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Spatial and temporal responses of swamp wallabies to roads in a human-modified landscape

Manuela Fischer, Milena Stillfried, Graeme Coulson, Duncan R. Sutherland, Stephanie Kramer-Schadt and Julian Di Stefano

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Roads can have significant impacts on wildlife populations by impeding movement, restricting access to resources and causing wildlife–vehicle collisions. In particular, wildlife–vehicle collisions represent a substantial conservation and social problem, and although mitigation measures are available, an increased understanding of the temporal and spatial patterns of animal movement around roads will enhance their effectiveness. We analysed GPS telemetry data from 47 swamp wallabies *Wallabia bicolor* on Phillip Island, south-east Australia, within patches of native vegetation dissected by roads. Our aims were to determine if (a) road crossing frequency was influenced by time period (day, night) or sex, (b) wallabies avoided roads, and if avoidance was influenced by time period or sex and (c) road crossing locations were associated with dense vegetation, and other habitat characteristics. We found that males crossed roads more often at night than during the day while females showed the opposite pattern. Further, wallabies avoided roads, with some evidence that avoidance increased at night ($p = 0.07$). The chance of a wallaby crossing roads with high speed limits ($80\text{--}100\text{ km h}^{-1}$) increased with vegetation density during the day but not at night. In contrast, vegetation density had no influence on crossing locations along roads with lower ($50\text{--}70\text{ km h}^{-1}$) speed limits during the day or night. Both vegetation density and vehicle speed may influence wallaby–vehicle collisions and suggest management strategies targeting these factors. Partial fencing guiding wallabies towards safer crossing locations, combined with other measures such as reduced speed limits and signage, could reduce collisions between vehicles and swamp wallabies on Phillip Island.

Keywords: correlated random walk, human–wildlife conflict, movement, road ecology, telemetry, *Wallabia bicolor*

The growing road network around the world represents a major form of environmental disturbance, which can have detrimental effects on wildlife (Forman and Alexander 1998, Spellerberg 1998, van der Ree et al. 2015). Roads can reduce and fragment habitat, and act as barriers to movement, causing animals to become isolated from vital resources and increased risk of death or injury from vehicle collisions (Forman and Alexander 1998, Spellerberg 1998, Shepard et al. 2008). For example, forest remnants in human-modified landscapes provide suitable habitat for many species, but are often surrounded and divided by roads, presenting a major obstacle to animal movement within and between remnants (Yokochi et al. 2016). Nevertheless, resource quality and quantity can be high

on roadsides (Forman and Alexander 1998), and while some species avoid roads (Whittington et al. 2005, Shepard et al. 2008, Stillfried et al. 2015), others are attracted to roadsides to access these resources (Grosman et al. 2011, Ben-Ami and Ramp 2013). However, attraction to roadside resources can increase the risk of road mortality. For instance, kangaroos in the Australian outback were killed more frequently along the road where they had come to forage on green roadside vegetation (Klößner et al. 2006).

Measures to reduce wildlife–vehicle collisions and increase landscape connectivity for wildlife, such as fencing, speed bumps and crossing structures, have been integrated into road designs for many years (Forman et al. 1997, Clevenger and Waltho 2000, Van Wieren and Worm 2001, Bond and Jones 2008). Less engineered mitigation measures can include seasonal wildlife signage, reduced speed limits, wildlife warning reflectors and road-side vegetation management (Pojar et al. 1975, Joyce and Mahoney 2001, Krisp and

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Durot 2007). However, it is critical to consider the temporal and spatial movement patterns of animals in the design of such mitigation measures (LaPoint et al. 2013).

Road crossings by wildlife, and hence patterns of wildlife–vehicle collisions, are often spatially and temporally aggregated. Patterns generally reflect the need of animals to access resources such as food, shelter and mates, and may be influenced by diurnal or seasonal cycles of species behaviour, road characteristics (e.g. speed limit, road size) and features of the surrounding landscape (Main and Allen 2002, Malo et al. 2004, Ramp et al. 2005, Gunson et al. 2011). For example, moose *Alces alces* showed bimodal daily road crossing peaks, as well as seasonal peaks during migration (Neumann et al. 2012), and the frequency of road-kills of common wombats *Vombatus ursinus* were associated with habitat features such as distance to water, elevation and slope (Ramp et al. 2005). Therefore, it is important to understand when, how frequently, and under what conditions animals will cross roads before effective management actions can be developed and implemented (Pojar et al. 1975, Malo et al. 2004, Ramp et al. 2005, Gunson et al. 2011).

Resource selection analysis offers a useful framework for identifying when, where and under what conditions animals cross roads, and thus will inform appropriate management action. Resource selection, the process underlying the use of resources by animals (Manly et al. 2002, Fahrig 2007), can be influenced by many factors, such as the risk of predation (Fischhoff et al. 2007), food quality (Di Stefano et al. 2009), intra- or inter-specific competition (Rosenzweig 1981), sex and reproductive status (Johnson and Bayliss 1981) and temporal activity patterns, whether seasonal (Singh et al. 2012) or daily (Di Stefano et al. 2009). Inherently, resource selection is linked to animal movement (Nathan et al. 2008, Van Moorter et al. 2016), with movement decisions influencing the efficiency with which individuals can access resources in the face of multiple pressures and threats (Fahrig 2007, Nathan et al. 2008). The need to acquire resources and the various impediments to their acquisition combine with an individual's motion and navigation capacity, resulting in a movement trajectory or path that can be measured by consecutively relocating an animal through time. In this study we use trajectories from swamp wallabies *Wallabia bicolor* to determine their interaction with roads in a human-modified landscape.

Swamp wallabies are solitary, medium-sized (10.5–24 kg) macropodid marsupials that are widely distributed throughout eastern Australia (Kirkpatrick 1970, Swan et al. 2008, Allen and Mitchell 2016). The species selects habitat with dense cover (Lunney and O'Connell 1988, Troy et al. 1992) to feed on nitrogen-rich vegetation (Osawa 1990). At a finer scale, habitat selection by swamp wallabies can change throughout the 24-h cycle (Swan 2008, Di Stefano et al. 2009). They are known to feed in open areas during the night and return to habitats with thick cover during the day (Edwards and Ealey 1975, Fischer et al. 2019), with nocturnal habitat selection by females positively related to forage quality (Di Stefano et al. 2009). Nevertheless, swamp wallabies are generalist herbivores with a mixed diet (Di Stefano and Newell 2008) enabling them to persist in human-modified landscapes. In such environments they often use roadside vegetation (Ben-Ami and Ramp 2013),

and are often observed crossing roads, making them an ideal model species to investigate road crossing activity.

Many studies have investigated animal road behaviour based on data collected from fatal wildlife–vehicle collisions (Mader et al. 1990, Main and Allen 2002) and only some focus on 'successful' road crossing events (Kämmerle et al. 2017). Here, we investigated 'successful' road crossings by swamp wallabies, using global positioning system (GPS) telemetry to link road crossing locations to landscape characteristics that are associated with crossing locations. Firstly, we tested for differences in the number of road crossings between day and night and between sexes. Because swamp wallabies are more active during the night and shelter in dense vegetation during the day (Kirkpatrick 1970, Edwards and Ealey 1975, Swan 2008) we predicted that there would be more crossings at night (prediction 1a). Road-kills of macropods are generally male-biased (Coulson 1997), and swamp wallaby road kills recorded along major roads in our study area also showed a bias towards males (Rendall et al. 2021). Hence, we predicted that males would cross roads more frequently than females (prediction 1b). Secondly, we tested whether swamp wallabies avoid crossing roads because roads are known to impede movement for wildlife (Richardson et al. 1997, Rondinini and Doncaster 2002, Rico et al. 2007). We predicted that the number of observed road crossings would be less than expected by chance movements (prediction 2). Thirdly, we expected specific landscape characteristics to be associated with crossing locations. Macropods use vegetation strips to move between remnant vegetation patches (Arnold et al. 1995) and swamp wallabies avoid risky areas and select landscape features with dense vegetation cover (Fischer et al. 2019). Hence, we predicted that the choice of crossing locations would be positively correlated with vegetation cover (prediction 3).

Methods

Study site

We conducted the study on Phillip Island (38°29'S, 145°15'E), a human-modified landmass (10 000 ha), located in Westernport Bay, south-eastern Australia (Fig. 1). Besides high tourist visitation rates (1.85 million annually) (Bass Coast Council Shire 2016), the island has a steadily growing human population estimated at 10 387 residents in 2016 (ABS 2016). Topography is mostly flat, and the maximum elevation is 112 m a.s.l. (Gliddon 1958). The island's native grass and bushland areas were largely cleared by early settlers in the mid 1800s (Head 2000). Currently, about 32% of the island is patches of bushland and coastal scrub surrounded by open grassland (50%), housing estates (13%) and waterbodies (3%) (Fig. 1). In addition to these main land use types, a well-established road network (2%) is present and roadside vegetation is often dominated by swamp paperbark *Melaleuca ericifolia*. The two main remnant bushland areas consist of native or revegetated eucalyptus woodlands; within these some locations have a thick understorey dominated by austral bracken *Pteridium esculentum* and hop goodenia *Goodenia ovata*. Coastal areas include coastal scrub and woodlands, and riparian and swampy scrub.

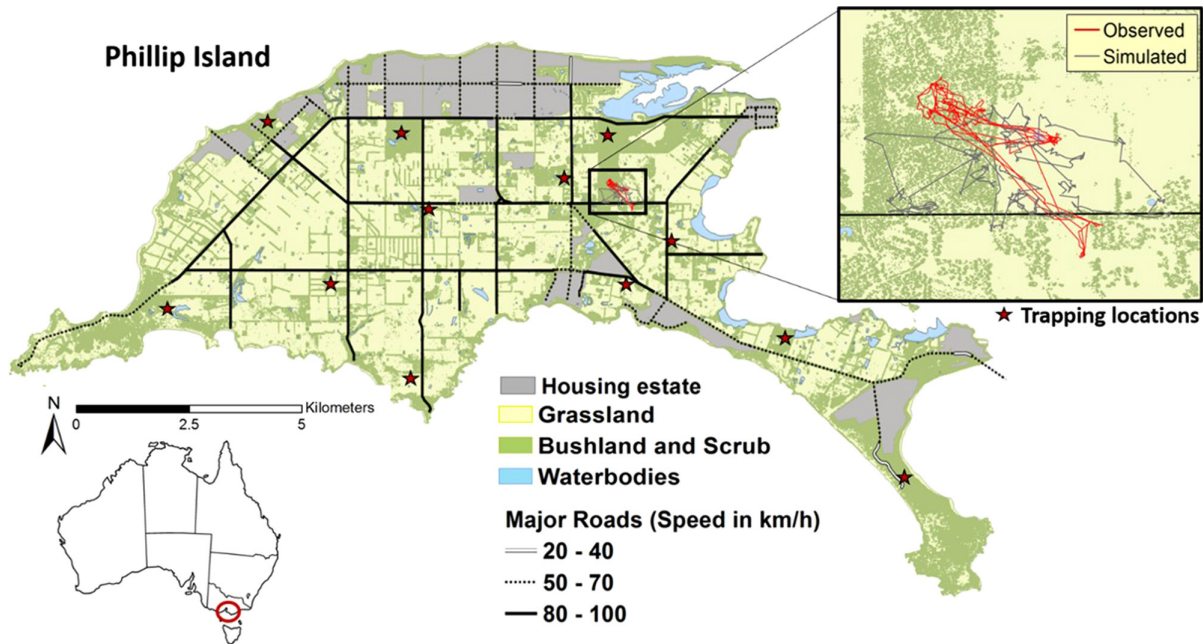


Figure 1. The study site (Phillip Island, Australia), showing the distribution of three dominant habitat classes and waterbodies. Red stars represent capture locations. The expanded map (right) indicates the observed trajectory of one wallaby (red) and the corresponding simulated trajectory (grey).

The largest native terrestrial mammal on the island is the swamp wallaby which is known to persist in human-modified landscapes (Di Stefano et al. 2009, Ben-Ami and Ramp 2013). Throughout their range, swamp wallabies have been recorded as frequent victims of vehicle collisions (Osawa 1989, Ben-Ami and Ramp 2013, Visintin et al. 2017), including on Phillip Island (Rendall et al. 2021).

Animal capture, handling and data collection

We captured wallabies (21 females, 26 males) from January 2015 to March 2017 across 12 locations on Phillip Island (Fig. 1). These locations were chosen so that they were evenly distributed across the island and stratified to be within or near two or more main land use types (Fig. 1). We captured wallabies using two methods. Some were captured in purpose-built double-layered traps (Di Stefano et al. 2005) set in the late afternoon, baited with carrots and checked the next morning. We sedated trapped wallabies with an intramuscular injection of Zoletil 100 (0.5 mg kg⁻¹) (Virbac Australia, Sydney). We darted other wallabies on foot during dusk and dawn using a tranquiliser gun (Pneu-Dart X-caliber), using the same dose of Zoletil as reported above.

We fitted healthy adult wallabies with custom-made GPS collars (Fischer et al. 2018). We scheduled the GPS collars with a 15-min fix interval, 24 h a day, seven days a week. GPS locations were sent remotely via the mobile phone network (Fischer et al. 2018). The life span of the collars was 3–10 days, and for each individual we sampled an average (\pm 95% CI) of 222 (\pm 39) locations during the day and 252 (\pm 44) locations at night. The Supporting information gives details of the captured wallabies and collected data. Targeted trapping allowed us to retrieve and redeploy some of the collars. We aimed for an unbiased sample across sexes and landscape features.

Data preparation

We collected 22 284 GPS locations from 47 swamp wallabies (21 females, 26 males) (Supporting information). We discarded fixes attained with < 3 satellites, horizontal dilution of precision > 8 , speed between fixes > 8 m s⁻¹ and elevation > 100 m a.s.l. using the online database Movebank (Wikelski and Kays 2014). We deleted GPS locations which occurred while trapping was being conducted and within 8 h after the sedation of an animal. Out of 23 496 locations, we discarded 1212 locations, including two fixes that were classified as biologically implausible.

An animal's movement trajectory or path is determined by species-specific motion and navigation capacity in combination with external factors influencing movement, such as the need to acquire resources, or the effect of pressures and threats. Movement trajectories can be estimated by consecutively relocating an animal through time. We used distributions of movement parameters (step length and turning angle) from observed wallaby movement trajectories as a basis for simulating plausible random trajectories to which observed trajectories could be compared. First, we created a polygon, which measured twice the square root of the 100% minimum convex polygon (MCP) derived from the original movement data. This buffered MCP100 determined the available area that could also have been potentially used by the wallaby, excluding unsuitable habitat such as ocean and water bodies (Roeleke et al. 2016, Stillfried et al. 2017). We then used an individual's observed movement trajectory, which represents the 'use' dataset, to generate correlated random walks (CRW) (Kareiva and Shigesada 1983, Stillfried et al. 2017). CRWs use the step length and turning angle of the observed trajectory to simulate random trajectories with identical sampling frequencies and time stamps. We generated one CRW per observed trajectory

with a randomly selected starting point within the available polygon, using the package ‘adehabitatHR’ (Calenge 2006) in the R statistical environment. These CRWs were used as the ‘availability’ datasets, which created a null model for the road avoidance and habitat characteristics analyses, while maintaining realistic movement distances and turning angles. The analysis of road crossing locations using CRWs allowed us to contrast the observed crossing locations and use of nearby habitat features with crossing locations and habitat features deemed available to each wallaby, corresponding to a classic use versus availability analysis.

To identify temporal differences in behaviour during the diel cycle we separated all data into day and night. We split the 24-h time cycle so that a day started at dawn and ended at dusk using the function *crepuscule* in the R package ‘maptools’ (Bivand and Lewin-Koh 2013). We then applied ‘points to lines’ to all data points using ArcGIS 10.4.1 (Esri 2011) to convert wallaby locations as well as the CRWs into trajectories (Fig. 1, 2). We used a road layer (Victoria State Government, Spatial Datamart, downloaded 29 May 2013) to classify major roads, categorised into three speed limits: 20–40, 50–70 and 80–100 km h⁻¹ based on road speed signs (VicRoads Transport Open Data API, VicRoads, downloaded 1 May 2017). We then identified intersections of the road layer with the trajectories and extracted the corresponding speed limit at each road-line intersection using the R package ‘rgeos’ and ‘sp’ (Bivand et al. 2017). No road crossing occurred at speed limits of 20–40 km h⁻¹ and we therefore excluded this category from the data set.

To determine whether crossing locations were spatially and temporally linked to specific land use types (housing estates, grasslands, bushland and scrub and waterbodies), we

extracted the percentage of each land use type (‘sf’ package, Pebesma 2018) within a 100-m radius circular area (3.14 ha) centred on crossing locations using the ‘rgeos’ package (Bivand et al. 2017). An area of this size was deemed large enough to account for the distance travelled between the two locations that defined each crossing; considering the four main portions of the data set separately (females day, females night, males day and males night) the maximum average distance between consecutive locations was ≤ 29.2 m and the 90th percentile of the distances was ≤ 72 m. Because the values for percentage of housing and water within the 3.14 ha sampling area were zero-inflated we converted the values to present (1) and absent (0) (Fletcher et al. 2005). Further, we used a point layer representing vegetation cover at 1-m resolution (Fig. 1) to estimate vegetation cover at crossing locations by calculating the number of points within each 3.14 ha sampling area. The layer was derived using colour spectral analysis of high-resolution aerial imagery to extract shadows cast by vegetation. All layers were plotted using R ver. 3.4.1 (<http://www.r-project.org>) and QGIS Desktop 2.18.12 (<http://qgis.osgeo.org>) with GRASS 7.2.1).

Data analysis

Road crossing frequency (prediction 1a and b; ‘use’ dataset)

We determined the association between the response variable ‘number of crossings per individual’, and the explanatory variables ‘sex’ (male, female) and ‘time’ (day, night) using a zero inflated negative binomial generalized linear mixed model (GLMM). Preliminary testing indicated that this model form was suitable to account for a substantial number

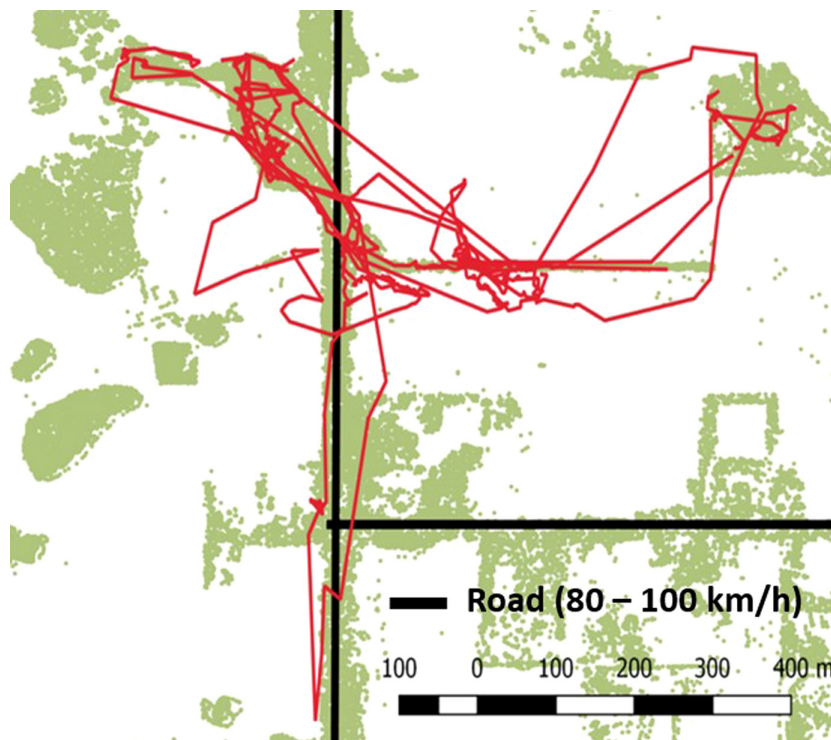


Figure 2. An example of a wallaby's movement path (red line) in relation to roads and vegetation cover (green). Crossing locations were defined as the point at which the movement path intersected the road.

of zeros in the data and also for underdispersion detected in a base Poisson model. A variable identifying each wallaby as a separate entity ('wallaby ID') was used as a random factor and, to account for unequal sampling effort between individuals, we included the total number of GPS locations per individual for each time period as an offset in the models. We built four models representing the effects of explanatory variables in single, additive and interactive combinations (models with interaction terms also contained the main effects of the interacting variables) and included a null model for reference.

Road avoidance (prediction 2; 'use' and 'availability' dataset)

For each individual, we subtracted the observed ('use') road crossing frequency from the corresponding simulated frequency generated by the CRW ('availability') so that a negative value reflected road avoidance. We used this quantity as the response variable in a linear mixed model (LMM) with Gaussian errors, building the same set of models described above. We tested model assumptions using graphical methods and no violations were detected.

Habitat characteristics (prediction 3; 'use' and 'availability' dataset)

We used a binomial response variable (observed crossings locations = 1 ('use'), simulated crossing locations = 0 ('availability')) to determine the effect of different habitat types on road crossing events. We included the presence or absence of housing estates, road speed limit (50–70 km h⁻¹, 80–100 km h⁻¹), time (day, night) and the vegetation cover index as predictor variables. We did not include the presence and absence of water as a predictor variable, as only four observed crossing locations included water within the 100 m buffer zone (Supporting information). We used a GLMM with a binomial error distribution and a logit link to contrast road crossing locations of wallabies with random crossings, with individual wallaby ID as a random factor. Based on previous research, we assumed that vegetation cover would be a key variable in influencing road crossing locations, therefore we produced a candidate set of models consisting of the null model, a vegetation cover only model and models including additive and interactive combinations between vegetation cover, housing, road speed and time.

We built models in the R statistical environment using the packages 'lme4' (Bates 2010) and 'glmmTMB' (Brooks et al. 2017) and for all three analyses (predictions 1, 2 and 3) selected the final models using Akaike's information criterion corrected for small sample size (AICc) and Akaike weights (ω_i) to indicate the degree of support within the model set (Burnham and Anderson 2002). Model fit was assessed by calculating marginal and conditional R² using the methods outlined by (Nakagawa and Schielzeth 2013). The marginal R² (R²m) refers to the variance explained by the fixed factors and the conditional R² (R²c) refers to the variance explained by both fixed and random factors. Model selection and R² calculations for mixed models were conducted using the package 'MuMin' (Bartoń 2016). For the zero inflated negative binomial model associated with prediction 1 we tested for overdispersion and underdispersion using the DHARMa package (Hartig 2019) and found no evidence of either. Because wallaby capture rate was low in winter (May–

November) (Supporting information), we did not include 'season' as a predictor variable in our models. The raw data are available from Movebank Data Repository: <<https://doi.org/10.5441/001/1.6ss053tn>>.

Results

Roads were accessible to 46 of the 47 individuals based on the polygon of available area calculated from their observed movements. Thirteen individuals crossed the road at least once whereas 32 individuals would have crossed roads based on simulated paths. In total, we identified 104 road crossings by wallabies and another 326 from simulated paths.

Road crossing frequency (prediction 1a and b; 'use' dataset)

The frequency of road crossings was most strongly influenced by the main effects of sex and time plus an interaction between sex and time (Table 1). However, the null model was within 1.3 AICc units and therefore had a similar level of support. Males crossed the road more often at night than during the day while females showed an opposite pattern, crossing the road more often during the day compared to the night (Fig. 3). Tests of our two predictions (1a; increased crossings at night and 1b; males cross more than females) using contrasts describing the difference in crossing frequency between males and females during both the day and night showed no clear support for either prediction (Table 2). Although males crossed roads 207% more frequently at night compared to the day (Fig. 3), the uncertainty associated with this effect was also large, preventing a clear conclusion.

Road avoidance (prediction 2; 'use' and 'availability' dataset)

On average wallabies crossed roads fewer times than expected based on simulated crossings generated from the correlated random walks, indicating road avoidance. The best AICc model included the main effect of time, providing some evidence that wallabies avoided roads more at night compared to the day (Table 1, Fig. 4). However, the null model was within 1.24 AICc units and therefore had a similar level of support; this model suggested that road avoidance was not influenced by time, sex or their interaction but that overall wallabies crossed roads 2.36 ± 1.44 (mean \pm 95% CI) fewer times than expected. This represents a 68% reduction in crossing rate compared to the rate expected from the correlated random walks.

Landscape characteristics (prediction 3; 'use' and 'availability' dataset)

The top ranked model in the model set included the predictor variables vegetation cover, time and their interaction, plus the additive effect of road speed limit. The chance of a wallaby crossing major roads with high speed limits (80–100 km h⁻¹) increased with vegetation cover during the day but not at night (Fig. 5A). In contrast, vegetation cover had little influence on crossing locations along smaller roads with

Table 1. Modelling summaries for the road crossing [1], road avoidance [2] and habitat characteristics [3] analyses. Models are ranked using Akaike's information criteria adjusted for small sample size (AICc), and models within 2 AICc units of the best are included, in addition to the null model. Akaike weights (ω_i) reflect the probability that the associated model is the best in the set. R^2_m is the variance explained by fixed effects while R^2_c is the variance explained by both fixed and random effects. Estimates and standard errors are included for the best model. Model terms include: time (day, night), sex (male, female), veg (index of vegetation cover), road speed limit (speed, 50–70 km h⁻¹, 80–100 km h⁻¹) and housing (present, absent).

Model	ΔAIC_c	ω_i	Terms	Estimate \pm SE	p-value	R^2_m (R^2_c)
[1] Road crossing frequency (response: number of crossings)						
Time \times Sex	0	0.49				0.27 (0.56)
			Male	-1.82 ± 0.82	0.03	
			Night	-1.10 ± 0.56	0.05	
			Male:night	2.22 ± 0.86	<0.01	
Null	1.13	0.28				
[2] Road avoidance (response: difference between observed and simulated crossings)						
Time	0.00	0.35				0.01 (0.68)
			Night	-1.19 ± 0.64	0.07	
Time \times Sex	0.52	0.27				0.03 (0.70)
Null	1.24	0.19				
[3] Habitat characteristics (response: road crossing index)						
Veg \times Time + Speed	0	0.50				0.08 (0.85)
			Veg	0.06 ± 0.02	<0.01	
			Night	1.81 ± 0.75	0.02	
			Speed 80–100	3.00 ± 1.69	0.07	
			Veg:night	-0.06 ± 0.03	0.05	
Veg \times Time + Veg \times Housing + Speed	1.19	0.28				0.13 (0.84)
Veg \times Time	1.80	0.21				0.01 (0.89)
Null	7.10	0.02				

lower (50–70 km h⁻¹) speed limits during the day or night (Fig. 5B). The second and third ranked models were within 1.8 AICc units of the best model and therefore had a similar level of support (Table 1). The second ranked model included the presence or absence as housing estates as a predictor variable, but examination of the model outputs demonstrated that it did not influence crossing location, either on its own (estimate \pm 95% CI: -5.02 ± 7.65 , $p=0.62$) or in interaction with vegetation cover (-0.21 ± 0.27 , $p=0.12$).

Discussion

Road crossing frequency (prediction 1a and b; 'use' dataset)

Based on previous research on habitat selection and sex-bias in road kills (Kirkpatrick 1970, Edwards and Ealey 1975, Osawa 1989, Coulson 1997, Swan 2008) we expected crossing frequency by swamp wallabies to be higher at night than

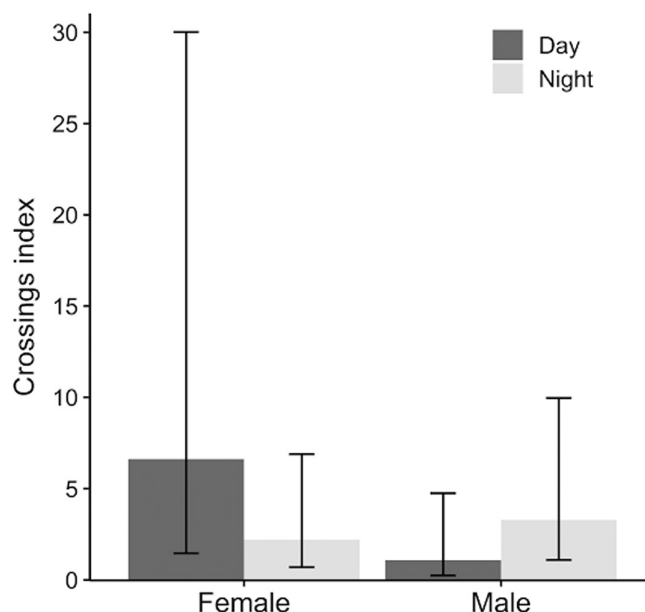


Figure 3. Predictions from a generalised linear mixed model representing the number of crossings (adjusted for unequal sampling effort) for females and males during the day and night. Error bars represent 95% confidence limits.

Table 2. Contrasts representing a test of prediction 1a (there will be more road crossings at night) for females and males, and a test of prediction 1b (males will cross roads more than females) during the day and night. A positive estimate means that the first-listed condition in the contrasts column has a higher value than the second-listed condition. 95 low and 95 upp are lower and upper 95% confidence limits.

Contrasts	Prediction	Estimate	95 low	95 upp	p-value
Female, day – female, night	1a	1.102	–0.013	2.217	0.05
Male, day – male, night	1a	–1.122	–2.352	0.1077	0.07
Female, day – male, day	1b	1.821	0.189	3.453	0.03
Female, night – male, night	1b	–0.403	–1.613	0.807	0.51

during the day (prediction 1a) and for males to cross roads more often than females (prediction 1b). Overall, our data did not support either prediction as the influence of time period on crossing frequency depended on sex; males crossed the road more often at night than during the day while females showed the opposite pattern. Consistent with prediction 1a, we observed a large (207%) increase in the number of male crossings at night compared to the day, but we could not be confident of this effect due to high variability among individuals. Additional data are required to confirm this response.

We lack a clear explanation for the patterns in crossing frequency that we observed for females. If females maximise their fitness by raising offspring to sexual maturity, they should attempt to minimise risk to their offspring and acquire high quality resources (Main et al. 1996). In the context of road crossing, risk should be reduced if roads are crossed when traffic volume is low, an assumption supported by several studies showing a positive correlation between the number of macropod deaths and traffic volume (Osawa 1989, Ramp et al. 2005, Klöcker et al. 2006). In most cases traffic volume is expected to be lowest at night, but in our study area the Penguin Parade, a major tourist attraction, results in high volumes of traffic along some roads around two hours after dusk as tourists return home after watching little penguins *Eudyptula minor* move from the ocean to their burrows. Although this only affected some roads for a small portion of the night, it may have acted to reduce noc-

turnal crossing frequency in females more than males due to the different factors influencing fitness. We did not treat females with pouch young separately from those without young (our sample was too small; Supporting information), but suggest that differentiating between females at different stages of the reproductive cycle may help to reveal the mechanisms underlying road crossing frequency in female swamp wallabies.

Our predictions were based on indirect information about the possible effects of time period and sex on crossing frequency from habitat selection and road-kill studies because studies using high-resolution tracking data for swamp wallabies or similar species are limited. We are aware of only one other GPS-based road crossing study of macropods, where the data showed no effect of time period on crossing frequency for four eastern grey kangaroos *Macropus giganteus* (Brunton et al. 2019). Similar studies on different species in other parts of the world are more numerous. For example, black bears *Ursus americanus* crossed paved roads five times more often at night than during the day and crossing frequency by roe deer *Capreolus capreolus* mirrored peaks in activity at dawn and dusk (Stillfried et al. 2015, Kämmerle et al. 2017). Further, in an urban population of bobcats *Lynx rufus*, males crossed roads more frequently than females (Poessel et al. 2014). Additional tracking studies on swamp wallabies and other macropods will help reveal the factors influencing road crossing frequency in this group of animals.

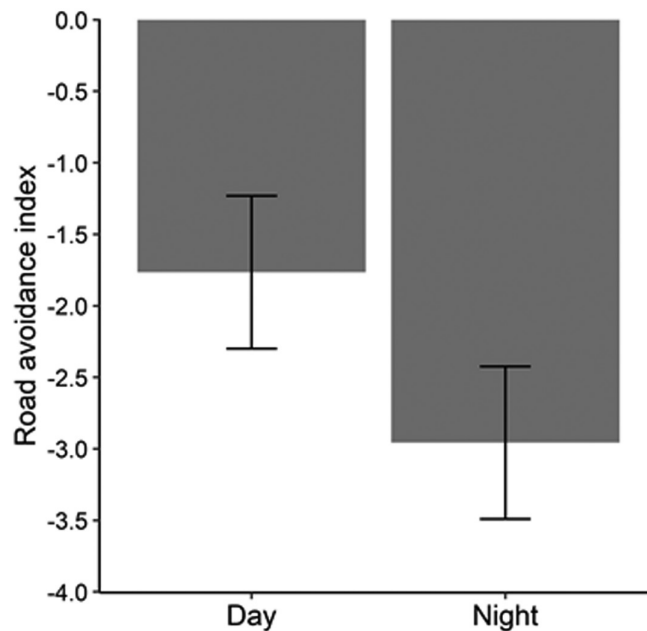


Figure 4. Predictions from a linear mixed model showing the influence of time period (day, night) on a road avoidance index. The index represents the difference between observed crossings and simulated crossings generated by a correlated random walk. Error bars represent 95% confidence limits.

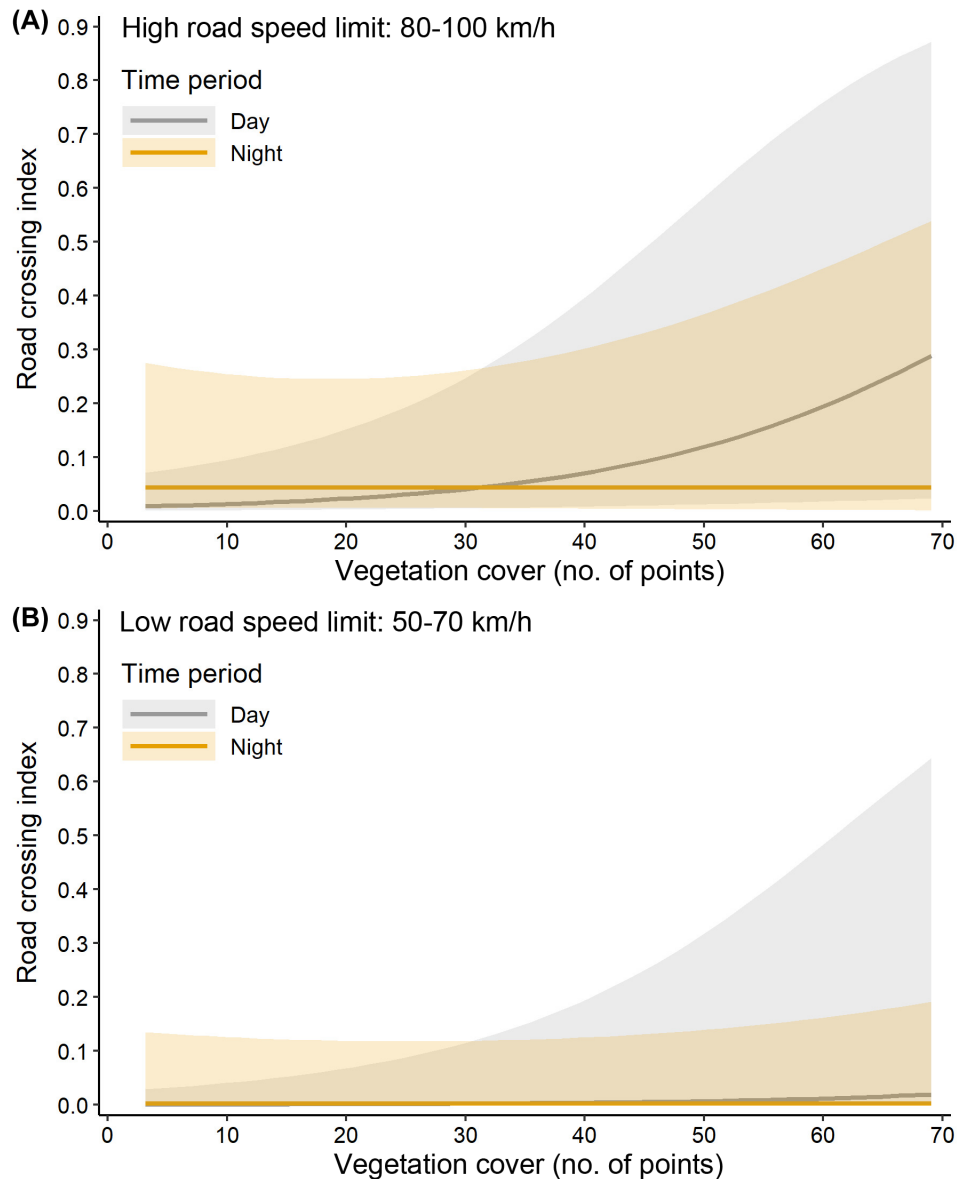


Figure 5. Predictions from a generalised linear mixed model showing the influence of vegetation cover on road crossings during the day and night. Effects varied among roads with higher (A) and lower (B) speed limits. Shaded areas represent 95% confidence limits.

Road avoidance (prediction 2; 'use' and 'availability' dataset)

We expected wallabies to avoid crossing roads (prediction 2), which was strongly supported by our findings and in line with other studies investigating road avoidance in macropods (Ben-Ami and Ramp 2013, Brunton et al. 2019) and other species (Rondinini and Doncaster 2002, Alexander et al. 2005, Shepard et al. 2008). For example, location data collected over a three-month period showed that only one of nine swamp wallabies crossed a nearby highway despite being habituated and potentially benefiting from the roadside environment (Ben-Ami and Ramp 2013). However, the propensity of species to cross roads is likely influenced by road size and traffic volume, with a higher number of deaths likely on roads with medium compared to high or low volumes of traffic (Burgin and Brainwood 2008). The

fact that swamp wallabies avoided road crossings indicates that the activity is perceived as risky, and is consistent with a substantial number of road-kills observed on Phillip Island (Rendall et al. 2021). Although swamp wallabies are common and widespread throughout their range, there is potential for road-kills to cause declines in local population, demonstrating the need to carefully consider management options in road-affected areas (Ramp and Ben-Ami 2006).

Habitat characteristics (prediction 3; 'use' and 'availability' dataset)

We showed that selection of crossing locations on roads with high speed limits (80–100 km h⁻¹) increased with vegetation cover during the day, providing partial support for our prediction. This is consistent with the selection of dense vegetation by swamp wallabies during the day

(Di Stefano et al. 2009, Fischer et al. 2019) which in landscapes with roads likely drives the positive correlation we observed between crossing locations and vegetation cover. We are not aware of any similar GPS tracking studies linking road crossing in macropods to landscape characteristics, although an analysis of road-kills showed that wallabies (including both swamp wallabies and red-necked wallabies *Notamacropus rufogriseus*) were more likely to be killed by vehicles at locations surrounded by a higher compared to a lower extent of forest (Ramp et al. 2005).

Nevertheless, we found that vegetation cover did not influence crossing location at night, which may be related to the lower reliance that swamp wallabies have on lateral cover during this time period (Swan 2008, Di Stefano et al. 2009, Fischer et al. 2019). We hypothesise that the perceived risk of road crossing in our study area is high during the day, but lower at night, removing the influence of vegetation cover on crossing location during nocturnal periods. Further, our findings suggest that the perceived risk of road crossing may be greater for roads with higher compared to lower speed limits as crossing locations along low-speed roads were not influenced by either vegetation cover or time period. Indeed, recent data from our study area show that swamp wallaby road kill numbers increase with speed limit (Rendall et al. 2021). Nevertheless, the relationship between road crossings by wildlife and speed limits is potentially confounded by variations in traffic volume and resulting road permeability (Alexander et al. 2005). Using both, traffic volume and speed as predictors of crossing location would be useful in future studies.

Management implications

Our main finding pertaining to management is the positive association between daytime crossing locations and vegetation cover along roads with a high speed limit. This finding implies that both vegetation cover and vehicle speed may influence wallaby–vehicle collisions and suggest mitigation measures targeting these two factors. Potential management options include (a) reducing vegetation cover, (b) establishing barriers (e.g. fences), (c) reducing vehicle speed and (d) providing signage. The first two options are designed to alter the behaviour of wallabies while the second two are designed to alter the behaviour of humans.

Fencing will be the most effective option as it provides a physical barrier to animal movement and has been shown to prevent wildlife from crossing roads (van der Ree et al. 2015). However, preventing road crossing may reduce access to important resources, potentially causing secondary detrimental effects to wallabies and perhaps other species (Putman et al. 2004). To overcome this issue, partially fencing stretches of road with dense vegetation may reduce collision probability while providing crossing opportunities at lower-risk locations (Ascensão et al. 2013). For example, partial fencing that guided elk *Cervus canadensis* to safe crossing locations, reducing collisions by 97% (Gagnon et al. 2015).

Positive synergies between partial fencing and other mitigation measures may exist. For example, if partial fencing guided wallabies to low-risk crossing locations, reduced speed limits and the addition of signage may have addi-

tional positive effects. Nevertheless, mitigation measures such as signage may have a limited effect if they are not carefully designed (Al-Kaisy et al. 2008, Bond and Jones 2013), and effective monitoring of management actions is essential to determine their utility. We suggest that partial fencing, possibly combined with other measures such as reduced speed limits and signage, could reduce collisions between vehicles and swamp wallabies on Phillip Island. Any management actions should be paired with monitoring to test their effectiveness, and to collect data to inform future management decisions.

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Author contributions

MF, MS, JD, GC and DS conceptualized the data. MF performed data curation. MF, MS, SKS and JD involved in formal analysis. DS and MF involved in funding acquisition. MF administered the project. JD, DS and GC supervised the study. MF visualized the data. MF involved in writing – original draft. MF, MS, SKS, JD, GC and DS involved in writing – review and editing.

Data availability statement

Data are available from Movebank Data Repository <<https://doi.org/10.5441/001/1.6ss053n>> (Fischer et al. 2021).

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Supporting information (available online as Appendix wlb-00691 at www.wildlifebiology.org/appendix/wlb-00691).