these analyses). Taxon-specific models were not run due to insufficient data. For the 2014 data, models were run for all roadkill combined and for the four taxonomic groups most

frequently detected: Swamp wallabies (*Wallabia bicolor*); possums (common brushtail possum (*Trichosurus vulpecula*) and common ringtail possum (*Pseudocheirus peregrinus*)); European rabbits (*Oryctolagus cuniculus*); and bird species. Like many other studies we had insufficient data on individual bird species to investigate more fine-scale trends. Additive models were chosen as it was expected 'distance' variables (i.e., distance to crest) and 'temperature' variables might have non-linear relationships with roadkill rates. Where there was no support for additive models, linear models were run (1998–1999 daily roadkill rate data only). Daily roadkill rates were calculated as the number of individuals within each taxonomic group killed on the road during a sampling period. These models were run with either a Gaussian or Poisson distribution depending on the data distribution. An offset was included within each model to account for unequal sampling periods (i.e., four weekdays versus three weekend days). Spatial roadkill rates were quantified as the number of individuals killed per 250 m road segment across the survey period; models were run with an underlying Poisson distribution. Where over-dispersion was present, a negative binomial distribution was used. All covariates were assessed for collinearity with all having a Pearson's correlation coefficient $r < 0.4$.

Global models were validated through visual assessment of residuals compared to fitted values, and residuals compared to each variable included within the model. Akaike's Information Criteria corrected for small samples sizes (AIC_c) backward selection was used to determine the most parsimonious model (Zuur et al., 2009), where the least influential variable is removed sequentially until the model no longer improves. Model selection results were screened for uninformative priors following Leroux (2019). Small sample size for the 2014 daily models meant global models were unable to be fit, we therefore considered competing models, including the effect of weekend and traffic volume in all models. All possible combinations of environmental parameters (mean maximum temperature, mean rainfall) were then considered across models. Models with a delta $AIC_c < 2$ were considered to have support. R-squared values were calculated to identify the explanatory power of each model.

All analysis was conducted in R (R Development Core Team, 2019) with GAMs conducted in 'mgcv' (Wood and Scheipl, 2014); model selection and R-squared values were calculated in 'MuMIn' (Barton, 2018).

3. Results

In 1998–1999, a total of 714 roadkill (1.59 mortalities per km per month) were observed on Phillip Island roads, compared with 688 (2.39 mortalities per km per month) in 2014. A total of 62 species were detected across both time periods including 13 mammals, 45 birds, three reptiles and one amphibian species (Table S2).

3.1. Compositional shift in roadkill rates

Roadkill rates of swamp wallabies (1998–1999: 0.06/km/month; 2014: 0.65/km/month); common brushtail possum (1998–1999: 0.03/km/month; 2014: 0.44/km/month), common ringtail possum (1998–1999: 0.01/km/month; 2014: 0.16/km/month), and masked lapwings (*Vanellus miles*) (1998–1999: 0.01/km/month; 2014: 0.07/km/month) all increased from 1998–1999 to 2014 (Fig. 1). To a lesser extent, overall bird roadkill rates have also increased (1998–1999: 0.29/km/month; 2014: 0.51/km/month). Roadkill rates for European rabbits and reptiles appear unchanged (Fig. 1; Table S2). Short-tailed shearwaters are the only species to have had a decline in roadkill rates (1998–1999: 0.65/km/month; 2014: 0.04/km/month).

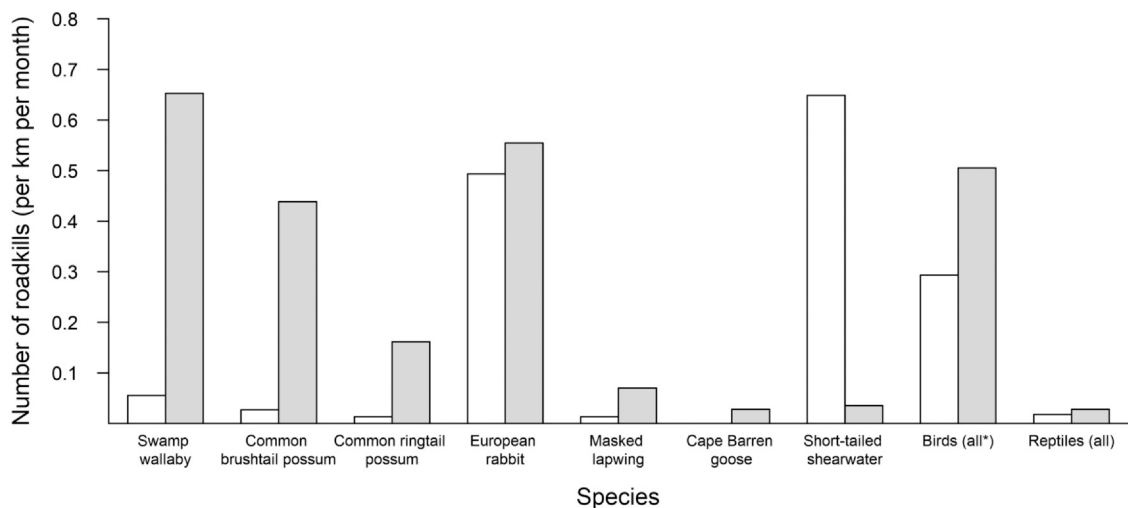


Fig. 1. The number of roadkill per kilometre per month between February and June 1998 and 1999 (white bars) and in 2014 (grey bars). Birds (all*) excludes short-tailed shearwaters.

3.2. Influence on daily roadkill rates in 1998–1999 and 2014

There was no support for the influence of either maximum daytime temperature or average rainfall on daily roadkill rates for the 1998–1999 data with the best supported model being a constant model (Table S3). The most supported model for all roadkill in 2014 included an effect of weekend versus weekday and maximum daytime temperature. There was limited support for an effect of traffic volume ($\Delta\text{AIC} = 2.29$; Table S3). Maximum daytime temperature had a positive influence on roadkill rates with more roadkill on days with higher temperatures ($\beta = 0.220$, 95%CI: 0.070–0.370). Roadkill rates were highest on weekends (6.89 roadkill per day; 95%CI: 5.53–8.58) compared to during the week (5.1; 4.09–6.36). This model explained 24.8% of the variation in these data.

3.3. Influence on spatial roadkill distributions in 1998–1999 and 2014

The best supported model for spatial distribution of roadkill in 1998–1999 included distance to crest, the level of urbanisation and road speed (Table S4). There was also support for more roadkill the further away from freshwater sources ($\Delta\text{AIC} = 1.84$; Table S4) although confidence intervals overlapped zero. Roadkill rates were greater further from crests ($\beta = 0.254$, 95% CI: 0.110–0.397), and highest at moderate speed limits (60–80 km/h) with lower roadkill rates at low (40 km/h) or high (100 km/h) speed limit roads. Rural areas had higher roadkill (2.95 per 250 m; 95% CI: 2.40–3.63) compared to urban areas (1.78 per 250 m; 95% CI: 1.23–2.56). The best supported model explained 19.5% of the variation.

The model for 2014 was similar to that for the 1998–1999 data with the exception of urban versus rural landscapes which was not supported (Fig. 2). The best supported model for roadkill in 2014 included an effect of road speed limit and distance to crest (Table S4). There was also support for an effect of roadside vegetation ($\Delta\text{AIC} = 0.81$) however, this was deemed an uninformative parameter. Road speed limit had a parabolic effect on roadkill rates with mortalities increasing along roads of 70–80 km/h before declining again along roads with speed limits of 100 km/h (Fig. 3). Roadkill was greater further from crests although confidence intervals overlapped zero ($\beta = 0.094$, 95% CI: -0.021 to 0.209). The top model of just road speed explained 15.6% of variation within these data.

3.4. Taxon-specific responses

Investigating taxon-specific trends, traffic volume was present in the top model for wallabies and possums (Table S5). As traffic volume increased, so did roadkill rates for both species with higher roadkill rates when there were more visitors (wallabies: $\beta = 0.274$; 0.039–0.508; possums: $\beta = 0.279$; -0.011 to 0.568). An outlier influenced the presence of a smooth term in the wallaby model suggesting roadkill rates plateaued at around 2000 daily visitors (Fig. S3), we therefore opted to exclude the outlier from these data. Maximum daytime temperature was in the best supported model for rabbits and birds, there was some support for an influence of temperature on possum roadkill; however, this was an uninformative parameter. Maximum day time temperature had a positive effect with roadkill rates increasing with increasing temperature for rabbits ($\beta = 0.517$, 0.222–0.812);

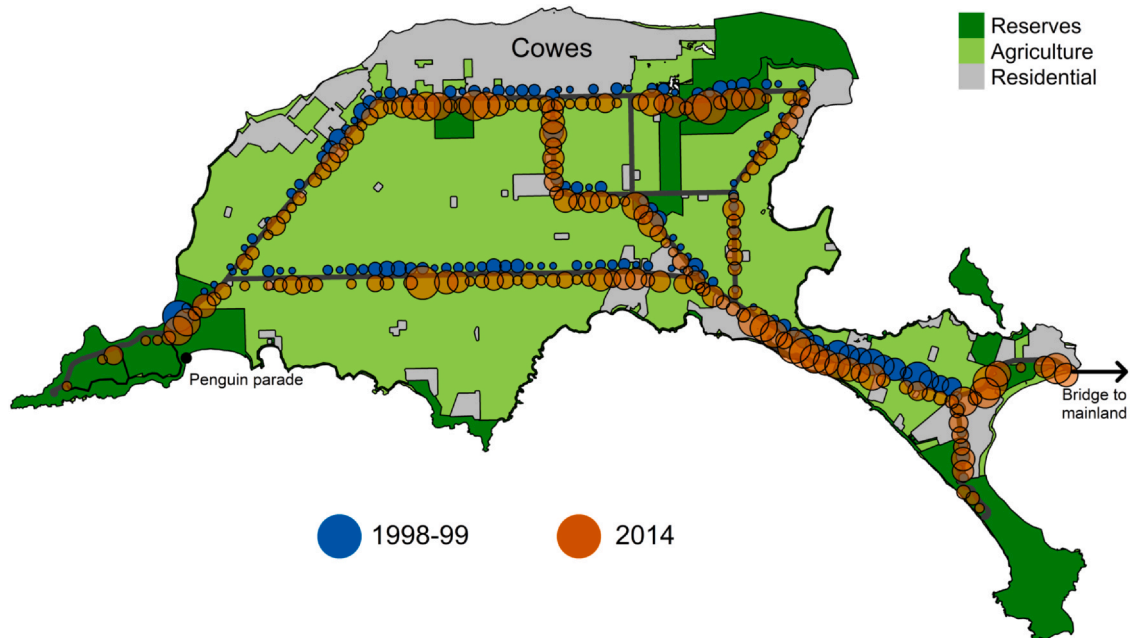


Fig. 2. Roadkill hotspots in 1998–1999 versus 2014 on Phillip Island between February and June. The size of dot represents the number of roadkill per segment per year (square root transformed). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

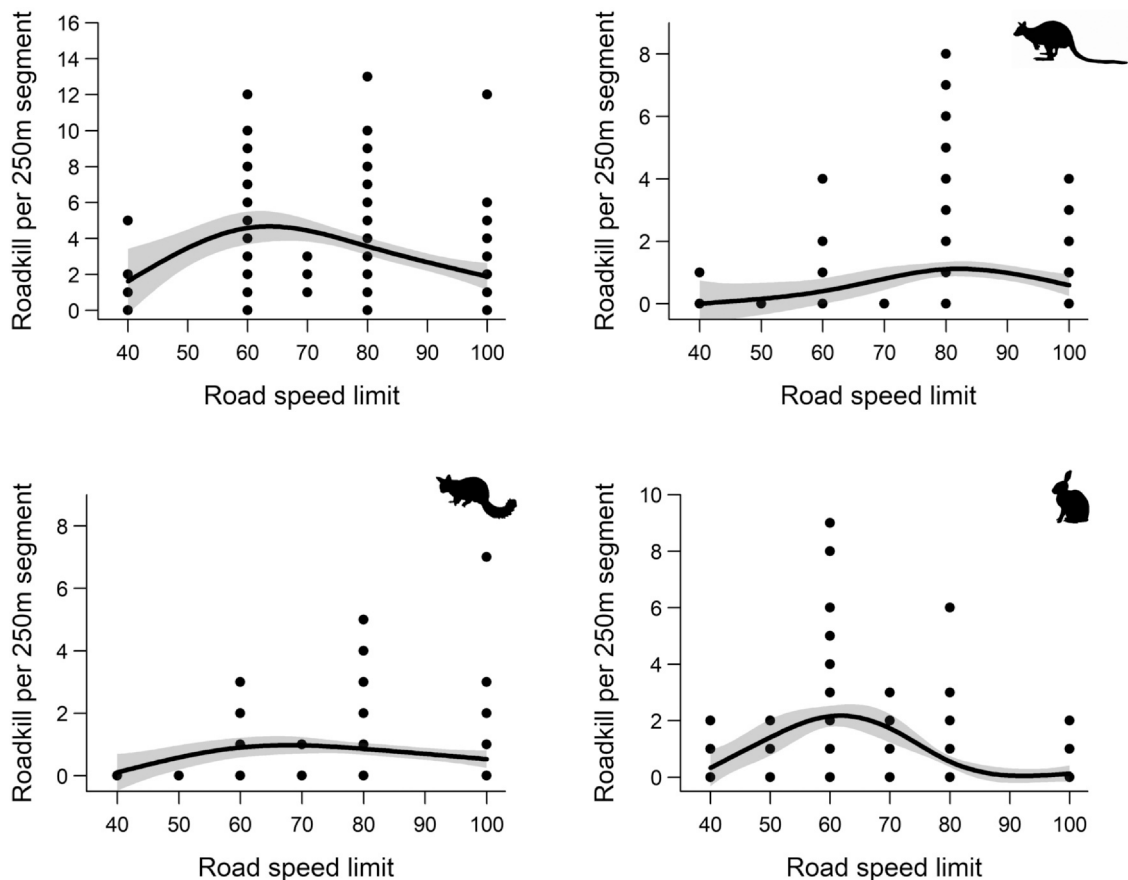


Fig. 3. Relationship between road speed and the number of roadkills (total, top left); for wallabies (top right), for possums (common ringtail possum and common brushtail possum, bottom left) and rabbits (bottom right) in 2014.

bird roadkill rates remained relatively constant at temperatures up to 20 °C but increased thereafter. Weekend versus weekday was in the top model for possums with some support for an effect on birds ($\Delta\text{AIC} = 1.14$; Table S5). Roadkill rates were greatest on the weekend for possums (weekend: 2.22 roadkill per day, 95%CI: 1.79–2.65; weekday: 1.47, 1.04–1.90) and birds (weekend: 1.24, 0.67–2.29; weekday: 1.09, 0.60–1.98). There was no support for an effect of rainfall in any taxon-specific models (Table S5).

The spatial influences on individual taxa roadkill rates differed (Fig. 4). Road speed limit was present in the top model for wallabies, possums, and rabbits (Table S6); however, was considered an uninformative parameter for bird roadkill rates. Peak road mortalities of swamp wallabies were observed at speed limits of 80 km/h, possum roadkill peaked at 60–80 km/h, and rabbits peaked at 60 km/h (Fig. 3). The level of urbanisation influenced roadkill for all species groups; for wallabies, roadkill rates were greater in rural environments (1.3 roadkill per 250 m, 95%CI: 0.98–1.78) when compared to urban environments (0.60, 0.34–1.04). Conversely, roadkill rates were greater in urban environments for possums, rabbits, and birds (possums = 1.06, 0.71–1.60; rabbits = 0.95, 0.68–1.35; birds = 0.92, 0.61–1.40) when compared to rural environments (possums = 0.75, 0.56–1.00; rabbits = 0.43, 0.32–0.58; birds = 0.66, 0.50–0.88). Roadside vegetation had a positive influence on possum roadkill rates with higher roadkill rates where more vegetation was present ($\beta = 0.267$, 95%CI: 0.077–0.456). In contrast, roadside vegetation had a negative influence on rabbit and bird roadkill rates with more mortalities where less vegetation surrounded road segments (rabbits: -0.198 , -0.434 to 0.039 ; birds: -0.1941 , -0.407 to 0.019 ; Fig. 5). Distance to crest had a positive influence on rabbit roadkill ($\beta = 0.149$, -0.023 to 0.320), but a non-linear negative influence on bird roadkill rates with higher rates close to crests declining sharply 900 m from the crest. There was no support for an influence of distance to water for any species. Distance to bend and wallaby density were both deemed uninformative parameters (Table S6).

4. Discussion

4.1. Compositional shift

Roadkill composition and volume shifted considerably from 1998–1999 to 2014. Increases in road mortalities of swamp wallabies, common brushtail possums, common ringtail possums and masked lapwings are evident. Two key changes occurred

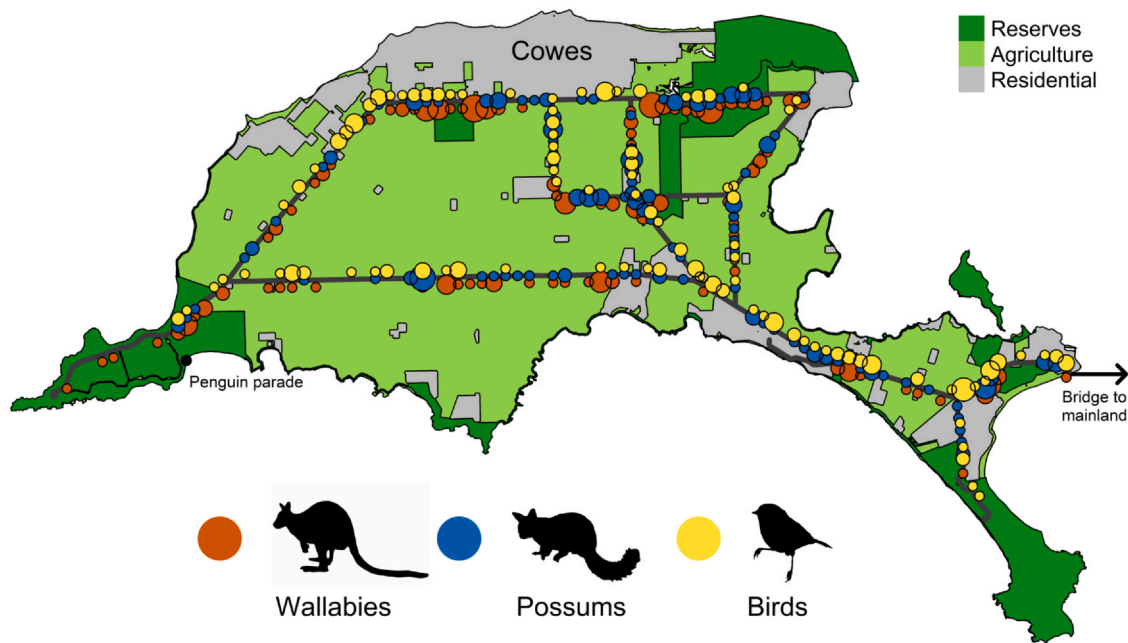


Fig. 4. Roadkill hotspots for different taxonomic groups across Phillip Island between February and June 2014. The size of the dot represents the number of roadkill (square root transformed) for Wallabies (orange), possums (blue) and birds (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between 1998–1999 and 2014 that likely contributed to this shift: 1) There has been an increase in road traffic volume due to increased human populations, both permanent residents and visitors; and 2) wildlife species composition and abundance has changed, potentially driven by shifts in top-down pressures associated with the effective control of red foxes and landscape changes. The clear shift in the amount and distribution of roadkill (Fig. 2) highlights the need for longitudinal studies to appropriately understand, and ultimately mitigate, road mortality of wildlife.

The increase in traffic volume across Phillip Island has likely increased the probability of roadkill. We found a limited relationship with traffic volume, although we did observe that weekends experienced greater roadkill frequencies than during the week, likely reflecting increased vehicle traffic on these days. This shift in roadkill has occurred despite speed limit reductions across many of the roads on Phillip Island since the 1990s. The increase in visitors between 1998–1999 and 2014 may therefore have contributed to higher roadkill rates due to a higher probability of a wildlife-vehicle collision (Farmer and Brooks, 2012; Taylor and Goldingay, 2010; Visintin et al., 2018). Dawn and dusk have been shown to correlate with increased mortality rates involving trains and wildlife (Visintin et al., 2018) and similar may be occurring on Phillip island with these periods coinciding with increased activity of nocturnal and crepuscular species. Therefore, the probability of a roadkill event may vary throughout the day and traffic pulses at certain times of the day may have a disproportionate effect on roadkill rates. However, there remains a paucity of data which consider the fine-scale timing of wildlife-vehicle collisions.

The composition of wildlife populations has shifted between 1998–1999 and 2014 and the abundance of several species has increased which may have led to the increased roadkill rates. Increased abundances of some species is potentially the result of successful fox control efforts (Kirkwood et al., 2014; Rout et al., 2014). The control or regulation of fox populations is correlated with increases in native species populations (Dexter and Murray, 2009; Robley et al., 2014) including swamp wallabies (Dexter et al., 2013) and possums (Dexter and Murray, 2009). On Phillip Island Cape Barren Geese have been observed to increase, a response correlated with fox suppression (Phillip Island Nature Parks, unpublished data), and predation events on little penguins (*Eudyptula minor*) have also decreased (Kirkwood et al., 2014; Sutherland and Dann, 2014). Hence an increase in wildlife populations around roads may result in increased wildlife-vehicle collisions, as has been shown with train-wildlife collisions (Visintin et al., 2018). We considered whether wallaby density directly influenced roadkill rates, although no clear trend was apparent within our data. Research has shown that wallabies frequently cross roads (Fischer, 2018), it may be that a finer-scale density distribution may be required to reveal these relationships. As species respond positively to control actions within conservation reserves, roadkill mitigation measures may need to be implemented pre-emptively to reduce mortality and facilitate dispersal (Barbosa et al., 2020; Yokochi et al., 2015).

4.2. Change in factors influencing roadkill rates

The spatial influences of roadkill changed between 1998–1999 and 2014. Roadkill rates in 1998–1999 were highest at moderate speed limits, further from crests and higher in more rural environments. In 2014, moderate road speed limits were

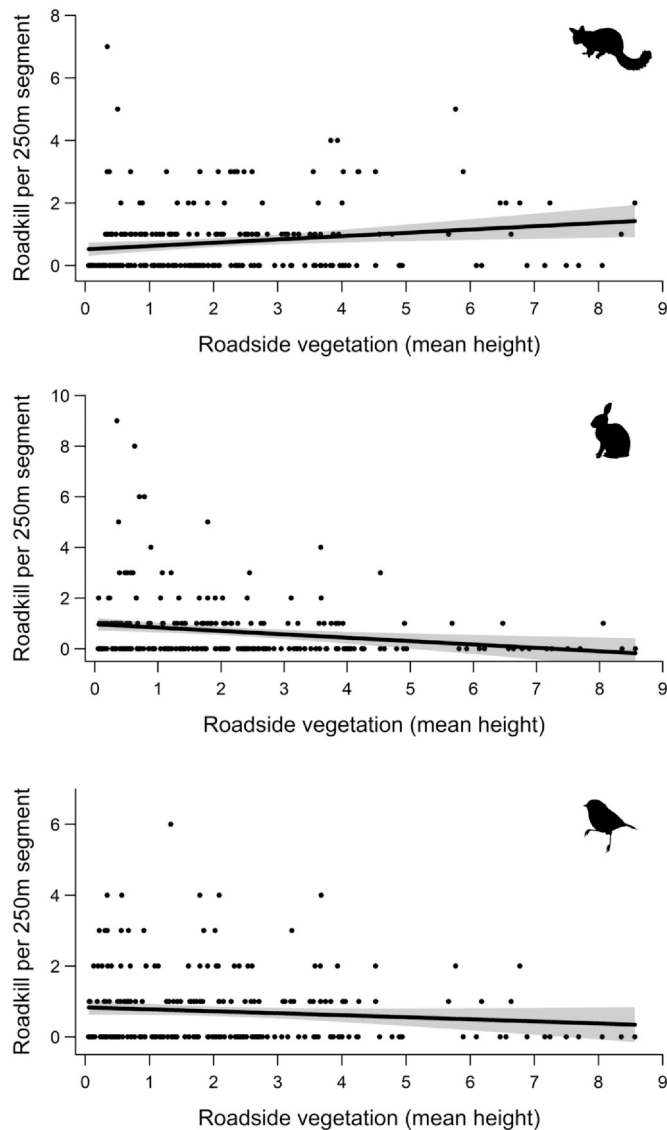


Fig. 5. Relationship between roadside vegetation and possums (common ringtail possum and common brushtail possum, top), rabbits (middle) and bird species (bottom).

found to influence roadkill rates with a similar effect of distance to crest, but there was no difference between urban and rural environments. Roadkill was higher in rural environments within the 1998–99 data, however, in 2014 possum, rabbit and bird roadkill were more prevalent within urban environments, while wallaby roadkill remained dominant in rural environments. This shift is likely attributable to increased wildlife abundances; this, in conjunction with fox control, is likely to have facilitated wildlife movement across Phillip Island and hence shift the prevalence of roadkill into more urban areas for some species, especially urban tolerant species like common brushtail and common ringtail possums (Isaac et al., 2014). It is likely that these contrasting species trends have contributed to the absence of urbanisation as influential within the 2014 model. Our results suggest that the spatial influences on roadkill rates may not change through time, with changes in roadkill more associated with landscape or population characteristics (Brockie et al., 2009; Canova and Balestrieri, 2019; Gehrt and Clark, 2003). Further research with the capacity to consider taxon-specific responses through time at varying population densities would assist in further understanding this outcome.

Daily roadkill rates in 2014 were positively associated with increased daytime temperatures, an association not observed in the 1998–1999 data. Bird roadkill rates increased notably at temperatures above 20 °C. Bird roadkill rates were higher in 2014 which may have contributed to a change in our capacity to detect a response. Species' activity is impacted by the prevailing weather conditions, and individuals often seek shelter during periods of peak heat (van Beest et al., 2012). However, birds, particularly insectivores, have been found to be more active as temperatures increase although this relationship is thought to be

limited in extreme heat (Lehmann et al., 2012). Hence, moderate temperatures likely reflect peak activity periods for birds increasing the likelihood of a collision. Daytime temperatures have also been found to influence rabbit activity periods; Villafuerte et al. (1993) showed that rabbits are often more active during mild temperatures, particularly at dawn. Conversely Ballinger and Morgan (2002) showed activity periods of rabbits decreased with higher temperatures. Our data suggests rabbits may be more active, and therefore more at risk of a wildlife-vehicle collision, at warmer temperatures, although it is likely this relationship may change at higher temperatures (Garriga et al., 2017).

4.3. Taxon-specific mortality

The drivers of roadkill showed contrasting results between taxa, supporting the idea that roadkill rates are taxon-specific (Bond and Jones, 2014). Road speed limits were the dominant influence on roadkill across taxa suggesting a reduction in road speed limits may provide the broadest benefits (Collinson et al., 2019). Higher speed limits reduce the reaction time of drivers and hence capacity to avoid a wildlife-vehicle collision (Collinson et al., 2019). Roadkill peaked at moderate speed limits for each species group. It is possible that these moderate speed limits already reflect higher risk areas for wildlife-vehicle collisions such as increased road traffic, particularly at night, and more roadside vegetation.

Roadside vegetation was influential for birds, possums, and rabbits, although responses differed. Possums were more likely to be recorded as roadkill in areas with a greater amount of roadside vegetation. These habitats likely influence roadkill through the provision of suitable resources close to the road network and the reduced visibility of wildlife to vehicle drivers. Animals are less conspicuous in roadside vegetation meaning driver response times are reduced making a collision more likely. Roadside vegetation may also provide valuable habitat for species (Carthew et al., 2013), improving body mass and possibly fitness in birds (Morgan et al., 2012) and mammals (Ben-Ami and Ramp, 2013). The resulting increases in abundance around the road network for such species could contribute to higher roadkill rates. Conversely, rabbits and birds were more frequently found as roadkill in open landscapes, likely reflecting their foraging modality with greater food availability in these landscapes. The weak trend of roadside vegetation and birds may reflect the diversity of birds detected including both ground-foraging (e.g. Cape Barren geese, masked lapwings) and aerial foragers (e.g. willie wagtail (*Rhipidura leucophrys*), wattlebird sp. (*Anthochaera* sp.)).

Swamp wallabies were the most frequently detected species (28% of all data). Road mortalities resulted in a loss of 4.9% of the total predicted population of the island within just four months of 2014. Previous studies have suggested that female road-mortality influenced population declines for swamp wallabies (Ramp and Ben-Ami, 2006), yet roadkill rates are male-biased (Coulson, 1997). Although wallabies were prevalent within our data, it is unclear whether road mortality has a population-level impact. The highest wallaby abundances are within faunal reserves where roads do not exist or are closed each night at dusk suggesting a population-level impact is unlikely, although wallaby density around roads are likely being limited (Fig. S2).

4.4. Management implications

Spatial models of roadkill offer directions for developing a management strategy to reduce interactions between wildlife and vehicles. Reducing roadkill rates can improve animal welfare outcomes, improve population viability (Barbosa et al., 2020), and reduce the economic or health impacts for motorists (Bissonette et al., 2008). However, no one mitigation method will be equally effective for all species, and its effectiveness may change through time, meaning wildlife managers may need to prioritise which species to focus on and the spatial influences that are most impactful. For Phillip Island, this is likely to be a trade-off between those species with the greatest human impact (i.e., wallabies) versus those species of specific conservation concern. Species such as rabbits are unlikely to warrant much consideration as an established pest animal in Australia.

The most direct way to reduce mortality for many species is through a reduction in the speed of vehicles (Collinson et al., 2019). Phillip Island could consider a two-speed road network, whereby high-risk conservation areas and urban centres are kept at or below 60 km/h and more rural areas at 80–100 km/h. Rural speed limits could then be reduced to 60 km/h around dawn and dusk when wildlife are most active. Train-wildlife collisions have been shown to be highest during periods of peak wildlife activity and suggested temporal timeframes of mitigation may be effective (Visintin et al., 2018). Time-specific mitigations around dusk, coinciding with increased activity of wallabies (Fischer et al., 2019), possums and peak traffic volumes on Phillip Island, may be most effective. The effectiveness of such measures are yet to be determined and represent a key area for future research.

Alternatives to speed-limit reductions may facilitate animals to avoid the use of the road network or prevent use altogether. For arboreal species such as possums, crossing structures like rope bridges placed in areas where vegetation structure is high on both sides of the road may reduce roadkill rates (Soanes et al., 2013). Although it is thought that these structures may assist in restoring functional connectivity (Soanes et al., 2018) there remains a need to determine the most effective configuration of these structures (Rytwinski et al., 2015). Road culverts have been used for terrestrial species like swamp wallabies (Ben-Ami and Ramp, 2013) and deer (Bissonette and Rosa, 2012) and are likely to be used by possums and birds. Despite culverts being used by a diversity of animals (Kleist et al., 2007), their effectiveness can vary (Delgado et al., 2018). Fencing readily prevents road crossings, reducing roadkill by up to 80% (Clevenger et al., 2001), however this fencing can also limit animal movements potentially having negative impacts (Jaeger and Fahrig, 2004; Jakes et al., 2018) including increased wildlife crossing at the ends of fences (Clevenger et al., 2001); fencing is therefore best implemented in conjunction with culverts (Bateman et al., 2017). Where fencing and culverts are constructed together roadkill reductions of 98.5% have been observed (Bissonette and Rosa,

2012), although predator-prey dynamics need to be considered; especially where predators are invasive (Harris et al., 2010). This combined approach is likely to be the most effective method to reduce roadkill rates in conjunction with rope bridges.

Birds represent the most complex group to mitigate roadkill for. A species' foraging modality, preferred habitat and morphological features all influence their roadkill rates (Santos et al., 2016) resulting in a wide diversity of responses. We, like many others, had insufficient data on birds with which to investigate species-specific responses, likely influencing some of the weaker trends in our data. The negative relationship with the structural complexity of roadside habitat, for example, is likely to be influenced by the high proportion of ground-foraging birds (i.e. Cape Barren goose, masked lapwing, purple swamphen (*Porphyrio porphyrio*), Table S1) who use open habitats. Alternatively this could reflect lower densities of some woodland birds around roads due to their sensitivity to noise pollution (Reijnen et al., 1995). Revegetation of roadside habitat may reduce habitat suitability for ground-foraging bird species but increase suitability for woodland birds and possums; hence decreasing roadkill rates for some while increasing it for others. Given the diversity of responses, targeted location-specific signage (Collinson et al., 2019) is recommended for areas with high roadkill rates of birds.

5. Conclusions

We demonstrate that within conservation landscapes roadkill rates can change in response to shifts in the conservation and tourism activities. To date, few studies consider the changing nature of roadkill rates and how these might influence the mitigation measures required (Zimmermann Teixeira et al., 2017). We reinforce, with a large sample size, that roadkill rates are taxon-specific and that combinations of mitigation methods are required to adequately address all roadkill. More research on taxon-specific roadkill rates and effective mitigation measures is required, and due to the frequency of roadkill, ecotourism destinations provide ideal locations in which to ask these important research questions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01530](https://doi.org/10.1016/j.gecco.2021.e01530).

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