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Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia

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Abstract. Roads can disrupt the population processes of vertebrate wildlife species through habitat fragmentation and vehicle collision. The aims of this review were to synthesise the recent literature on road impacts on wildlife, to identify gaps in our understanding of this topic and to guide future research and management in Australia. We reviewed 244 published studies from the last decade on road and vehicle impacts on wildlife conducted worldwide. A geographic bias was evident among the studies, with 51% conducted in North America, 25% in Europe, 17% in Australia and 7% across several other countries. A taxonomic bias was evident towards mammals (53%), with far fewer studies on birds (10%), amphibians (9%) and reptiles (8%), and some (20%) included multiple taxonomic groups. Although this bias is partly explained by large insurance and medical costs associated with collisions involving large mammals, it is also evident in Australia and signals that large components of biodiversity are being neglected. Despite a prevalence of studies on wildlife road mortality (34%), population impacts are poorly described, although negative impacts are implicated for many species. Barrier effects of roads were examined in 44 studies, with behavioural aversion leading to adverse genetic consequences identified for some species. The installation of road-crossing structures for wildlife has become commonplace worldwide, but has largely outpaced an understanding of any population benefits. Road underpasses appear to be an important generic mitigation tool because a wide range of taxa use them. This knowledge can guide management until further information becomes available. Global concern about the decline of amphibians should lead to a greater focus on road impacts on this group. Priorities for research in Australia include (1) genetic studies on a range of taxa to provide an understanding of life-history traits that predispose species to barrier effects from roads, (2) studies that examine whether crossing structures alleviate population impacts from roads and (3) studies that describe the behavioural response of frogs to crossing structures and that identify factors that may promote the use of suitable structures. A national strategy to mitigate the impacts of roads on wildlife populations is long overdue and must ensure that research on this topic is adequately funded.

Introduction

Roads and traffic are ubiquitous features of the modern landscape. Over 32 million kilometres of road partition the earth's surface (CIA 2007), imposing enormous habitat loss and landscape fragmentation (Spellerberg 1998; Forman *et al*. 2003). Roads reduce habitat quality, encourage the spread of invasive species and provide greater human access to undeveloped areas (Trombulak and Frissell 2000; Coffin 2007; Laurance *et al*. 2008). It is now well recognised that roads can potentially disrupt the population processes of vertebrate wildlife in several fundamental ways. First, population sizes may be reduced or population dynamics impaired when habitat is removed for roads and the quality of habitat remaining is altered (Benayas *et al*. 2006; Laurance *et al*. 2006; Ament *et al*. 2008). Second, vehicle-induced mortality (road-kill) may lead to a decrease in local population size. There is now a very large number of studies that document species that are susceptible to road-kill, although the extent that this may threaten populations is not well understood (e.g. Massemin and Zorn 1998; Hels and Buchwald 2001; Dique *et al*. 2003; Ramp *et al*. 2005; Hobday and Minstrell 2008). Third, roads may act as a filter or barrier to animal movement, thereby affecting home-range use and migration (e.g. Roe *et al*. 2006; van der Ree 2006; Gagnon *et al*. 2007; Timm *et al*. 2007; Wilson *et al*. 2007). Disruptions to migration or home-range use may result in changed social structure and reduced reproduction (e.g. Mansergh and Scotts 1989). Last, roads may alter patterns of gene flow and lead to genetic isolation, resulting in genetic drift and inbreeding (e.g. Reh and Seitz 1990; Epps *et al*. 2005; Lesbarrères *et al*. 2006; Riley *et al*. 2006; Sillero 2008). The consequence of these genetic changes is that population viability may be threatened. Despite the potential severity of these impacts, and recognition that not all species will be affected (e.g. Meunier *et al*. 1999; Bellamy *et al*. 2000; Dean and Milton 2003), we are only beginning to understand how widespread these effects are and how predictable they might be across taxa (see Fahrig and Rytwinski 2009).

Road impacts on wildlife are a truly global concern. Road networks are expanding in most countries throughout the world. Impacts will not be uniform across taxa and may vary geographically, owing to variation in the natural environment, as well as to variation in the physical characteristics of roads in

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different countries. Such variability requires that studies be conducted throughout the world on a broad range of species. This has occurred (e.g. Mumme *et al*. 2000; Carr and Fahrig 2001; Hels and Buchwald 2001; Dique *et al*. 2003; Goosem 2004; Laurance *et al*. 2008), although further research is needed.

Concurrent with studies that identify impacts on species is the need to conduct studies that consider how such impacts might be mitigated. Road agencies worldwide are paying increased attention to impact mitigation and in many cases are installing structures to mitigate road impacts, even when the effectiveness of those structures for particular taxa may be unknown (e.g. Taylor and Goldingay 2003; van der Ree *et al*. 2007). Studies that examine how species respond to the mitigation of road impacts have been conducted at two levels; one is simply where data are collected to show a behavioural response of individual species (e.g. use of a crossing structure) and the other is to demonstrate that there is a population response to the mitigation. Both are complementary in that understanding the behavioural response is important if improvements to design are needed (e.g. Woltz *et al*. 2008), whereas the population response is the ultimate test of how effective the mitigation is.

In the present paper, we review studies published in the past 11 years describing road impacts on wildlife and their mitigation. We started in 1998, because two significant literature reviews on roads and wildlife were published then (Forman and Alexander 1998; Spellerberg 1998). We aim to synthesise research in this field and identify gaps in knowledge. We begin with an assessment of the geographic and taxonomic biases of the literature and then review the literature according to the following four broad topics: (1) wildlife road mortality, (2) adverse landscape effects, (3) impact mitigation and (4) landscape-level strategic road planning. In contrast to earlier reviews, we endeavour to highlight species and taxonomic groups most affected and make much stronger connections between the broader population consequences of road-barrier effects, particularly as they relate to an Australian context. In so doing, we highlight taxa that have been disproportionally neglected from research efforts (e.g. arboreal mammals), something that was not a feature of earlier reviews (e.g. Forman and Alexander 1998). Finally, we examine how research activity in Australia compares with that overseas and use this to guide future research in Australia.

Geographic and taxonomic biases

We confined our attention to published peer-reviewed English-language papers on roads and vertebrate wildlife for the years 1998–2008. We refer to several 2009 papers that provide key insights on particular topics. We have not included conference proceedings in this review, although we acknowledge that those arising from the International Conference on Ecology and Transportation (ICOET) (e.g. 2003, 2005, 2007) and Infra Eco Network Europe Meetings (IENE) (e.g. 2001, 2003, 2008) provide a valuable record of research projects conducted over the past 10 years. We chose not to include these studies because they are not peer-reviewed, many describe works in progress, and there was a predominance of studies from the USA and Europe where the conferences were held. We have not considered non-English language journals and acknowledge that this may cause a partial bias. We searched the Web of Science database with many keywords relating to roads and wildlife, and also checked the reference lists of any papers we obtained to provide further references.

We located 244 papers and note that only those that are cited specifically in our text are included in our reference list. We found that research involving roads and wildlife has grown steadily over the past 11 years from <10 papers per annum in 1998/99 to ~40 per annum in 2006–08 (Fig. 1). North America (n = 124), Europe (n = 60) and Australia (n = 42) were the primary sources of published research, and the growth in attention has occurred in each area. The remaining 18 papers were derived from the vast geographic areas of South-east Asia, Africa and South America. This shows that, globally, there are large geographic biases in research effort, with vast areas of the globe relatively ignored. On the basis of population size (i.e. North America ~340 million, Europe ~830 million, Australia ~20 million), Australia has shown a relatively high level of research activity (i.e. 0.3% of global population and 17% of papers) compared with Europe (12% and 25%, respectively) and North America (5% and 51%, respectively).

The most frequently studied vertebrate class was mammals (53% of studies), with ungulates (predominantly deer) the most frequently studied single taxonomic group (14% of studies). Reptiles represented 8% of studies whereas birds accounted for 10%. Despite the growing international recognition that amphibians are more threatened and declining more rapidly than either mammals or birds (Stuart *et al*. 2004), they represented only 9% of studies. Multiple taxonomic groups (e.g. mammals and herpetofauna) accounted for 20% of studies.

If we consider the expected number of studies for each vertebrate class against the relative proportion of total described taxa, a clear bias towards mammals is evident. That is, mammals represent 18% of global land-vertebrate species (Chapman 2009) and 53% of the studies. The other vertebrate classes are each similarly under-represented (i.e. birds 33% of the species and 10% of the studies; reptiles 28% of the species and 8% of the studies, and amphibians 21% of the species and 9% of the studies).

The focus on mammals is likely to be due to the high medical and vehicle-repair costs arising from collisions with large mammals. However, on the basis of numbers of declining species worldwide, amphibians may be particularly sensitive to road effects (e.g. Lesbarrères *et al*. 2006; Arens *et al*. 2007; Glista *et al*. 2008; Fahrig and Rytwinski 2009). The relative inattention they have received precludes generalisation, particularly given that as a group they vary substantially in morphology and ecology. Arboreal mammals also require more attention because their general reliance on continuity of forest cover makes them highly sensitive to landscape fragmentation and many species are threatened (see Goosem 2004; Wilson *et al*. 2007; Ball and Goldingay 2008).

We divided the literature into the following four broad topics: (1) wildlife road mortality, (2) adverse landscape effects, (3) impact mitigation and (4) landscape-level strategic road planning. There were obvious geographic differences in the spread of these topics (Fig. 2). Australian studies were dominated by road-mortality investigations (45%), and paid little attention to aspects of strategic planning (4% of studies).

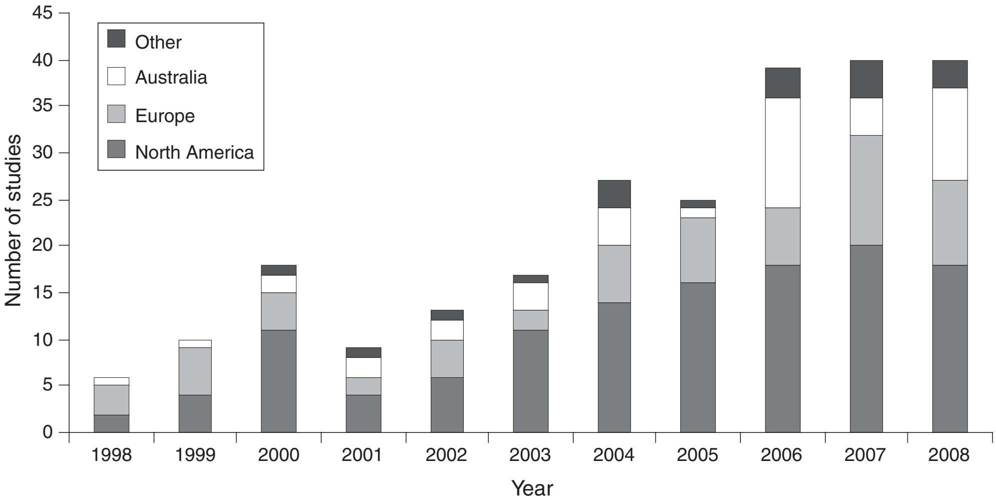

Fig. 1. Number of published studies by year and region on vertebrate wildlife and roads during 1998–2008. 'Other' includes Asia, Africa, South America and New Zealand.

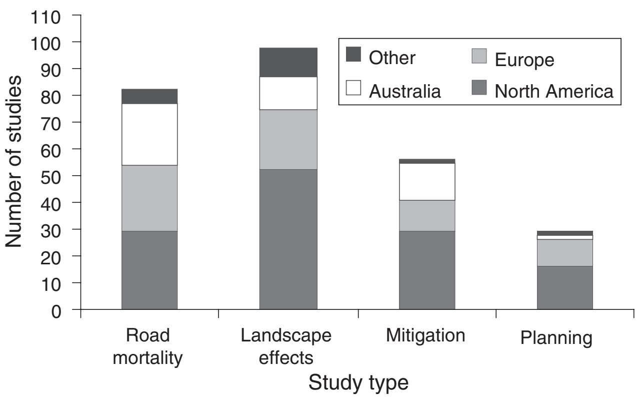

Fig. 2. Number of published studies by region and study type on vertebrate wildlife and roads. Some papers included more than one study type.

Studies in North America were spread across all topics, although with an emphasis on landscape effects (41% of North American studies). European research was spread across the four topics, although with an equivalent emphasis on landscape effects (33% of studies) and road mortality (36% of studies).

Wildlife road mortality

Road-killed taxa and population effects

Assessment of wildlife road mortality is fundamental to understanding road impacts, both in identifying species in need of detailed population studies and as a means of determining the effectiveness of impact mitigation. We identified 82 studies documenting road-kill, including mitigation studies that reported road-mortality data as part of their investigation. Most ($n = 45$) of these studies targeted individual species or fauna groups (e.g. amphibians). Twenty-eight studies were generic in nature, with an aim of simply describing the species that occur as road-kill. Thirteen of these studies identified species that may be vulnerable to road-kill, particularly those that are listed as threatened.

Concern about adverse population effects from road mortality was expressed in 50 of the 82 studies, which is a proportion similar to that reported recently in a review of the effects of roads on animal abundance (see Fahrig and Rytwinski 2009). However, only 26 of the 82 studies analysed and/or calculated how local wildlife populations may be affected. These studies reported 32 instances where populations were affected negatively, compared with seven documenting no effect (some studies assessed more than one species). Negative effects were reported more frequently in amphibians ($n = 11$) and mammals ($n = 11$) than in reptiles ($n = 9$) and birds ($n = 1$), which is a distribution similar to that noted by Fahrig and Rytwinski (2009). Given that amphibians occurred in few studies, compared with other taxonomic groups (see above), the frequent negative impacts reported for amphibians suggest that this group is particularly vulnerable to road impacts and warrants further attention.

Factors associated with wildlife road mortality

Studies of factors, or attributes, associated with wildlife road mortality essentially attempt to identify road-kill black-spots, or hot-spots (i.e. locations of road-kill clusters) as a way of identifying locations where mitigation is needed. This type of analysis is a necessary complement to population impacts because it can provide an indirect way of understanding local factors associated with high road-kill. Such studies may also reveal preferred locations for the placement of crossing structures (i.e. where local populations will benefit the most). Most of the 52 studies we reviewed involved assessments of road-mortality locations according to a range of road, landscape or life-history attributes. The development of spatially explicit models to predict likely black-spots has been a more recent addition to attribute investigations (e.g. Jaeger *et al*. 2005; Litvaitis and Tash 2008; Ramp and Roger 2008).

Traffic volume ($n = 28$) and roadside vegetation cover ($n = 20$) were the attributes most commonly identified across all wildlife groups, as associated with higher road mortality. Therefore, roads with these attributes are the ones likely to cause greater population impacts on wildlife and require mitigation measures. The impact of minor roads may be greater for some species (e.g. badgers; see van Langevelde *et al*. 2009), and relevant for mammals in peri-urban and regional areas of Australia (Burgin and Brainwood 2008). The key point here is that even if road-kill rates are substantially lower on minor roads, the overall impact may be substantial because of the number of such roads.

Although road-kill rates are used to suggest black-spots or to correlate with road attributes, some caution is needed in interpreting their significance. High road mortality may simply indicate high population density that may be able to withstand high road mortality. Such species may not benefit significantly from mitigation measures. Alternatively, road sections with low road mortality may be associated with low population density, and low population viability. Mitigation measures that reduce mortality and improve connectivity may substantially benefit population viability at such locations.

Clearly, this is an issue warranting further investigation to gain a better perspective on overall population impact. Nonetheless, recognising the impacts of large, high-volume roads indicates that mitigation is needed when such roads are being constructed through native vegetation. A range of attributes was assessed in different studies, although the number of studies is currently too few to allow generalisation. This approach has considerable merit in identifying locations where mitigation may be focussed. Life-history attributes may also help explain the vulnerability of some species to road mortality although too few studies have assessed this to allow any generalisations.

Adverse landscape effects

Barrier effects

Roads may act as a barrier or filter to the movement of vertebrates (e.g. Mansergh and Scotts 1989; Alexander and Waters 2000; Rondinini and Doncaster 2002; van der Ree 2006; Rico *et al.* 2007). Animal movement may involve daily travel through a home range, seasonal migration associated with changes in habitat use or breeding events, or the dispersal of individuals from their natal areas. We have not attempted to separate these forms of movement in this section because too few studies have been conducted to warrant it; however, dispersal movement is the primary consideration when population effects are considered below.

A barrier effect may result from a behavioural aversion to a road (e.g. reindeer, *Rangifer tarandus*, in Norway: Dahle *et al.* 2008) or from a reduced dispersal because of high road mortality (e.g. amphibians in Indiana: Glista *et al*. 2008). The inclusion of tall 'sound-barrier' walls along some major roads may enhance the physical barrier to some terrestrial vertebrates. Forty-four studies have explored barrier effects, including nine on genetic effects. Mammals ($n=29$ studies) dominate investigations compared with herpetofauna (mostly frogs) ($n=7$), birds ($n=6$) and multiple taxa and/or modelling ($n=3$).

Although it is tempting to view the behavioural response to roads as an all-or-nothing scenario, this is unlikely to be the case for many species. For example, whereas increased traffic volume reduced highway-crossing frequency for elk (*Cervus canadensis*), this effect depended on season and the proximity of high-quality foraging areas (Gagnon *et al*. 2007). Numerous studies have demonstrated that roads severely inhibit the movement of a range of species across all fauna classes. These include salamanders (deMaynadier and Hunter 2000), species of snake (Andrews and Gibbons 2005), rainforest birds (Laurance *et al*. 2004), several rodent species (Goosem 2001; Rico *et al.* 2007; McGregor *et al*. 2008) and a range of tropical fauna (see Laurance *et al*. 2009). This is largely due to behavioural avoidance of open areas and a preference for dense habitats.

Behavioural studies have confirmed the effect of traffic volume and road width, which tend to co-vary and are difficult to separate. Bank voles (*Clethrionomys glareolus*), yellow-necked mice (*Apodemus flavicollis*) and hedgehogs crossed two-lane highways but not three-lane highways of a similar volume (Rondinini and Doncaster 2002; Rico *et al*. 2007). Mammalian carnivores crossed low–medium-volume two-lane roads but showed some avoidance of high-volume two- and three-lane roads (Alexander *et al*. 2005; Dickson *et al*. 2005). However, grey wolves (*Canis lupus*) and grey foxes (*Urocyon cinereoargenteus*) regularly crossed three-lane, high-volume highways (Blanco *et al*. 2005; Riley 2006), albeit major roads may increase the tortuosity of their movements (Whittington *et al*. 2004). Ungulates crossed medium–high-volume two-lane highways but were greatly inhibited by very high-volume two-lane highways (Alexander and Waters 2000; Alexander *et al.* 2005).

Edge-dwelling birds were not affected by a forest road, whereas forest-interior birds were partially inhibited (Laurance 2004). However, by the use of playback and translocation, forest birds (St Clair 2003) and understorey rainforest birds (Laurance and Gomez 2005) crossed busy two- and three-lane highways. Small snakes and salamanders were partially inhibited by low-volume two-lane roads, whereas anuran movement was reportedly unaffected (deMaynadier and Hunter 2000; Shine *et al*. 2004; Andrews and Gibbons 2005), and migrating leopard frogs (*Rana pipiens*) took longer and were less successful at crossing roads in response to increased traffic volume (Bouchard *et al*. 2009).

Behavioural studies of barrier effects provide an important complement to other studies because they may reveal more readily which species show an aversion to crossing roads and which factors may alleviate inhibition. Currently, few studies of this kind have been conducted in Australia, and those that have, reveal that a diversity of responses can be expected among mammalian taxa. Rodents of different genera showed a gradient of responses to crossing road clearings, from no inhibition to severe inhibition (Goosem 2001). Squirrel gliders (*Petaurus norfolcensis*) regularly crossed a high-volume two-lane highway, whereas females appeared to be inhibited from crossing a high-volume four-lane highway with a median strip (van der Ree 2006). Wilson *et al*. (2007) demonstrated, by translocating lemuroid ringtail possums (*Hemibelideus lemuroides*) across roads and powerline easements, that gaps in rainforest canopy posed substantial barriers to the return of many individuals (see also Laurance *et al*. 2009). Many further studies and studies involving other vertebrate classes are needed.

Population effects of road barriers

The most compelling evidence demonstrating an adverse population effect resulting from roads as barriers comes from recent genetic studies. Research on desert bighorn sheep (*Ovis canadensis*) (Epps *et al*. 2005), bank voles (Gerlach and Musolf 2000), coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Riley *et al*. 2006), Scottish Highland red deer (*Cervus elaphus*) (Pérez-Espona *et al*. 2008), grizzly bears (Proctor *et al*. 2005) and frogs (Lesbarrères *et al*. 2006; Arens *et al*. 2007) has demonstrated significant genetic subdivision in populations separated by highways. Loss of connectivity between these smaller patches causes the loss of genetic diversity (Forman *et al*. 2003). For long-lived species, such as desert bighorn sheep, there was a reduction in genetic diversity from as little as 40 years of road-induced isolation (Epps *et al*. 2005). For short-lived species, such as frogs, the genetic effect of highway development was evident in as little as 7–10 generations (~21 years) (Lesbarrères *et al*. 2006). This isolation effect is likely to be most severe for very small populations and rare species (Riley *et al*. 2006). Such evidence of genetic isolation suggests that demographic processes have become impaired. Thus, roads may create an unstable metapopulation, by fragmenting formerly large continuous areas into a series of smaller patches (Hanski 1998; Gerlach and Musolf 2000). The viability of these smaller, isolated populations is reduced and they are vulnerable to extirpation from stochastic events (e.g. Goldingay and Sharpe 2004; Patten *et al*. 2005; Taylor and Goldingay 2009).

Riley *et al*. (2006) suggested that the observed migration rates across anthropogenic barriers, such as major roads, may be poor surrogates for gene flow. They found that despite moderate levels of migration by coyotes and bobcats across the Ventura Freeway in Los Angeles, populations on either side of the freeway were genetically differentiated, implying that individuals that crossed the freeway, rarely reproduced. These authors concluded that highways impose artificial home-range boundaries on territorial and reproductive individuals and hence decrease genetically effective migration. This study highlighted how little is known about road-mediated changes to dispersal behaviour. The study by Riley *et al*. (2006) suggested that assumptions based on observed crossings of roads may be untenable. Many further studies are needed to determine whether there are life-history traits that might predict incongruities between observed crossings and population genetic consequences.

Currently, no published studies in Australia have examined the effects of roads on gene flow of wildlife populations. Studies should focus on a range of taxa to examine whether particular life-history traits predispose species to barrier effects from roads. Such species should be examined under a range of road types (e.g. size, traffic volumes, time since road isolation). Such information is fundamental to guiding mitigation strategies.

Impact mitigation

Foremost in efforts to reduce the barrier effect of roads and increase landscape permeability has been the installation of wildlife road-crossing structures (Figs 3, 4). Published studies have been undertaken in Australia, Europe and North America, and have involved a total of 329 crossing structures (Table 1).

Fig. 3. (*a*) Aerial view of one of the five 50-m-long rope bridges installed on the Pacific Highway, Karuah, New South Wales. (*b*) Aerial view of wildlife-crossing structures installed at Compton Road, Brisbane, Queensland. Shown here are one of three rope bridges and a land-bridge that contains eight glider poles. Photos: Google Earth.

Various below-road crossing structures comprised 82% of all crossing structures studied. These ranged in size from small drainage pipes up to dry passage bridges. Box drainage culverts were the most commonly studied (26%) of all crossing-structure types. Over-road structures (overpasses) have taken the form of wildlife-dedicated land or green bridges, combined wildlife and vehicle overpasses, pole bridges, and rope bridges (e.g. Goosem 2004; Clevenger and Waltho 2005; Krawchuk *et al*. 2005; Mata *et al*. 2008). Canopy rope bridges are a recent innovation (Fig. 3) and featured in just one study (Goosem 2004). Studies of under-road structures were more common in North America ($n = 15$) than in Europe ($n = 5$ studies) or Australia ($n = 3$). Overpasses were infrequently studied in Europe ($n = 5$ studies) and North America ($n = 4$). Within our review period, there was only a single published study on overpasses in Australia (Bond and Jones 2008). However, another study has recently been published (see Hayes and Goldingay 2009).

Although research on the usage of crossing structures has focussed primarily on mammals (Table 2), there is evidence of use

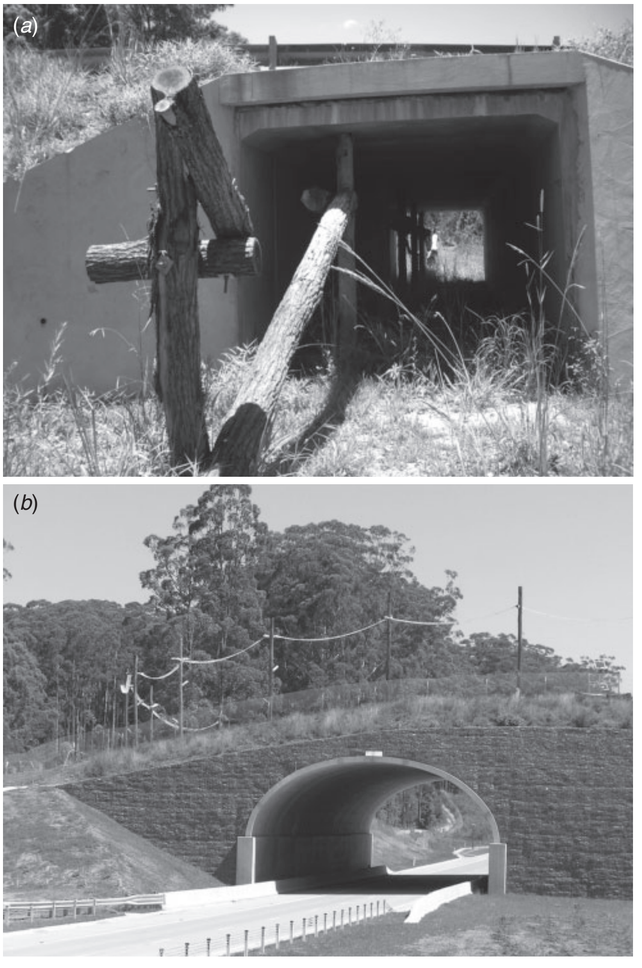

Fig. 4. (*a*) Dedicated wildlife underpass with rail for arboreal mammals under the Pacific Highway, Yelgun, New South Wales (NSW). (*b*) Land-bridge installed on the Pacific Highway at Bonville, NSW. This bridge supports a set of wooden poles linked by a rope bridge. The poles have a side arm to allow koalas, the target species, to rest. Photos: (*a*) B. Taylor and (*b*) I. Hayes.

by a broad range of taxa (e.g. Mathiasen and Madsen 2000; Popowski and Krausman 2002; Taylor and Goldingay 2003; Ng *et al*. 2004; Bond and Jones 2008). Pipes were used by small to medium-sized vertebrate groups and by some canids. All vertebrate groups have been recorded in culverts and underpasses, though some amphibians and mustelids were not recorded in some drainage culverts and wildlife underpasses (e.g. Dodd *et al*. 2004). Overpasses were commonly used by a range of large mammals, whereas their use by small and medium-sized vertebrate groups was less consistent (see McDonald and St Clair 2004*a*). Despite these demonstrations of use by many species, there is a need for behavioural studies that attempt to understand how species respond to structures, whether widely used or novel structures (e.g. Woltz *et al*. 2008). There is some evidence of aversion of some structures by some groups (e.g. small mammals on overpasses; Table 2); however, further studies are needed.

Fifteen studies have investigated factors that influence the use of underpasses. Structural, landscape and road-related attributes influence the pattern of usage, which may be species-specific. Underpass openness, and usage generally, related to an animal's body size (see Mata *et al*. 2005), although medium-sized carnivores preferred larger passages (Grilo *et al*. 2008). Funnel-fencing and/or walls adjoining underpasses were positively related to use by herpetofauna and small–medium-sized mammals, but not by wide-ranging bobcats (Cain *et al*. 2003; Dodd *et al*. 2004). Wild carnivores appear to utilise culverts away from human settlements and noise, whereas domestic carnivores show an opposite usage pattern (Clevenger and Waltho 2005; Ascensão and Mira 2007; Grilo *et al*. 2008). Vegetation cover near an underpass entrance appears to encourage the use by small–medium-sized mammals and reptiles, whereas it may discourage the use by grizzly bears and some ungulates (e.g. Clevenger and Waltho 2005). Underpasses adjoining areas of greater natural habitat show higher levels of usage by carnivores and deer (e.g. Ng *et al*. 2004; Grilo *et al*. 2008). Structural attributes (i.e. physical dimensions of the crossing structure) better explain patterns of underpass usage for a range of taxa than do landscape- or human-related factors (Mata *et al*. 2005; Clevenger and Waltho 2005).

Studies have suggested that usage of overpasses by ungulates and canids was positively related to the proximity of vegetation cover, negatively related to the proximity of croplands and showed no relationship to the proximity of a mountain (Popowski and Krausman 2002; Peris and Morales 2004; Mata *et al*. 2005). Ungulate usage was also positively related to the proximity of a creek or river (Popowski and Krausman 2002),

Table 1. The number of studies of different types of crossing structures by broad geographic area
The number of crossing structures investigated is in parenthesis. In all, 14 of the 30 published papers investigated multiple structure types, which resulted in a total of 52 studies of different structure types

Structure type	Function	North America	Europe	Australia	Total
Pipe	Drainage	3 (18)	2 (41)	–	5 (59)
Box drainage culvert	Drainage	5 (52)	1 (34)	–	6 (86)
Adapted culvert	Drainage and adapted for wildlife	2 (11)	2 (17)	2 (14)	6 (42)
Wildlife underpass	Use by wildlife	8 (24)	4 (11)	1 (4)	13 (39)
Bridge underpass	Rural roads and livestock paths	5 (24)	2 (19)	–	7 (43)
Overpass	Rural roads	1 (2)	3 (34)	–	4 (36)
Wildlife overpass	Use by wildlife	4 (5)	5 (16)	1 (1)	10 (22)
Canopy-rope bridge	Use by arboreal mammals	–	–	1 (2)	1 (2)
Total		27 (134)	19 (172)	5 (21)	52 (329)

Table 2. Use of different types of crossing structures by different taxa as recorded in 30 published papers
The first value shows the number of studies where that taxonomic group was recorded using the structure; the second value shows the number of studies where that group was present, but not recorded using the structure

Taxon/taxa	Pipe	Drainage culvert	Adapted culvert	Wildlife underpass	Bridge underpass	Overpass	Wildlife overpass	Rope bridge
Amphibians	2–0	4–1	3–0	1–0	1–0	1–0	0–1	0–0
Reptiles	4–0	9–0	4–0	1–1	3–0	2–0	1–1	0–0
Small mammals	6–1	5–0	5–0	3–1	2–1	2–2	4–3	0–0
Arboreal mammals	1–1	4–0	4–0	0–0	1–0	0–0	1–0	1–0
Medium mammals	8–3	12–1	8–0	6–2	6–1	4–1	5–2	0–0
Large mammals								
Omnivores	1–0	0–1	1–0	1–0	1–0	2–0	3–0	0–0
Carnivores	5–2	9–0	8–0	11–0	10–1	4–1	11–0	0–0
Herbivores	0–1	2–0	2–0	12–0	3–0	3–1	9–0	0–0

although narrow overpasses (<6 m wide) were not used by wolves and deer (Peris and Morales 2004; Mata *et al*. 2005).

Crossing structures are generally combined with exclusion fencing or barrier walls (see Dodd *et al*. 2004; Olsson and Widen 2008) that attempt to prevent animals from entering a road and funnel them towards the crossing structure. Although rigorous experiments on the efficacy of 'funnel-fencing' are lacking, some underpass studies inferred a positive funneling effect for large mammals (e.g. Ascensão and Mira 2007) and herpetofauna (Aresco 2005). Highway mitigation fencing in Canada led to a 78% reduction in moose highway incursions and an 80% reduction in ungulate–vehicle collisions (Clevenger *et al*. 2001; Leblond *et al*. 2007), although concerns have been raised about the potential barrier effect (Olsson and Widen 2008). In Florida, a drift-fence system was successful in preventing road incursion and funnelled a variety of herpetofauna to underpasses (Aresco 2005). The combined funnelling effect of fencing and crossing structures has also raised concern that they may act as prey traps, although Little *et al*. (2002) found scant evidence for this.

It is apparent from crossing-structure research that few studies have rigorously evaluated their efficacy (see Clevenger 2005; van der Ree *et al*. 2007). Clevenger and Waltho (2005) stressed that such studies often fail to address masking effects of confounding variables, such as variation in human activity, density of crossing structures along the highway corridor and equality of species' perceived access to each crossing structure. Of the 30 studies on crossing structure usage we reviewed, 16 simply described the species or guilds of wildlife and the frequency of use (e.g. Mathiasen and Madsen 2000; Krawchuk *et al*. 2005; Bond and Jones 2008), 12 studies identified factors that influence or facilitate the use by particular species or guilds of wildlife, and three studies conducted behavioural experiments on the usage (see Lesbarrères *et al*. 2004; McDonald and St Clair 2004*b*; Woltz *et al*. 2008). Importantly, only one study determined whether wildlife-crossing structures enhanced the population viability of the species. Van der Ree *et al*. (2009) used Population Viability Analysis (PVA) modelling to demonstrate that a tunnel built under a road at Mount Higginbotham for the mountain pygmy-possum (*Burramys parvus*) reduced, but did not eliminate, the negative effects of the road.

Investigating the extent to which a mitigation measure reduces the risk of local extinction and conducting cost–benefit analyses of mitigation measures (e.g. Huijser *et al*. 2009) are obvious areas of research that are lacking. In terms of taxonomic groups, frogs and arboreal mammals have not been adequately catered for by the design of crossing structures or by research into their requirements. These fauna groups are the ones requiring research in Australia because many have populations that are likely to be affected by roads (e.g. Goldingay and Sharpe 2004; Goldingay and Taylor 2006, 2009) and many are listed as threatened species.

Landscape-level road planning

Concomitant with the growing concern for landscape fragmentation by roads (Vos and Chardon 1998; Forman *et al*. 2003; Epps *et al*. 2005) has been the development of GIS-based information technologies that allow coordination of ecological and transportation networks at multiple scales (Clevenger 2005; Frair *et al*. 2008). Several countries have incorporated these technologies into strategic spatial planning to assess the potential impact of linear infrastructure on landscape permeability and connectivity. Road authorities in the north of Spain investigated at both a local and regional scale how the main transport-infrastructure network affected horizontal ecological flows, such as the movement of large mammals (Serrano *et al*. 2002). This approach allowed integration of regional-scale fragmentation and connectivity, and local-scale information on road-mortality black-spots and wildlife movement patterns. This information was then used to guide assessments of future transport-infrastructure proposals. Researchers in Austria and the Czech Republic evaluated the permeability of their national motorway network for large and medium-sized mammals and developed recommendations for existing and future motorways that ensure landscape connectivity, particularly by the inclusion of minimally spaced crossing structures (Woess *et al*. 2002; Hlavac 2005).

Other GIS-based strategic-planning approaches have been developed for specific taxa or fauna groups. Benayas *et al*. (2006) developed a matrix that compared distributional data of herpetofauna across Spain with planned linear infrastructure. They identified 'alert planning units', where planned infrastructure coincided with areas of high diversity or presence of threatened species. These areas were recommended for either habitat protection or a range of mitigation strategies.

Studies of migratory water snakes (Roe *et al*. 2006) and pond-breeding amphibians (Timm *et al*. 2007) have demonstrated that maintaining population persistence requires a landscape-level approach that considers the permeability of terrestrial corridors between wetlands because roads through such corridors may account for significant levels of mortality. An extension of addressing road permeability involves identifying appropriate criteria, such as an animal's vagility, to guide the placement and frequency of crossing structures (see Bissonette and Adair 2008).

GIS-generated, expert-based models were used to identify habitat linkages and to plan migration passages for black bears (*Ursus americanus*) on a major road-widening project on the Trans-Canada Highway (Clevenger *et al*. 2002). The utility of such habitat models could be enhanced by the complementary use of predictive models that identify wildlife-fatality black-spots (e.g. Kramer-Schadt *et al*. 2004; Malo *et al*. 2004; Ramp *et al*. 2005; Litvaitis and Tash 2008). Lee *et al*. (2006) demonstrated the utility of a internet-based GIS to enable community members to report wildlife-crossing observations for a highway in Canada, which revealed that wildlife successfully crossed the highway in areas not identified by wildlife-mortality data. Spatially explicit genetic data that reveal effective dispersal may further refine the efficacy of predictive models (Epps *et al*. 2007).

The approach adopted thus far in Australia is best exemplified by the on-going conversion of the Pacific Highway in New South Wales (NSW) to a dual carriageway from immediately north of Sydney to the Queensland border. Much of this has involved the development of new transportation corridors, which have fragmented once continuous natural habitats. The landscape-level planning that has taken place has focussed on species listed under the *NSW Threatened Species Conservation Act* (1995). Location records of species deemed vulnerable to road mortality and road barriers have been used to determine the location of wildlife-crossing structures (Sinclair Knight Merz 1998). The structures installed have largely been chosen in the absence of knowledge about their effectiveness (see Taylor and Goldingay 2003; Hayes and Goldingay 2009). Such an approach has been a necessary starting point, given the poor state of knowledge in Australia when this road project began in the early 1990s. However, a more sophisticated approach is now needed, based on a more rigorous assessment of vulnerability, that aims to maintain local population viability of wildlife.

Conclusions and future research

The present review has demonstrated that the study of roads and wildlife is a burgeoning research area. Concern about the following three factors seems to be driving this growth: (1) human costs associated with collisions with large mammals, (2) impacts on vertebrate wildlife from road-mediated landscape fragmentation and (3) impacts on sensitive or threatened species from road-kill. Despite this growth in research, there are still major gaps in our understanding. Indeed, the rate of deployment of road-crossing structures to mitigate impacts appears to have outpaced ecological research on the use and population benefits of such structures (see also van der Ree *et al*. 2007).

A taxonomic bias is evident among studies, with ungulates and large mammalian carnivores dominating all areas of research. Small mammals and arboreal mammals have received little research attention, particularly in regard to road-mortality impacts and mitigation. Amphibians feature in relatively few studies, despite global concern that this class of vertebrates is highly threatened. Several studies in the USA and Europe have demonstrated adverse genetic effects of roads on amphibian populations, suggesting that road impacts may be widespread for this group. Reptiles require studies on life-history attributes that may be associated with heightened vulnerability to road mortality and also the effect of road barriers on populations. Birds are largely absent from mitigation studies and need to be considered in association with barrier effects, especially for interior-dwelling species.

Worldwide, adverse impacts of roads on wildlife populations are frequently implicated, although not well demonstrated, largely because of weaknesses in study design (see Roedenbeck *et al*. 2007; Fahrig and Rytwinski 2009). The use of PVA may assist in revealing long-term impacts (e.g. Ramp and Ben-Ami 2006) and in determining population benefits of mitigation measures (e.g. Taylor and Goldingay 2009; van der Ree *et al*. 2009). Modelling of road-kill data can assist in identifying parameters associated with higher road-kill, whereas analysis of life-history attributes can help understand factors that may be shared by vulnerable species. Studies of mitigation measures commonly suffer from a lack of replication and a control group. Better-designed studies (such as before–after–control–impact) are needed and will require close collaboration with road authorities during the strategic phase of road development.

Underpasses have been deployed worldwide and demonstrated to be used by a broad range of taxa; so, an obvious generalisation is that underpasses have value as a generic mitigation measure. However, research is largely lacking in assessing whether the deployment of underpasses leads to changes in population impacts or enhanced population viability. There is currently no published account of the willingness of any Australian frog species to use underpasses or trials of amphibian tunnels that are routinely used in Europe and North America. The population benefits that derive from wildlife overpasses and newer crossing structures such as canopy bridges also need to be demonstrated. Notwithstanding this, it is evident that large, high-volume roads create movement barriers for a range of terrestrial and arboreal taxa and their construction should include crossing structures for a range of functional groups. Underpasses appear to offer the best solution for routine inclusion in new road projects, until research suggests otherwise.

GIS-based predictive models that integrate landscape- and patch-level attributes show promise in broader application, although their utility is highly contingent on the precision of the input data. This highlights the importance of local-level data, such as road-kill, species' distribution and fine-grain habitat data. Australian researchers need to identify species vulnerable to local extirpation from road mortality and their life-history attributes (e.g. Jones 2000; Taylor and Goldingay 2004; Goldingay and Taylor 2006). Information on the distribution of these at-risk species should then be combined with that for existing or proposed road networks to identify locations requiring mitigation (see Litvaitis and Tash 2008). The development and refinement of predictive models should enable extrapolation across different geographic regions (e.g. Ament *et al*. 2008; Frair *et al*. 2008).

Australian research is conspicuous for its lack of published accounts on the effect of roads on gene flow across the landscape or on how crossing structures may facilitate effective dispersal across a road barrier. Therefore, we suggest that road agencies need to fund genetic studies on representative taxa from different functional groups to understand which road types (e.g. major, minor) are barriers or allow movement, and whether road-crossing structures contribute to gene flow for populations separated by a road barrier.

Australia is lagging well behind North America and Europe in developing a national strategy for managing the impact of linear infrastructure (roads, rail, powerlines) on wildlife movement and population viability. A national research body needs to be established in Australia that includes all three levels of government, road-construction companies and researchers from around the country. Such a body could establish research priorities and fund projects. Currently, research is conducted on an *ad hoc* basis and largely reflects the interests of individual researchers. Road agencies need to fund on-going research rather than the current practice of evaluation of potential road impacts and mitigation measures through short-term surveys conducted by private consultants. Furthermore, there should be continued study of installed structures that are now permanently embedded in the landscape, to assess their ecological performance (see also Clevenger 2005) and this information should be used to guide future projects. An attempt to promulgate a national approach may be emerging, with the first national road-ecology symposium ('*Breaking the Barriers*') held in Brisbane during May 2009, attracting over 200 delegates. This meeting recognised the fundamental importance to biodiversity conservation of continued research in this area.

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