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Review

Roads and macropods: interactions and implications

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Abstract. Understanding the impacts of roads on wildlife and the natural environment is of increasing importance. Macropods (mostly kangaroos and wallabies) are a diverse and widespread taxon in Australia that has been significantly affected by the presence of roads in various ways. We reviewed the available literature on macropods and roads, assessing 60 scientific journal articles, reports and theses. Studies on road mortalities were the most prevalent ($n = 29$, with 12 on macropods only), revealing both spatial and temporal patterns in occurrence. Behavioural studies in relation to the road environment are limited ($n = 2$) yet could help our understanding of patterns of road-kill and other impacts. Some macropod populations are critically affected by the presence of roads (e.g. brush-tailed rock-wallaby, *Petrogale penicillata*) due to either proportionately high road mortalities and/or population fragmentation, and may face continued decline unless effective road-mitigation measures are implemented. Investigations of various types of road mitigation focussed on wildlife-exclusion fencing and road crossing structures as the most effective option, although the high cost of these measures appears to limit their implementation. Further research into several areas was identified, particularly on species where severe road impacts are likely to result in population declines.

Additional keywords: fauna crossing structures.

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Introduction

Roads are now widely accepted as being a major source of environmental change. These changes can include destruction and fragmentation of habitat, rerouting and pollution of waterways, erosion and pollution of soils, wildlife mortality, disturbance from sound and light, facilitation of the dispersal of invasive species and the severing of connectivity between previously continuous habitats (Forman *et al*. 2003). Some of these disturbances can penetrate hundreds of metres, or even over a kilometre, into the adjacent habitat (Forman and Deblinger 2000; Forman *et al*. 2003; Biglin and Dupigny-Giroux 2006; Beckmann and Hilty 2010).

The level of impact on wildlife associated with these disturbances varies greatly, ranging from little or negligible influence to being severely detrimental to resident populations. Some species cannot cope with the associated changes to their environment, and so avoid the road entirely, whereas other species can be attracted to the road by resources that may be limited in their habitat (e.g. water, high-quality food, salt: Lee 2006; Barrientos and Bolonio 2009; Grosman *et al*. 2009). Other species may attempt to cross roads to access favoured resources available in habitat on the other side (e.g. mates, water, quality food, unoccupied territories), thereby increasing the risk of traffic-related mortality (e.g. Gagnon *et al*. 2007). Terrestrial species that migrate, in particular, are often faced with the task of safely crossing numerous roads in order to reach their seasonal breeding grounds (Forman and Deblinger 2000; Sullivan *et al*. 2004; Dahle *et al*. 2008). Conversely, some non-migratory species can face this risk on an almost daily basis in areas of high road densities, where various resources are located on either side of roads or roads have divided animal home ranges (e.g. Klar *et al*. 2009; Jones *et al*. 2012).

With ~50 species living in Australia (Coulson and Eldridge 2010), macropods (Macropodidae) are present in most landscapes, whether arid or forested, rural or urban. The general public and tourists are familiar with some macropod species and regard them as iconic and valued wildlife (Tisdell *et al*. 2005, 2006). However, due to their wide-ranging distributions and high mobility, macropods may be especially vulnerable to the disturbances associated with roads (Ramp 2010). Further, because of their perceived 'commonness', macropods in general are not often considered as being of conservation concern (Coulson 2007).

Comparisons can be made between macropods and ungulates, indicating the similarity of their ecological roles and relationship with road environments. Many species of both taxa are large-bodied animals that aggregate in open areas to graze (Pays *et al*. 2007; Favreau *et al*. 2010), inhabit a variety of landscapes, can be attracted to roads by resources (Lee 2006; Grosman *et al*. 2011), can cause large problems in wildlife–vehicle collisions (Seiler 2005; Ramp and Roger 2008), and may present similar challenges for widespread road mitigation (Putmam 1997; Ramp 2010). Although macropods are not migratory, they often have large home ranges, and road crossings can be frequent, even in areas with low road densities (e.g. Lee 2006).

The perception that high road-kill rates equate to abundant populations remains widespread (see Forman *et al*. 2003) despite considerable evidence to the contrary (e.g. Coulson 1989; Jones 2000; Vijayakumar *et al*. 2001; Schwab and Zandbergen 2011). As well as causing severe injury or death to the animals involved, macropod–vehicle collisions, particularly those involving larger species, can also result in severe human injury or death and great damage to vehicles (e.g. Abu-Zidan *et al*. 2002; Ramp and Roger 2008). Some research has been conducted on the impacts of roads on macropods, particularly with regard to macropod–vehicle collisions (e.g. Coulson 1982, 1989; Osawa 1989; Buchanan 2005; Chambers *et al*. 2010; Lee *et al*. 2010), but many crucial aspects remain largely unstudied. This review aims to summarise the body of research conducted to date and to evaluate where future research is needed to provide a better understanding of the interactions between roads and macropod species, whether widely abundant or critically endangered.

First, however, some important terms related to the field of road ecology must be defined (see Forman *et al*. 2003 for further details). The road corridor consists of the road surface and roadsides where road construction and maintenance alter the land. The road verge is the area between the road and adjacent blocks of land that includes the road shoulder, ditches and areas altered by road maintenance. The road-effect zone is the area within which the road impacts on the surrounding environment, with its size being dependent upon the size and traffic volume of the road, the impacts being investigated and the species, taxa or ecological process of concern. Finally, the road barrier effect occurs when a road corridor forms a partial or complete barrier to water, plant and animal movement and dispersal, effectively separating previously continuous populations.

A web-based search resulted in a total of 60 scientific journal articles, reports and theses that included some study of the impact or interactions between macropods and the road environment (Table 1).

Table 1. Number of studies that investigate relationships between macropods and roads assessed in this review

Topic		No. of studies
Roadkill	Macropods only	12
	Include macropods	17
Roadkill factors	Traffic volume	4
	Local road attributes	5
	Landscape attributes	3
	Temporal variations	11
	Behavioural factors	2
	Demographic biases	6
	Human aspects	6
Road movements		1
Roadside behaviour		2
Population impacts	Modelling	5
	No modelling	3
Mitigation measures	Overpasses	3
	Underpasses	14
	Acoustic deterrents	3
	Olfactory deterrents	1
	Warning signs	2
	Warning reflectors	4
Total		60

Fig. 1. A road-killed red-necked wallaby in Redland, south-east Queensland.

Road-kill

By far the most conspicuous impact of roads on wildlife, including macropods, is mortality due to collisions with vehicles (Fig. 1). This has also been the most commonly researched aspect of road impacts. In Australian studies, macropods sometimes contribute a large percentage of total native mammal road-kill, though low proportions have also been reported (see Table 2).

Traffic volume

One of the most frequently discussed factors contributing to wildlife–vehicle collision hotspots is that of traffic volume (Taylor and Goldingay 2010). Low levels of traffic are usually of little significance as the risks of collisions for most species are relatively low (Burgin and Brainwood 2008). Medium-level traffic volume roads, on the other hand, have been associated with high incidence of road-kill for many species (not only macropods) (Burgin and Brainwood 2008). It has been suggested that medium traffic volumes are low enough for animals to cope with the disturbance, yet high enough for many animals to become injured or killed during crossing attempts (Huijser and McGowen 2010). Very high traffic volumes, however, often result in little wildlife mortality as continuous traffic leads wildlife to avoid the high disturbance associated with these roads. For example, in periurban and rural areas of New South Wales, macropod road-kills were significantly more frequent on roads with medium traffic volumes than those with high or low volumes (Burgin and Brainwood 2008). On North Stradbroke Island in Queensland, higher incidences of swamp wallaby (*Wallabia bicolor*) road-kills were aligned with the relatively higher traffic volumes during the holiday periods, compared with the very low levels at other times (Osawa 1989). Road-kills also increased with average weekly night-time traffic volumes during a drought in north-western New South Wales (Lee *et al*. 2004; Klöcker *et al*.

Table 2. Percentage of macropods (of total native mammals) reported in Australian road-kill studies included in this review

Location	% macropods	Source
Snowy Mountain Highway, NSW	94.3	Ramp *et al*. (2005)
Redland City, south-east Qld	79.7	Buchanan (2005)
Various peri-urban and regional locations in NSW	75.0	Burgin and Brainwood (2008)
Redland City, south-east Qld	58.2	Dexter *et al*. (2009*a*, 2009*b*)
Redland City, south-east Qld	49.1	Dexter (2007)
Royal National Park, NSW	43.8	Ramp *et al*. (2006)
Narrabeen Catchment, Sydney, NSW	40.0	Harris *et al*. (2008)
Pacific Highway between Woodburn and Ferry Park, NSW	30.0	Hayes and Goldingay (2009)
Several highways in eastern Tasmania	27.4	Hobday and Minstrell (2008)
North-eastern NSW	5.6	Taylor and Goldingay (2004)
Between Gungahlin and Lake Cowal, NSW	5.5	Vestjens (1973)
Pacific Highway between Yelgun and Cudgera Creek, NSW	0	Hayes and Goldingay (2009)

2006). These were the only studies to date to specifically investigate the influence of night-time traffic volumes, which is when most macropod–vehicle collisions occur (Osawa 1989), and among the few to include temporal variations in traffic volume. Across these studies there is evidence demonstrating that traffic volume can influence rates of macropod road-kills both spatially and temporally, which emphasises the importance of this variable in predicting and mitigating against road-kills (Taylor and Goldingay 2010).

Local road attributes

Both landscape and local roadside physical features can influence road-kill rates along some roads or sections of roads. For example, visibility of the road verge and the immediate road ahead is known to contribute to the detectability of animals at the roadside (Mastro *et al*. 2010). Sharp bends or corners in the road may reduce the driver's ability to view the road immediately ahead, and therefore result in potential hotspots for road-kill (Lee *et al*. 2004; Klöcker *et al*. 2006). Obstructions along the roadside can also greatly reduce the visibility of macropods nearby or may temporarily trap macropods on the road. In some cases, dense vegetation, such as shrubs or long grass can be such an obstruction to driver visibility (Lee *et al*. 2004). Additionally, the presence of impermeable or wildlife-unfriendly fencing and road cuttings may cause macropods to panic when faced with an approaching vehicle (Lee *et al*. 2004; Klöcker *et al*. 2006; Burgin and Brainwood 2008).

Vegetation along the roadside verge can also play a role in attracting macropods to the roadside to forage. This was evident during a drought when Klöcker *et al*. (2006) found that pasture cover, height and greenness were greater at locations of road-kill incidents than at locations that were free from kangaroo fatalities. Similarly, Lee (2006) found kangaroos to be killed more often on sections of road where shrubs were present and overall pasture greenness was high. Swamp wallabies on North Stradbroke Island were found to select forage with higher nitrogen content, the preferred grasses of which occurred mostly in roadside verges and nearby areas (Osawa 1990). Another study (Burgin and Brainwood 2008) found more macropod road-kills in areas where the road verge was of mown grass, as opposed to longer unmown grass, although no other parameters relating to verge vegetation were considered.

Chambers *et al*. (2010) addressed two largely ignored localised road factors, road verge width and speed limit. These investigations found a positive correlation between tammar wallaby (*Macropus eugenii*) road-kills and verge width on Garden Island in Western Australia. Higher road-kill rates were also found on 60 $km\,h^{-1}$ roads than roads with speeds of 50 $km\,h^{-1}$ and 80 $km\,h^{-1}$

Landscape attributes

Landscape attributes can also contribute to determining road-kill hotspots. Gullies, creek crossings, drainage lines and the presence of other water bodies can be areas of regular movement for macropods and other wildlife (Lee *et al*. 2004). Land use and the type of habitat on either side of the road can also determine where different species are likely to come into contact with the road environment, and therefore are more likely to be involved in a vehicle collision. For example, in a study of road-kill along the Snowy Mountains Highway in New South Wales, eastern grey kangaroos (*M. giganteus*) were more likely to be killed in flat areas with little forest, and where the road was closest to a large dam (Ramp *et al*. 2005). Alternatively, swamp wallabies and red-necked wallabies (*M. rufogriseus*) (combined) were far more likely to be killed where there was a high proportion of forest, presumably because these species often browse and prefer the cover of nearby forest (Ramp *et al*. 2005). In a rural–urban area to the south-east of Brisbane, red-necked wallabies were more likely be killed on roads in areas where both forest and rural properties bordered the road (Buchanan 2005). Red-necked wallabies were also slightly more frequently killed in areas where only rural habitats bordered the road than where only forest bordered the road. Alternatively, swamp wallabies tended to be killed in areas where rural and forest habitats and only forest bordered the road more than in rural habitats (Buchanan 2005). Proximity to forested cover and gullies can likewise influence the location of deer–vehicle collisions (e.g. Finder *et al*. 1999; Found and Boyce 2011).

Temporal variations

In general, seasonal patterns of macropod road-kills are usually not apparent, although some studies have observed seasonal peaks. Reported macropod–vehicle collisions over a 10-year period (1996–2005) in New South Wales were highest from April to August (Ramp and Roger 2008). During a five-year period (1975–79) eastern grey kangaroo road-kills peaked in autumn during two separate years (1975 and 1978) in central Victoria (Coulson 1982). Similarly, tammar wallaby road fatalities over five years (2000–04) on Garden Island, Western Australia, were noticeably greater between March and August (Chambers *et al*. 2010). Further investigation of this pattern showed that daylength (number of daylight hours) was significantly negatively correlated with wallaby road-kill numbers (Chambers *et al*. 2010).

Peaks in road deaths of eastern grey kangaroos have also been related to lunar phase, with significantly higher numbers of deaths around full moon than during any other times (Coulson 1982; Lintermans and Cunningham 1997). In an eight-week study of road-kill patterns in periurban landscapes in south-east Queensland, Buchanan (2005) initially found no clear relationship between road mortality of mammals and lunar phase. However, when data from this study were combined with 12 months of community and council records, road-kill rates of mammals (with 75% of the fatalities being macropods) were significantly higher around full moon (Buchanan 2005). In contrast, however, Osawa (1989) found no evidence of swamp wallaby road-kill occurrence being related to lunar phase.

Preceding rainfall levels also appear to influence macropod road-kill rates. Six-month road-kill surveys conducted during and following drought conditions along a section of the Silver City Highway at Fowlers Gap, north-western New South Wales, found road-kill rates to be significantly higher during the drought (20.8 per month) than after the drought (2.6 per month) (Lee *et al*. 2004). This increased road-kill rate was attributed to a much higher presence of all species of kangaroos at the roadside during drought, perhaps due to higher quality and quantity of food at the roadside than further from the road (Lee 2006). Eastern and western grey (*M. fuliginosus*) kangaroos were killed in similar proportions to their roadside presence both during and outside drought, yet red kangaroos (*M. rufus*) and euros (*M. robustus erubescens*) were killed at a higher proportion to their presence at the roadside during drought (Lee *et al*. 2004). Similarly, during a four-year drought in central Victoria, the road-kill rate of eastern grey kangaroos increased significantly compared with pre- and postdrought surveys (Coulson 1989). The occurrences of swamp wallaby road-kills also increased but were too few for statistical analysis. Further investigation revealed that low rainfall levels would result in higher kangaroo road-kill incidence in the following season, and high rainfall levels would result in lower incidence (Coulson 1989).

On the Snowy Mountains Highway in New South Wales, road fatalities of eastern grey kangaroos and swamp and red-necked wallabies (wallaby species pooled) were negatively correlated with rainfall over the previous six months (Ramp *et al*. 2005). This study also found eastern grey kangaroo fatalities to be negatively correlated with the Southern Oscillation Index, suggesting that road-kill rates are higher during El Niño periods when eastern Australia experiences reduced rainfall (Ramp *et al*. 2005). Lintermans and Cunningham (1997) also discovered similar increases in road-kills of eastern grey kangaroos around Canberra following months of below-average rainfall. These observations further support the contention that periods of low rainfall generally lead to greater road deaths in macropods.

Such patterns suggest that macropods are more susceptible to collisions with vehicles during periods of poor environmental conditions as they have to travel further in search of sufficient resources (Norbury *et al*. 1994) and tend to move into more open habitats (Hill 1982). This idea is also supported by increased incidence of road-kill following bushfires. During a study of swamp wallaby road-kill on North Stradbroke Island, Queensland, a bushfire occurred along one section of the main road, resulting in small increases in collisions along several sections of the road during the following months (Osawa 1989). Although rainfall has emerged as playing a significant role in the frequency of macropod road-kills, a study of tammar wallabies living on a small island in Western Australia found daylength to be correlated with rainfall (Chambers *et al*. 2010). Once this was accounted for, rainfall was no longer a significant factor in predicting road fatalities for this location.

Few other climatic conditions have been related to macropod road-kills, although this may be due to the lack of studies including such factors. One study that did include other climatic parameters found that high barometric pressure and high-speed wind gusts were associated with increased kangaroo road mortalities in north-western New South Wales (Lee 2006). When considering only red kangaroo road-kills, however, low night-time temperature and high night-time humidity increased the probability of road-kills (Lee 2006).

Behavioural response to vehicles

The behavioural response of an animal to an approaching vehicle can play a significant role in determining the end result of the encounter. Although this research was limited to a single locality (the Silver City Highway in north-western New South Wales: Lee 2006; Lee *et al*. 2010), a relatively strong relationship was found between the generalised level of flightiness of a species and the proportion of road mortalities of that species. These studies showed that red kangaroos and grey kangaroos (eastern and western species combined) had high percentages of individuals that fled from an approaching vehicle, took flight at a greater distance from the vehicle and fled the furthest distance (Lee 2006; Lee *et al*. 2010). These species also had the highest mortality rates on the highway.

Demographic biases

Numerous studies on macropod road-kills have reported some level of bias towards males being killed on roads. This bias was known initially only for the eastern grey kangaroo (60%: Coulson 1982; 65%: Coulson 1997), where adult males dominated the data. However, varying levels of male bias have now been reported for western grey kangaroos (70%), swamp wallabies (73%), red-necked wallabies (92%) and red-bellied pademelons (*Thylogale billardierii*) (80%) (Coulson 1997). In contrast, no such bias was found for red kangaroos (42%) (Coulson 1997). Road-kills records for eastern grey kangaroos in Canberra based on adventitious encounters and reports from the public also showed a large bias towards males (71%), particularly immature males (39%) (Lintermans and Cunningham 1997). Macropod road-kill surveys in a semirural area south-east of Brisbane revealed a strong male bias (94% of 18 sexed carcasses) in red-necked wallaby fatalities, but almost parity of the sexes in swamp wallabies (Buchanan 2005). This study did, however, reveal a strong age bias for swamp wallaby road-kills with 95% of animals being adults, though less pronounced for red-necked wallabies (68% adults) (Buchanan 2005). Lee (2006) and Lee *et al*. (2010) also found male biases in the road-kills of eastern grey kangaroos and euros along the Silver City Highway in north-western New South Wales, although sample sizes from these species were very low. However, road-kills of eastern and western grey kangaroos and red kangaroos showed no sex bias along the same section of highway (Lee *et al*. 2004; Klöcker *et al*. 2006). In the same studies, male euros were killed more than females; however, this was attributed to their higher presence at the roadside (Lee *et al*. 2004; Klöcker *et al*. 2006). It has been suggested that a likely reason for such consistent bias across species and regions is that males in many species have larger home ranges and often move larger distances than females (Arnold *et al*. 1992; Evans 1996; Lintermans and Cunningham 1997; Paplinska *et al*. 2009). This greater travel may result in an increased chance of encountering more roads more frequently.

Human aspects of macropod–vehicle collisions

It is also critical to discuss the impact of wildlife–vehicle collisions on humans. In the case of medium to large animals, it is almost always in the best interest of drivers to avoid wildlife collisions, as not only is damage caused to the vehicle, but vehicle occupants can be injured and even killed. Indeed, in the USA, wildlife–vehicle collisions – primarily with various species of deer – cause 26 000 human injuries, 200 human deaths and cost an estimated US$8388 million every year (Huijser *et al*. 2008).

Similarly, macropod–vehicle collisions, particularly those involving large species, can cause injury and even death to the vehicle occupants (e.g. Abu-Zidan *et al*. 2002). Despite this, remarkably few data on these incidents are available, apparently as the causes of many crashes are not recorded in detail (e.g. Berry and Harrison 2008; Henley and Harrison 2009). The following figures come from a variety of sources giving, at best, a fragmentary picture. A sample of 46 patients admitted to Perth Royal Hospital, who had been involved in collisions with a macropod, reported that 19 had actually hit the animal while 27 were able to avoid the animal (Abu-Zidan *et al*. 2002). For all these incidents, 16 (35%) hit secondary objects and 15 (33%) rolled over. Patients who were in crashes where the macropod was avoided had a significantly higher incidence of neck injuries and tended to also have more head injuries, but there was no significant difference in the severity of injuries between those who avoided and those who hit a macropod (Abu-Zidan *et al*. 2002). One patient of the 46 died as a result of injuries sustained in the collision with a macropod (Abu-Zidan *et al*. 2002).

Data from the Traffic Accident Database System for New South Wales for 1996–2005 showed high proportions of macropods to be involved in animal-related accidents (41%) (Ramp and Roger 2008). Additionally, of the 22 animal-related collisions that resulted in human fatality, 13 (59%) of these involved macropods, and of those resulting in human injury, 38% were attributed to macropods (Ramp and Roger 2008). Of all crashes, 57% occurred between 17:00 and 24:00 hours, significantly more crashes occurred from April to August, and on the weekend than on weekdays except Friday (Ramp and Roger 2008). Further investigation into the variation across each year revealed that the mean length of natural darkness (time between sunset and sunrise) was positively correlated with the number of animal-related collisions (at the scale of month) and explained 89% of variation in crash rate (Ramp and Roger 2008).

Rowden *et al*. (2008) collated data on vehicle collisions with animals in Australia, with data from most states and territories covering the five-year period 2001–05. From the Queensland data (which was the most detailed), the period when the largest proportion of animal–vehicle collisions occurred was between 18:00 and 23:59 hours and most incidents occurred in 100–110 km h^{-1} speed zones (Queensland Transport 2007 in Rowden *et al*. 2008). High proportions of these incidents were reported to involve kangaroos or wallabies: 47% in New South Wales and 45% in Queensland (Rowden *et al*. 2008). Statistics on the type of animal involved from crashes in other states and territories were not reported.

It is clear from these data that kangaroos and wallabies should be of the most concern for Australian motorists. Collisions involving macropods comprised the highest proportion of reported crashes and a high proportion of injury-related crashes.

Movement and behaviour around roads

Very little research has been conducted on the behaviour and movements of macropods around roads, and some potentially relevant work has focussed mainly on ecotourism impacts rather than road impacts. Lee (2006) approached these topics by investigating the temporally varying conditions under which road crossings are more likely to occur and the behavioural responses of kangaroos to approaching vehicles. Road crossings by kangaroos were investigated using laser and heat/movement sensor devices attached to a nearby fence, and were influenced by barometric pressure, wind gusts and dew-point temperature (Lee 2006). High-speed wind gusts may create conditions in which kangaroos have more difficulty detecting predators, and thus may travel less during these conditions (Lee 2006).

In response to an approaching vehicle, red kangaroos and grey kangaroos (eastern and western species combined) were much more flighty than euros (Lee *et al*. 2010). In general, kangaroos were more likely to react to an approaching vehicle with flight than vigilance at night than during the day (Lee *et al*. 2010). When kangaroos did flee, during both day and night, over 75% of them fled away from the vehicle, with the next most common direction being across the path of the approaching vehicle (Lee 2006). Kangaroos tended to flee across the path of the vehicle more at night, with a negligible proportion fleeing towards the vehicle (Lee 2006). During the day, a small proportion of kangaroos also fled in a parallel direction to the vehicle, but this behaviour was never displayed during the night (Lee 2006). Kangaroos were also more likely to flee when confronted along a small dirt track (that was used very infrequently) than the highway, during spring and when the vehicle was travelling at low speeds. Grey kangaroos were also significantly less likely to take flight if they were in groups of three or more and if they were partially obscured by cover; these factors did not change the flightiness of red kangaroos and euros (Lee *et al*. 2010). Similar responses to vehicles have been observed in ungulates (Horejsi 1981; Blackwell and Seamans 2009).

Some studies have also investigated macropod behaviour while being approached by slow-moving tour vehicles in sanctuaries. Bridled nailtail wallabies (*Onychogalea fraenata*), red-necked wallabies and swamp wallabies all significantly reduced time spent performing maintenance activities, such as feeding, resting, grooming and socialising, when approached by a vehicle (King *et al*. 2005). Another study found that red kangaroos and euros fled from a slow-moving vehicle 41% of the time, with euros allowing closer approach before flight and fleeing for shorter distances than red kangaroos (Wolf 2009; Wolf and Croft 2010).

Evidence of the spatial extent of the road-effect zone was reported by Pocock and Lawrence (2005) in Bendigo Regional Park, Victoria, where the presence of eastern grey kangaroos and swamp wallabies was found 10 m and 25 m from a two-lane arterial road, respectively. This suggests that these larger macropod species do not avoid the road, and can even be found very close to it, potentially increasing their susceptibility to collisions with vehicles.

The impact of roads on the viability of macropod populations

Population viability analyses are often conducted in situations where populations appear to be in decline and are sometimes used to predict the impact of different management strategies on the viability of the population in question (Hanski 2002; Ben-Ami and Ramp 2005). A population viability analysis conducted on a semiurban swamp wallaby population in the Royal National Park near Sydney revealed that the viability of the population was very sensitive to the number of deaths of females (Ramp and Ben-Ami 2006). By reducing road mortality of females by only 20%, the model predicted that the population decline could be reversed and carrying capacity restored (Ramp and Ben-Ami 2006). Reducing the wallaby road mortality was by far the most effective management option for this population when compared with high levels of fox control. It must be noted, however, that the population involved in this modelling was assumed to be closed, a condition not necessarily valid given the geography of the site. Thus, the conclusions reached may be less concrete than were articulated in the study.

Conversely, although road-kill was a significant contributor to the mortality of a semiurban swamp wallaby population in Muogamarra Nature Reserve, also near Sydney, other pressures on the population were found to be more important (Ben-Ami 2005; Ben-Ami *et al*. 2006). The population viability analysis showed that even if all road mortalities were prevented (and no other management action taken), the population would continue to decline (Ben-Ami 2005; Ben-Ami *et al*. 2006). Population modelling conducted on tammar wallabies living near a naval base on Garden Island, Western Australia, revealed that road-kill rates significantly decreased the population growth rate, but not during all years (Chambers 2009; Chambers and Bencini 2010).

Roads may play a significant role in decreasing the viability of vulnerable and endangered populations (e.g. Hayward *et al*. 2005; Hazlitt *et al*. 2006; Ramp and Ben-Ami 2006). The Proserpine rock-wallaby (*Petrogale persephone*) is listed as endangered by the IUCN, the Commonwealth and in Queensland, and is one such species where roads contribute to its decline. In the national recovery plan for the species (Department of Environment and Resource Management 2010) road mortality is listed as a moderate threat, and in the previous recovery plan (2000–04, Nolan and Johnson 2001) reduction of road mortality was listed as the second threat management priority. Road mortalities in some areas have been attributed to guinea grass (*Panicum maximum*) attracting the wallabies to graze in road verges and wallabies crossing a road to access irrigated grass in a picnic area (Department of Environment and Resource Management 2010). Efforts to reduce guinea grass in road verges and to provide alternative irrigated grazing areas appeared to reduce road-kill rates, although further monitoring has not yet been reported.

The brush-tailed rock-wallaby (*Petrogale penicillata*) is listed as vulnerable by the IUCN and in Queensland, where its populations are the most stable in Australia (Hazlitt *et al*. 2006). On a road near one population of ~20–25 individuals in south-east Queensland, at least seven individuals were killed from collisions with vehicles during a single year (2004) (Hazlitt *et al*. 2006). Despite this apparently low number of road-kills, they represent a substantial proportion (~28–35%) of the small and genetically constrained population of the species (Hazlitt *et al*. 2006).

The quokka (*Setonix brachyurus*) is also listed as vulnerable by the IUCN, and although it has a stable population on Rottnest Island, Western Australia, the small surviving metapopulations on the mainland are subject to much greater threats (Hayward 2002; Hayward *et al*. 2003, 2005, 2007). In a study of survivorship in the northern jarrah forests, eight of 58 radio-collared individuals died, with two of these deaths being attributed to collisions with vehicles (Hayward *et al*. 2005). The risk of mortality of quokkas from vehicle collisions was high at two of the remaining populations where roads with high traffic volumes and speeds bisect the swamp habitat of the quokkas (Hayward *et al*. 2005). Road-kills of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*), which is listed as near-threatened in Queensland, have also been recognised as a significant threat to their populations in the wet tropics (Newell 1999; Goosem *et al*. 2005).

Road crossing structures and other mitigation devices

Many approaches have been used to attempt to mitigate the impacts that roads have on wildlife, including: wildlife warning road signs, road markings, ultrasonic devices, roadside reflectors, wildlife fencing, wildlife underpasses and retrofitted culverts, and wildlife overpasses (e.g. Magnus *et al*. 2004). Mitigation structures and devices aim to change either the behaviour of the wildlife near roads or the behaviour of drivers. Their effectiveness, however, has been shown to be highly variable and dependent on the location of the measure, strategic implementation for the targeted wildlife and continued maintenance (see Huijser and McGowen 2010 for North American review).

Wildlife warning signs

Wildlife warning signs are the most commonly implemented approach to mitigation of wildlife road-kills (Huijser and

McGowen 2010). Typically, they depict a silhouette of the species of concern on a yellow background, although larger and more conspicuous signs also exist. On some occasions these images are deployed in conjunction with signs indicating reduced speed limits during the times when animals are most susceptible to collisions (Gleeson and Gleeson 2012). The main aim of such signage is to alert drivers to the possibility of encountering wildlife on or near the road and thus make the driver more vigilant and reduce speed.

Despite warning signs being commonly used, there is little evidence that they significantly change driver behaviour and reduce road-kill rates (Dique *et al*. 2003; Al-Ghamdi and AlGadhi 2004). Standard kangaroo warning signs were ineffective at reducing macropod road-kill rates immediately following erection along the Northern Highway in central Victoria in 1978 (Coulson 1982). On a Wyoming highway (speed limit 105 km h^{-1}), USA, the use of deer signs with flashing lights when deer were detected near the road succeeded in reducing vehicle speeds, but only by an average of 6% without lights and 7% when lights were flashing (Gordon *et al*. 2004). Magnus *et al*. (2004) developed and installed a new wildlife warning sign design that included a greatly reduced recommended speed from dusk to dawn. Unfortunately, the vehicle speed data collected were incompatible with presign data, though, anecdotally, speeds were thought to be reduced, at least in the short term. Magnus *et al*. (2004) did, however, highlight the importance of investigating alternative sign designs that may be more informative and meaningful to drivers.

Crossing structures and fauna fencing

Underpasses and overpasses that are purpose-built or retrofitted for wildlife can be successful in providing safe movement across roads. These structures, however, function well only when used in conjunction with wildlife-exclusion fencing and are designed so that wildlife are not deterred from using them (Fig. 2). Table 3 summarises reported evidence of macropod species using underpasses and overpasses. Kangaroos and wallabies have used underpasses with a wide range of dimensions. Although wallabies and kangaroos used fauna culverts as small as 1.2 m high × 2.4 m wide (Taylor and Goldingay 2003), a minimum of 3 m in height should be recommended to allow animals to stand upright and hop unimpeded (Figs 3, 4). The influence of the length of the underpasses has only been assessed on a few occasions, but one culvert 62.5 m in length has been used, suggesting that wallabies and kangaroos may not be deterred by long structures (Hayes and Goldingay 2009). Unidentified kangaroos or wallabies have also been detected using viaducts and culverts for creek and drainage flow on the Gold Coast, Queensland, although no dimensions for these structures were reported (Leopold-Wooldridge 2008). The three overpasses used by wallabies and kangaroos varied in minimum width, but wider overpasses with continuous habitat limit disturbance from the traffic and encourage regular use. Smaller macropods such as pademelons, potoroos and bettongs, have been recorded less commonly than large macropods (AMBS 2001*a*, 2001*b*, 2001*d*, 2002*a*), while overseas studies have suggested that smaller animals tend to prefer shorter structures (e.g. Yanes *et al*. 1995; Ascensão and Mira 2007). Underpass length, however, does not appear to constrain use by these smaller macropods, as pademelons, potoroos and bettongs all used structures at least 52 m in length (AMBS 2001*b*, 2001*d*, 2002*a*). To date, there has been no evidence of potoroos and bettongs using overpasses, although there is potential for overpasses to be used by smaller macropods if continuous dense vegetation covers the structures. Wildlife-exclusion fencing associated with most of these structures was integral in encouraging macropods to use such road crossing structures, particularly for larger wallabies and kangaroos, which readily make direct road crossings (Buchanan 2005; Bond and Jones 2008).

Fig. 2. An example of a fauna overpass (land bridge), with fauna-exclusion fencing, connecting habitat across Compton Road in Brisbane, Queensland.

Fauna-exclusion fences aim to prevent animals from entering the roadway and have different specialised features, depending on what taxa are targeted and their ability to breach a standard fence. In some fence designs, animals are prevented from climbing over the fence by having a 'floppy top' that flops back towards a climbing animal, or by running metal sheeting along the top that is wider than the species' reach (Department of Transport and Main Roads 2010; Gleeson and Gleeson 2012). Similarly, animals can be prevented from digging under the fence by a thick plastic strip that is dug slightly into the ground, or the bottom of the mesh is attached to a block of cement running under the fence (Department of Transport and Main Roads 2010). When well designed and maintained, such fencing along roads has been proven to reduce road-kill rates of many taxa (Clevenger *et al*. 2001*b*; Jaeger and Farhig 2004; Dodd *et al*. 2007; Leblond *et al*. 2007; Bond and Jones 2008). Not only does wildlife-exclusion fencing reduce wildlife–vehicle collisions, it can also be strategically placed to funnel wildlife to road-crossing structures and increase successful road crossings via these structures (Dodd *et al*. 2007).

The use of fencing alone is often cautioned against, however, as it also creates an impermeable barrier to most animals, thus inhibiting animal movement across the road and creating smaller isolated populations without the possibility of gene flow (Jaeger and Farhig 2004). Although fauna-exclusion fencing may reduce wildlife–vehicle collisions where it is present on both sides of the road, it can also cause road-kill hotspots at the fence ends (Clevenger *et al*. 2001*a*). Additionally, on occasion when an animal may breach the fence, they then become trapped on the roadway unless one-way escape gates or ramps are installed at

Table 3. Use of a range of road crossing structures by macropod species

EGK: eastern grey kangaroo (*Macropus giganteus*); RNW: red-necked wallaby (*Macropus rufogriseus*); SW: swamp wallaby (*Wallabia bicolor*); UWK: unidentified wallaby or kangaroo (*Macropus* sp. or *Wallabia bicolor*); RLP: red-legged pademelon (*Thylogale stigmatica*); UPa: unidentified pademelon (*Thylogale* sp.); LNP: long-nosed potoroo (*Potorous tridactylus*); UPo: unidentified potoroo (*Potorous* sp.); UB: unidentified bettong (*Bettongia* sp.); LTK: Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*)

Species	Structure type	Dimensions	Fencing	Location	Source[A]
EGK	Forest bridge	20 m base, 15 m mid width, 70 m long	Yes	Karawatha Forest, Kuraby, south-east Qld	12, 13
RNW	Culvert	2.8 m diameter, 47.8 m long	Yes	Taree Bypass, NSW	9
	Forest bridge	20 m base, 15 m mid width, 70 m long	Yes	Karawatha Forest, Kuraby, south-east Qld	12, 13
SW	Culvert	4 m high, 3.2 m wide, 20 m long	Unknown	Wollongong, NSW	1
	Underpass	10 m diameter, unknown length	Yes	Brisbane Water National Park, NSW	2
	Culvert	3 m high, 3 m wide, 40–52 m long	Yes	Pacific Hwy, Bulahdelah to Coolongolook, NSW	4, 6
	Span bridge underpass	5.5 m high, 75 m wide, 21 m long	Yes	Petrie, south-east Qld	15
	Span bridge underpass	3 m high, 12 m wide, 14 m long	Yes	Victoria Point, south-east Qld	15
	Culvert	3.7 m high, 3 m wide, unknown length	Yes	Capalaba, south-east Qld	15
	Culvert	3–3.1 m high, 3–3.1 m wide, 55 m long	Yes	Gateway Mwy, Mackenzie, south-east Qld	16
	Forest bridge	20 m base, 15 m mid width, 70 m long	Yes	Karawatha Forest, Kuraby, south-east Qld	12, 13
UWK	Culvert	3 m high, 3 m wide, 40–52 m long	Yes	Pacific Hwy, Bulahdelah to Coolongolook, NSW	4, 6, 8
	Arch underpass	18.3 m diameter, unknown length	Yes	Pacific Hwy, Bulahdelah to Coolongolook, NSW	4
	Culvert	2.8 m diameter, 47.8 m long	Yes	Taree Bypass, NSW	7, 9
	Culvert	1.2 m high, 2.4 m wide, 18 m long	Yes	Brunswick Heads, NSW	3
	Span bridge underpass	3 m high, 10 m wide, unknown length	Yes	Brunswick Heads, NSW	3
	Span bridge underpass	Unknown dimensions	Yes	Herons Creek Deviation, NSW	5
	Culvert	1.2 m high, 2.4 m wide, 18 m long	Yes	Brunswick Heads, NSW	10
	Underpass	2.4 m high, 2.5 m wide, 48 m long with raised cement level 1.6 m wide, 2 m clearance	Yes	Karawatha Forest, Kuraby, south-east Qld	12, 13
	Culvert	3 m high, 3 m wide, 42.3 m long	Yes	Marshall's Ridges, Yelgun, NSW	14
	Culvert	3 m high, 3 m wide, 62.5 m long	Yes	Tagget's Hill, Cudgera Creek, NSW	14
	Span bridge underpass	1.5 m high, 8 m wide, 12 m long	Yes	Gold Coast Hwy, Arundel, south-east Qld	15
	Forest bridge	20 m base, 15 m mid width, 70 m long	Yes	Karawatha Forest, Kuraby, south-east Qld	12, 13
	Forest bridge	9.4–37 m wide, unknown length	Yes	Marshall's Ridges, Yelgun, NSW	14
	Forest bridge	35 m wide, unknown length	Yes	Tagget's Hill, Cudgera Creek, NSW	14
RLP	Arch underpass	3.4 m high, 3.7 m wide, unknown length	Unknown	Wet Tropics World Heritage Area, north Qld	11
UPa	Culvert	3 m high, 3 m wide, 40–52 m long	Yes	Pacific Hwy, Bulahdelah to Coolongolook, NSW	4, 6
	Arch underpass	18.3 m diameter, unknown length	Yes	Pacific Hwy, Bulahdelah to Coolongolook, NSW	4
LNP	Culvert	3 m high, 3 m wide, 40–52 m long	Yes	Pacific Hwy, Bulahdelah to Coolongolook, NSW	8
UPo	Culvert	1.2 m high, 2.4 m wide, 18 m long	Yes	Brunswick Heads, NSW	3
UB	Culvert	3 m high, 3 m wide, 40–52 m long	Yes	Pacific Hwy, Bulahdelah to Coolongolook, NSW	8
LTK	Arch underpass	3.4 m high, 3.7 m wide, unknown length	Unknown	Wet Tropics World Heritage Area, north Qld	11

[A]Source: 1, Hunt *et al*. (1987); 2, AMBS (1997); 3, AMBS (2001*a*); 4, AMBS (2001*b*); 5, AMBS (2001*c*); 6,AMBS (2001*d*); 7, AMBS (2001*e*); 8, AMBS (2002*a*); 9, AMBS (2002*b*); 10, Taylor and Goldingay (2003); 11, Goosem *et al*. (2005); 12, Bond and Jones (2006); 13, Bond and Jones (2008); 14, Hayes and Goldingay (2009); 15, Jones *et al*. (2012); 16, Jones *et al*. (2013).

regular intervals in the fence (Department of Transport and Main Roads 2010).

Warning reflectors, acoustic repellents and scent repellents

Studies on other mitigation devices such as wildlife warning reflectors and vehicle-mounted acoustic repellent devices have shown varying results. In some studies, wildlife warning reflectors were found to have little effect on the roadside behaviour of deer, with little change in the rates of road-kill (Waring *et al*. 1991; D'Angelo *et al*. 2006), whereas in others, deer–vehicle collisions were reduced dramatically (Putmam 1997). For macropods, the effectiveness of both red and white reflectors from two brands (Strieter-Lite and Swareflex) were assessed on captive red kangaroos and red-necked wallabies (Ramp and Croft 2006). The red Strieter-Lite reflectors elicited significantly increased vigilance in red kangaroos and increased flight from the road in red-necked wallabies (Ramp and Croft 2006). However, despite these results being statistically significant, overall responses to the wildlife warning reflectors were very low, and therefore were deemed ineffective (Ramp and

Fig. 3. Swamp wallaby using a 3 m × 3 m box culvert under the Gateway Motorway in Brisbane, Queensland. (Photo: Applied Road Ecology Group, Environmental Futures Centre.)

Fig. 4. The entrance of a box culvert used by swamp wallabies under the Gateway Motorway in Brisbane, Queensland. (Photo: Applied Road Ecology Group, Environmental Futures Centre.)

Croft 2006). Roadside reflectors were installed in northern Queensland where endangered Proserpine rock-wallabies were at risk from being hit by vehicles. Initially, the reflectors were thought to be reducing road-kills of the species (Nolan and Johnson 2001; Johnson *et al*. 2003), but were later assessed and revealed to be ineffective (Department of Environment and Resource Management 2010). Swareflex wildlife warning reflectors were also installed with a range of other mitigation measures in Cradle Mountain–Lake St Clair National Park in Tasmania (Jones 2000). Road-kill rates were reduced along the road, but the different mitigation measures installed were not independently tested from one another (Jones 2000), so the reduction in road-kill rates cannot be attributed to the reflectors alone.

Vehicle-mounted acoustic repellent devices claim to repel animals by emitting a high-frequency sound (Bender 2003; Magnus *et al*. 2004; Muirhead *et al*. 2006). Such devices have been tested to assess their effectiveness in Australia, generally resulting in little or no response from animals (Bender 2003; Magnus *et al*. 2004; Muirhead *et al*. 2006). The electronic Roo-Guard® sound emitter was tested on captive and free-ranging eastern grey kangaroos, captive red kangaroos (Bender 2003) and temporarily captive tammar wallabies (Muirhead *et al*. 2006). Exposure to the sound emitted from the Roo-Guard® elicited no significant response from all species, including free-ranging eastern grey kangaroos (Bender 2003; Muirhead *et al*. 2006).

Another device, the Hobi ultrasonic animal alert whistle, an air-driven vehicle-mounted whistle, was tested for its ability to change wildlife roadside behaviour and reduce the number of animals hit (Magnus *et al*. 2004). During the tests, the driver was unaware as to whether the device was turned on or off, in order not to bias driver behaviour. This device did not alter roadside behaviour of animals and failed to significantly reduce the number of animals hit (Magnus *et al*. 2004). Additionally, the whistle sound emitted was found to be only slightly louder than the sound of the vehicle, suggesting that the sound produced may have been insufficient (Magnus *et al*. 2004).

Scent repellents have not been well researched with regard to deterring macropods from roads. Gibson (2008), however, investigated the reaction of red-necked wallabies to various scent repellents under captive conditions. First, four different scent repellents were compared in their effectiveness in deterring the wallabies from a food source, with two performing well: Plant Plus (based on the chemistry of dog urine) and an egg formulation (Gibson 2008). Captive trials revealed that Plant Plus was the most effective repellent (from a limited food source). Furthermore, habituation of wallabies to the scent over a period of six weeks was minimal and Plant Plus continued to persist and be effective for up to 10 weeks after application (Gibson 2008). Field trials of the repellent were attempted, but failed due to unavoidable and unpredicted site disturbance and lack of interest by free-ranging macropods in artificial food sources (Gibson 2008).

Research gaps

From the material summarised in this review, it is evident that there are numerous areas of research that need to be investigated further with regard to the relationship between macropods and roads, and in road ecology in general. First, although many road-kill studies have been conducted, some of which include modelling, there is a lack of species-specific road-kill modelling. Modelling has been conducted on pooled road-kill data (e.g. Ramp *et al*. 2005), but this often fails to consider species differences in habitat preferences, behavioural responses to roads and general ecology of the various species recorded. By conducting species-specific road-kill modelling, more accurate predictions and conclusions can be drawn. Additionally, more research that includes seasonal variation and investigation of daylight length on road-kill rates would be beneficial to concentrating mitigation efforts when resources are limited.

In general, behavioural and animal movement studies relating to roads have been rare in Australia (although see King *et al*. 2005; Lee 2006; Wolf 2009), but these are very important in developing a profile on how different species perceive roads and vehicles and the contributing effect of roads on a day-to-day basis. Such behavioural studies also have the potential to contribute significantly to understanding road-kill risks and to the design and location of mitigation measures. Data on animal movements around roads in particular are lacking, and should be prioritised as this can potentially reveal road avoidance and/or attraction, road permeability, regular road crossing locations (where road-kills may not be prevalent, e.g. Lewis *et al*. 2011; Neumann *et al*. 2012), and quantification of road exposure (using time budgets).

Research on the overall impact of roads on the viability of species populations in Australia is also lacking (see Taylor and Goldingay 2010). Population viability analyses can be a useful tool for quantifying and prioritising the pressures on populations, particularly in urban landscapes, where there are numerous pressures from human sources (Ben-Ami and Ramp 2005; Ben-Ami *et al*. 2006). To date, population modelling has been performed on only three macropod populations where the impact of roads has been investigated (Ben-Ami *et al*. 2006; Ramp and Ben-Ami 2006; Chambers and Bencini 2010). Two of these studies were conducted on swamp wallaby populations; similar studies need to be conducted on other macropod species, particularly where declines in the populations may easily go unnoticed. Further research needs to be conducted on population impacts, particularly on species of conservation concern where severe road impacts may be occurring, for example, as has been conducted for a squirrel glider (*Petaurus norfolcensis*) metapopulation (Taylor and Goldingay 2012). Additionally, however, preventing population decline in currently abundant road-impacted species should also be a management goal through ongoing long-term research.

Use of road-crossing structures (both pre-existing and purpose-built) by wildlife has been explored only in recent decades in Australia. To date, research has mostly been limited to documenting use by various taxa and not actual effectiveness in creating pathways for movement between populations (van der Ree *et al*. 2007). Ideally, efforts need to be invested in long-term BACI (Before–After–Control–Impact) studies that involve investigating metapopulation dynamics through population genetics (Lesbarrères and Fahrig 2012). Unfortunately, such research is both time expensive and financially expensive, and so is rarely conducted. Even so, smaller short-term (~3–5 years) research in this area would be highly valuable (e.g. van der Ree *et al*. 2009; Taylor 2010; Torres *et al*. 2011).

Another poorly researched area is that of identifying the road-crossing structure preferences and tolerance limits of different species. It is vitally important that when road-crossing structures are being designed, that the target taxon's preferences for using structures of varying design are considered. This should include structures of various dimensions (an openness index is often used), vegetation type and proximity, light penetration (for underpasses), and ground substrates (e.g. Woltz *et al*. 2008). Such research could then be used to design appropriate and targeted (whether to one species or many) road-crossing structures that are likely to be more successful than the generic structures commonly deployed as part of road upgrades.

Further research on other road-mitigation measures is also needed. As mentioned above, wildlife warning signs are the most commonly implemented mitigation measure, yet research on their effectiveness paints an uncertain picture and there is little evidence that they reduce wildlife road-kill rates in the long term. Despite this, it is likely that they will continue to be frequently implemented due to their relatively inexpensive cost. With this in mind, research into other potential sign designs that may be more effective at eliciting desired responses from drivers should be conducted (Magnus *et al*. 2004). Additionally, scent repellents may be appropriate to use in some small areas of particularly high road mortality, yet field tests are needed to be performed on a variety of species before they can be seriously considered as a mitigation option (Gibson 2008).

Genetic studies investigating the potential barrier effects of roads have been completely deficient on macropods, to the best of our knowledge (Taylor and Goldingay 2010). Such research would be highly informative in quantifying the permeability of roads to wildlife populations, whether limited gene flow caused by road barrier effects is likely to cause population collapse and evaluate the facilitation of gene flow by road-crossing structures (Simmons *et al*. 2010).

Conclusion

Research in the field of road ecology is still in its relative infancy in Australia (see Taylor and Goldingay 2010), and much more wide-spread attention is needed in many areas of this field to be comparable to Europe and North America. Although a moderate volume of research has been conducted on the interactions between macropod species and roads in Australia, it is a fraction of the research effort conducted on large mammals in Europe and North America (Seiler 2001; Forman *et al*. 2003; Fahrig and Rytwinski 2009; Beckmann *et al*. 2010). Research that encompasses a variety of aspects of interactions between roads and macropods (and wildlife in general) is needed to broaden our perspective on impacts and mitigation. Not only is Australian research in limited volume, but it mainly comprises simple short-term studies. Road ecology research in Australia needs to be broadened to include longer-term studies that assess a higher level of complexity and impact.

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