

Review

Do wildlife passages act as prey-traps?

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Abstract

A number of studies have proposed that wildlife passages beneath roads and railway lines might be exploited by mammalian predators as ‘prey-traps’ with prey-species being effectively funnelled into areas of high concentration. This proposition has raised the possibility that use of passages by predators may reduce the effectiveness of passages in conserving other forms of wildlife. We review the literature and conclude that evidence for the existence of prey-traps is scant, largely anecdotal and tends to indicate infrequent opportunism rather than the establishment of patterns of recurring predation. Most passage studies record no evidence of predation in or around passages. Conversely, there is some evidence that predator species use different passages than their prey.
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1. Introduction

Wildlife passages are being increasingly promoted as a means of mitigating the impacts of roads and railways on animal populations (Bekker et al., 1995; Forman and Hersperger, 1996; van Boheman, 1998; van der Grift, 1999) and are now becoming a routine requirement for major road and rail corridors. In Europe, the inter-governmental framework for European Co-operation in the field of Scientific and Technical Research has implemented Action 341 (COST 341) entitled “habitat fragmentation due to transportation infrastructure”. The main objective of COST 341 is to promote a safe and sustainable pan-European transport infrastructure with the aim of conserving biodiversity and reducing vehicular accidents and resulting fauna casualties (Button et al., 1998). In the USA, the Transportation Equity Act for the 21st Century (TEA-21), expands the funding of transportation enhancement activities to include projects to reduce vehicle-caused wildlife mortality (US Department of Transportation, 1999). In Australia, State transport legislation such as the New South Wales Transport Administration Act 1988 requires that where transport activities affect the environment, operations need to be in compliance with the principles of ecologically sustainable development (Johnson, 2000). There are also State and Federal requirements for the environmental assessment of road and rail corridor proposals having particular regard to potential impacts on threatened animal and plant species. However, decision making by land managers and transportation planners regarding the effective design and success of passage structures is hampered by the dearth of information currently available (Gloyne and Clevenger, 2001).

Studies of the effectiveness of wildlife passages have generally focused on examining the influence of passages in reducing road- and rail-kill (Jackson and Tynning, 1989; Foster and Humphrey, 1995; Boarman and Sazaki, 1996; Rodríguez et al., 1996), facilitating movement (Reed et al., 1975; Singer and Doherty, 1985; Clevenger and Waltho, 2000), and ameliorating other adverse effects on populations (Mansergh and Scotts, 1989). Whether being designed to reduce road-kill and barrier effects, to facilitate movement, or to increase population viability, it is usually assumed that passages provide a safer environment for animals than the roads and railways they cross.

By their very nature, wildlife passages are likely to result in concentrations of animals or at least high rates of transit. Therefore, if predators do prey on species that use the passages, the probability of encountering prey may increase in proximity to frequently used passages. As a result, it has been hypothesized that passages may be exploited by predatory mammals, such as foxes (*Vulpes vulpes*), dogs (*Canis familiaris*) and cats (*Felis catus*), with these predators effectively using the

tunnels as ‘prey-traps’ (Hunt et al., 1987; Reading, 1989; AMBS, 1997). If proved true, this supposition has the potential to stigmatise the use of passages as effective measures for mitigating road and rail impacts. Wildlife passages are costly, particularly when designed for large fauna, and such criticism may deter transportation agencies from implementing such structures.

The possibility of passages acting as ‘prey-traps’ is beginning to draw attention to this issue as a matter for consideration in research and monitoring studies (AMBS, 1997; Finegan, 1997; Norman et al., 1998). It is also drawing attention in environmental impact statements (EISs) for new road and rail proposals. For example, between January 1991 and October 2001, 29 of 71 EISs produced in New South Wales for new road and rail proposals proposed construction of wildlife passages (including culverts and bridges modified or designed to provide for animal thoroughfare). Six of these identified predation as an issue for passage sites or in passage design (unpublished data available from the authors on request).

The objective of this review is two-fold. Firstly, we critically examine and evaluate the evidence that passages are exploited as prey traps. Secondly, we evaluate the evidence regarding whether predator and prey species use different passages and explore whether this reflects possible predator-prey avoidance behaviour.

2. Literature survey

We conducted a literature survey in July 2000 using BIOSIS (Biological Abstracts) and searching for the following key words: *wildlife* with any of the following additional terms: *passage*, *tunnel*, *culvert*, *underpass*, *overpass*, and *ecoduct*. Additional papers were obtained by examining the literature cited in the references and from considering the Proceedings of the First, Second and Third International Conference on Wildlife Ecology and Transportation (Evink et al., 1996, 1998, 1999). Informal contact was also made with a number of colleagues. We then examined the available literature for evidence of exploitation of passages as prey-traps, as well as information on predator-prey interactions associated with passage studies.

3. Passages as prey-traps

3.1. Do predators use artificial structures to facilitate hunting success?

The response of predators to artificial structures such as roads and other utility corridors is varied. Native carnivores have been reported avoiding artificial structures such as roads and developed areas (McLellan and

Shackleton, 1988; Apps, 1999; Sweanor et al., 2000). Local populations of native predators can become drastically reduced and in some cases extirpated, by road building and consequent road-kill [e.g. Florida panther, (*Puma concolor coryi*) Foster and Humphrey, 1995; eastern quolls, (*Dasyurus viverrinus*), and Tasmanian devils, (*Sarcophilus laniarius*), Jones, 2000]. However, road construction areas may be used by other native predator species [e.g. wolves (*Canis lupus*), and lynx (*Lynx canadensis*)] to facilitate greater access to prey (Parker, 1981; Thurber et al., 1994; James and Stuart-Smith, 2000). The creation of new roads may also favour the dispersal of exotic predator species such as foxes, potentially exposing local populations of native animals to increased predation (May and Norton, 1996). Roads may be incorporated as part of a predator's home range boundary (Meek and Saunders, 2000), and can increase the foraging opportunities for predators through the availability of road-kill carrion, although they themselves may become victims of road-kill (Bennett, 1991; AMBS, 1997; Jones, 2000; Meek and Saunders, 2000). The response of carnivorous mammals to transport infrastructure corridors therefore appears to vary between the attraction exhibited by the most generalist species, and its avoidance by those most sensitive to human interference (Rusch, 1985).

Predators are known to opportunistically exploit fauna surveys (e.g. pitfall traps) and artificial utility corridors (e.g. pipelines and roads) to increase their foraging opportunities. Reading (1989) reported opportunistic predation by brown rats (*Rattus norvegicus*) on migrating common toads (*Bufo bufo*) caught in pitfall traps. There have also been reports of predation (evidenced by partly eaten wildlife) and 'patrolling' by cats and foxes, along pipeline trenches (Ayers and Wallace, 1997; Woinarski et al., 2000). Wolves are known to use roads to facilitate the hunting of prey [e.g. caribou (*Rangifer tarandus*)] as roads provide greater access to prey (Thurber et al., 1994; James and Stuart-Smith, 2000).

Predators are known to enhance hunting success by exploiting wildlife mitigation structures constructed to alleviate road impacts on fauna. For example, wolves and coyotes (*Canis latrans*) are known to chase and trap ungulates against wildlife exclusion fencing (Woods, 1990; Gibeau and Heuer, 1996; M. Hebblewhite, personal communication). There have also been reports that high levels of use of wildlife tunnels by introduced predators coincide with low levels of prey species' use (Hunt et al., 1987). This has led to speculation that wildlife passages may be used by predators as 'prey-traps' (Hunt et al., 1987). It appears therefore that predators can and will take advantage of artificial structures to increase their foraging opportunities. However, this is not evidence that wildlife passages themselves facilitate prey capture.

3.2. Use of passage structures by predators and prey

Recent attention has focused on the role and design of wildlife passages to sustain populations of native predator species (Foster and Humphrey, 1995; Broekhuizen, 1996; Land and Lotz, 1996; Hewitt et al., 1998; Ruediger et al., 1999; Tewes and Blanton, 1998; Clevenger and Waltho, 2000). Movement of predator species through passages has been documented in studies of both specific wildlife passages (Hunt et al., 1987; Fehlberg, 1994; Foster and Humphrey, 1995; AMBS, 1997; Hewitt et al., 1998; Clevenger and Waltho, 2000; Gloyne and Clevenger, 2001) and non-wildlife passages (e.g. drainage culverts; Camby and Maizeret, 1985; Yanes et al., 1995; Rodríguez et al., 1996, 1997; Clevenger et al., 2001). It has been shown that individuals can learn to frequent the same passages. For example, Florida panthers will repeatedly pass through passages within their home range (Foster and Humphrey, 1995; Land and Lotz, 1996). Spotted genets (*Genetta genetta*) have been observed showing preferences for specific passages and avoiding others (Yanes et al., 1995). Wolves, cougars (*P. concolor*) and grizzly bears (*Ursus arctos*) are known to frequent a variety of passage types (Clevenger and Waltho, 2000). Cougars are also known to select home ranges based on the presence of their prey [mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*)] and have been found to frequent the same passages as these species (Gloyne and Clevenger, 2001). This indicates that predators will use passages for movement and incorporate them into their territories. There is also evidence that they will use passages for shade and shelter, for example, bobcats (*L. rufus*) use culverts as day-beds in southern Texas (Hewitt et al., 1998).

Wildlife passages have also been designed to allow the dispersal of, and maintain connectivity between, populations of non-predator species such as large mammals [e.g. mule deer, Reed et al., 1975; mountain goats (*Oreamnos americanus*), Singer and Doherty, 1985], small and medium-sized mammals [e.g. mountain pygmy-possum (*Burramys parvus*), Mansergh and Scotts, 1989; koala (*Phascolarctos cinereus*), Moon, 1998] and amphibians (Langton, 1989). Potential prey species are known to move through wildlife passages (Reed et al., 1975; Olbrich, 1984; Ballon, 1985; Singer and Doherty, 1985; Hunt et al., 1987; Mansergh and Scotts, 1989; Foster and Humphrey, 1995; AMBS, 1997; Clevenger and Waltho, 2000) and non-wildlife passages such as culverts (Hunt et al., 1987; Yanes et al., 1995; Rodríguez et al., 1996; AMBS, 1997; Boarman et al., 1998; Clevenger et al., 2001). Movements by prey species through passages can be associated with seasonal migration and dispersal (Reed et al., 1975; Mansergh and Scotts, 1989; Jackson and Tying, 1989) or the movement of resident individuals that incorporate the

passages as part of their territories for daily transit (Singer and Doherty, 1985; Hunt et al., 1987; Boarman et al., 1998).

3.3. Direct and indirect evidence of hunting in and near passages

Predators have been reported hunting in or near wildlife passages. Chervick (1991) reported a single coyote hunting field mice beneath a beltline structure near a conveyor underpass in Colorado. Foster and Humphrey (1995) photographed a bobcat in a wildlife underpass in Florida with a hispid cotton rat (*Sigmodon hispidus*) in its mouth and suggested that the bobcat may have been foraging in the underpass. They also commented that barred owls (*Strix varia*) may have been using underpasses for feeding as the authors photographed several owls apparently swooping down on prey. There is also one record of a cougar-killed elk (*Cervus elaphus*) at an underpass in Banff National Park (A. Clevenger, personal observation). However, evidence that foraging occurs in or near a passage does not confirm that the passage environment increases predation risk nor that the passage acts as a prey-trap.

As far as we are aware, the only confirmed report of tunnels increasing predation risk is in Australia where a corridor and two tunnels (cross section 0.9×1.2 m) were constructed beneath a road to reconnect fragmented habitat and restore annual movements associated with the breeding and dispersal of the mountain pygmy possum (Mansergh and Scotts, 1989). The tunnels were filled with rocks (0.3–0.7 m height) to mimic adjacent habitat and provide protection for the possum. An area within one of the tunnels was cleared to photograph use of the tunnel. The tunnel was used by the possums (Mansergh and Scotts, 1989), however, one fox was photographed within the tunnel, having traversed 7 metres of rock-filled tunnel to the cleared area (I. Mansergh, personal communication). Following this incident, predator proof grills were fitted on both ends of the tunnel complex to reduce predation risk (Mansergh and Broome, 1995).

If passages are being exploited as prey-traps, then there should be an increase in predator density or activity in proximity to passages compared with control areas away from passage sites. Similarly, we would also expect an increase in predation rates at passage sites relative to control sites. We could not find any study that has specifically examined predator activity, predator densities, or predation rates at passage sites relative to control sites away from passages. Also, no study has examined predator-induced prey mortality at passage sites compared with control areas away from passages to ascertain whether predators are affecting prey population viability. Moreover, we were unable to find a single study examining predator–prey interactions

before and after passage construction. To our knowledge, there are no records of prey species' population decline that have been attributed to passage use either by prey or predator species. In light of the limited evidence available, predation, if and when it occurs, appears to be incidental and opportunistic. There is no evidence to suggest recurring patterns of predation in or near passage sites nor any evidence that predation at passages has adversely affected the population viability of any prey species. However, these conclusions need to be treated cautiously as there is an absence of scientific studies examining whether predator density and behaviour are influenced by passage presence and whether wildlife passages do or do not act as prey-traps. This is therefore an area where further research is required.

Most studies report the successful thoroughfare of target and non-target species and made no reference to the presence of animal remains, blood or carrion which if present might suggest that passages were used by predators to trap prey (Hunt et al., 1987; Niewenhuizen and van Apeldoorn, 1995; Yanes et al., 1995; Rodríguez et al., 1996, 1997; Clevenger and Waltho, 1999, 2000; Clevenger et al., 2001). The lack of reference to animal carcasses (and similar evidence of attack) in passage studies may suggest that animals are not preyed upon in the passages themselves. However, it is not clear whether observation of such events was a consideration during these studies.

AMBS (1997) and Finegan (1997) specifically considered whether predators were using wildlife passages as prey-traps when monitoring underpasses and culverts along the F3 freeway in New South Wales, Australia. Both studies recorded a low incidence of feral animal movement through the passages. AMBS (1997) observed that there were no carcasses or indications of predation detected in the passages, despite the movement of feral predators (cat, dog, fox) and one native predator (tiger quoll, *Dasyurus maculatus*) through the passages. AMBS (1997) and Finegan (1997) considered that feral predators did not appear to be using the underpasses as prey-traps but noted that the results were not conclusive.

4. Predator–prey avoidance

4.1. Do prey species avoid passages frequented by predators?

Predators can have important effects on the community structure of prey species (Lima and Dill, 1990; Doncaster, 1994; Stapp, 1997). For example, in the rural areas of southern England, hedgehogs (*Erinaceus europaeus*) tend to be rare or absent where badgers (*Meles meles*) persist (Doncaster, 1992, 1994, 1999). White-tailed deer are known to survive population declines by

keeping to the periphery of wolf territories (Hoskinson and Mech, 1976; Mech, 1977). It is plausible then that the use of passages by predator and prey species reflects larger scale predator–prey interactions influencing the population and abundance of these species at passage sites.

From observational studies, it is known that prey species will use the same passages as their predators (Fehlberg, 1994; Foster and Humphrey, 1995; Nieuwenhuizen and van Apeldoorn, 1995; Land and Lotz, 1996; Roof and Wooding, 1996; AMBS, 1997). However, when experimental studies are considered, it appears that the coincidental use of passages by predator and prey species may be masking true patterns in the structure of the faunal communities and the response of predator and prey species to various habitat and passage structural attributes.

Clevenger and Waltho (2000) found differences in passage use between predator and prey species in Banff National Park, Canada. Large carnivores [wolves, cougars, black bears (*U. americanus*) and grizzly bears] had a greater tendency to use underpasses at drainages for cross-highway travel whereas prey species (ungulates) avoided them. As drainage systems are known travel routes for wildlife, particularly in narrow glacial valleys such as in their study area, the authors suggested that the inverse relationship between carnivores and ungulates with respect to drainage may be due to predator–prey avoidance rather than landscape attributes. However, recent examination of cougar use of wildlife passages revealed a positive correlation with use by mule deer and white-tailed deer (Gloyne and Clevenger, 2001).

Research in Banff National Park also found similar differences in passage preference between small carnivores [American marten, (*Martes americana*), weasel (*Mustela* spp.)] and their prey species [red squirrel (*Tamiasciurus hudsonicus*), snowshoe hare (*Lepus americanus*), voles (*Arvicolidae*)] to the use of dry drainage culverts along roads of varying traffic volumes (Clevenger and Waltho, 1999; Clevenger et al., 2001).

Similarly, in their study of non-wildlife passages across a high-speed railway in Spain, Rodríguez et al. (1996) found differences in passage preferences between carnivores and small mammals. In this case, the presence of cover at passage entrances favoured use by carnivores while small mammals preferred narrow passages. The authors argued that the latter may indicate lower predation risk for vulnerable species. Examining the individual responses of fox and European wildcat (*Felis sylvestris*) in more detail, Rodríguez et al. (1997) found a significant preference by foxes and wildcats for passages in scrubland than passages in border and farmland vegetation. Interestingly, Yanes et al. (1995), who also studied non-wildlife passages in Spain, observed that all spotted genet crossings and approximately half the wildcat crossings occurred in one pas-

sage (located in an area of pasture) when at least eight culverts coincided with the distribution of both species.

Observational studies in Australia have also revealed different passage usage between predator and prey species. Hunt et al. (1987), who examined mammal passage through culverts and fauna tunnels beneath a railway line in New South Wales, observed that feral predators (dog, fox, cat) predominated at tunnel sites while all but the cat were absent from culvert sites. Conversely, small native mammals were found to be using the culverts and were absent from the tunnels. It was suggested by the authors that the vegetation cover at passage entrances and passage size could have influenced predation risk and that this may have accounted for the differences in predator and prey use of the passages. AMBS (1997) also found differences in introduced predator (cat, dog, fox) usage between three passage sites although native prey species such as the swamp rat (*Rattus lutreolus*) and bush rat (*Rattus fuscipes*) were recorded from all three passage sites. However, reasons for the difference in predator usage between passage sites were not explored.

In light of the evidence currently available it would appear that predator species may use different passages than their prey. The relationship between predator and prey use of passages needs to be investigated further giving particular consideration to separating the influence of habitat and passage structural attributes on species' use and examining use in relation to larger scale predator and prey interactions.

4.2. Do prey species use passages at different times than predators?

Few experimental or even quantitative observational studies have examined whether prey species alter their diel patterns of foraging activity in response to a predator (Lima and Dill, 1990). However, Caldwell (1986) has suggested that during periods of intense hawk predation, herons (*Ardeidae*) switch their foraging to safer periods (during rainfall or at dusk). Brown rats (*Rattus norvegicus*) have also been found to time their activity to avoid predation from red foxes (Fenn and Macdonald, 1995). As far as we are aware, no studies have yet examined whether the timing of use of passages by predator and prey species corresponds with their normal periods of activity and whether predator–prey avoidance behaviour is being exhibited.

We have been able to find only two observational studies that have considered passage use in relation to predator and prey species' daily activity: one in Florida (Foster and Humphrey, 1995), the other in New South Wales (AMBS, 1997; Finegan, 1997). In their study of wildlife passages in Florida, Foster and Humphrey (1995) found that Florida panthers used wildlife passages exclusively at night, while raccoons (*Procyon lotor*) and bobcats usually crossed from dusk to dawn,

and white-tailed deer most often crossed during the day (particularly morning). Conversely, while studying wildlife passages beneath a freeway in New South Wales, AMBS (1997) and Finegan (1997) found fox and most native mammal activity to be nocturnal, while cat and dog activity occurred both during day and night. Although there is little evidence available, we postulate that timing of passage use may reflect predator–prey avoidance behaviour where predator and prey species have co-evolved. However, this may not hold for situations where introduced predators occur with native prey species. We propose that the timing of passage use as a predator–prey avoidance strategy is therefore less likely to occur in Australia where introduced predators (cat, dog, fox) now predominate.

4.3. Mechanisms for predator avoidance at passage structures

Successful survival of a prey species depends on the ability of prey individuals to detect and avoid the predator, or successfully escape the predator after an encounter (Lima and Dill, 1990). Both morphological and behavioural adaptations influence the successful foraging by the predator and the successful survival of the prey species (Sih, 1985; Endler, 1991; Corley et al., 1995).

For prey species, some morphological attributes can influence the chance of being attacked and may influence capture frequency (Endler, 1991; Corley et al., 1995). For example, locomotion of desert rodents plays a central role in the ability of different species to escape from predator approaches (Djawdan and Garland, 1988; Corley et al., 1995). Prey species can also exhibit anti-predator behavioural adaptations that can reduce their potential vulnerability and increase their chance of survival (Dickman, 1992; Jedrzejewski et al., 1993; Corley et al., 1995; Fenn and Macdonald, 1995).

Prey behavioural adaptations can be considered in terms of two categories: predator avoidance behaviour and prey escape behaviour (Sih, 1985). The most common examples of avoidance behaviours include the use of protected habitats and active use of refuges (Wywiłowski, 1987; Brown, 1988; Lima and Dill, 1990). Prey species are also known to disperse or aggregate to avoid attack (Bertram, 1978; Caldwell, 1986). Differences in diurnal and nocturnal activity patterns have been reported as influencing the chances of prey species encountering a predator (Brown, 1993; Fenn and Macdonald, 1995). Many prey species are also known to react negatively towards the scent of a known predator and thus may avoid areas predators frequent (Dickman and Doncaster, 1984; Jedrzejewski et al., 1993; Ward et al., 1997; Kats and Dill, 1998).

Escape behaviours can also be utilized by prey species to avoid capture. For example, aggressive defence behaviour is known to reduce cat predation of larger

mammal species such as bandicoots (*Isodon* spp.) and Tasmanian devils (Dickman, 1996). Crypsis is also particularly relied upon to avoid being eaten (Edmunds, 1974; Endler, 1991).

If we consider these morphological and behavioural attributes against the environment created by wildlife passages, we find that many of these adaptations can be limited by the nature of the wildlife passage environment. Wildlife passages are generally exposed, restricted, and often narrow environments. They potentially increase prey vulnerability by reducing the effectiveness of mechanisms available to prey species to avoid detection or escape. Protected habitats and refuge sites are mostly unavailable within passage confines while cryptic colouration and shading are likely to be of limited effectiveness in such exposed areas. Escape mechanisms such as locomotion may also be less effective given only two paths of exit. Habitat and cover adjacent to passage entrances may favour prey species through the presence of protected habitats but may also make such areas prone to predators that employ ambush to catch prey (e.g. felids). For wildlife passages then, successful predator–prey avoidance mechanisms would appear to be particularly dependant upon avoidance responses, i.e. early detection of predators before the prey species enters the passage environment.

While prey may respond to cues from predators in any sensory modality, early detection of predators relies on prey response to visual, acoustic and olfactory cues. Visual predator recognition can sometimes depend on simple cues such as predator morphology and therefore elicit a response in a potential prey species irrespective of whether the predator and prey species have co-evolved (Curio, 1993; Coss and Goldthwaite, 1995; McLean et al., 1996; Blumstein et al., 2000). However, acoustic and olfactory recognition appears to depend on relatively specific cues. Thus, prey species may be less able to respond to the sounds and scent of evolutionary and ontogenetically novel predators (Dickman, 1993; Banks, 1998; Berger, 1998; Blumstein et al., 2000). Such predator-naïve species are likely to be more prone to predation due to the reduced abilities of the prey to recognise potential predators.

Numerous studies have shown that where predators and prey species have co-evolved, predator scent can act as a deterrent for prey species (Gorman, 1984; Calder and Gorman, 1991; Jedrzejewski et al., 1993; Kats and Dill, 1998). For example, black-tailed deer (*Odocoileus hemionus columbianus*) are known to reduce feeding effort when exposed to odours of coyotes and other predator species (Muller-Schwarze, 1972; Sullivan et al., 1985). In Australia, the yellow-footed antechinus (*Antechinus flavipes*) and ash-grey mouse (*Pseudomys albocinereus*) avoid the faeces of western quolls (*Dasyurus geoffroyi*; Dickman, 1993). In Europe, hedgehogs react negatively to badger odour (Ward et

al., 1996, 1997) and this has led Doncaster (1999) to speculate that hedgehogs are likely to avoid using tunnels that are frequented by badgers. Based on this evidence, we postulate that predator scent could act as a deterrent for prey species using passages frequented by predators in circumstances where the predator and prey species have co-evolved.

However, predator–prey avoidance behaviour from olfactory cues may not be prevalent if the predator and prey species have not co-evolved. In Australia, for example, the introduced house mouse (*Mus domesticus*) shows strong avoidance of odours to introduced predators (cat and fox) compared with the western quoll despite the mouse having co-existed with the quoll for > 150 years (Dickman, 1992). The fox and cat are also known to be major predators of small native mammals and macropods in Australia (Triggs et al., 1984; Lunney et al., 1990; Dickman, 1996; Banks et al., 2000). However, small mammals such as native bush rats and brown antechinus (*A. stuartii*) show no response to fox odour despite the fox co-existing with these species for > 140 years (Banks, 1998). Dickman (1993) also reports no response of yellow-footed antechinus and ash-grey mouse to the odour of feral cats. The absence of co-evolution therefore may be an important feature in limiting the responses of native prey to an introduced predator (Banks, 1998).

For wildlife passages this means that in island countries like Australia, where the main predators have not co-evolved with the native wildlife, predator–prey avoidance mechanisms are less likely to be exhibited by native prey species. We hypothesize that the potential for passages to act as prey-traps may be greater in countries like Australia. We also consider that for Australia, any differences in the response of predator and prey species to passages may be more a direct effect of population abundance of the species and its preferences to passage structure and habitat types, rather than predator–prey avoidance behaviour.

5. Influence of human activity

There is some evidence that human activity affects the use of passages by predator and prey species. Native carnivore species can be hunted or controlled in areas close to human habitation, especially if such carnivores pose a threat to humans (Mech, 1996; Berger, 1998). Native carnivores are also known to avoid areas of human activity (Elgmork, 1978; van Dyke et al., 1986).

Humans can influence animal use of passages by directly using the same passages for thoroughfare, or indirectly, through the influence of human activity (hiking, horse-riding, residential occupation) in proximity to passage sites. How human presence influences predator and prey use of passages has been evaluated in a number

of recent studies (Rodríguez et al., 1996, 1997; Clevenger and Waltho, 2000; Gloyne and Clevenger, 2001).

In their study of non-wildlife passages (culverts) in Spain, Rodríguez et al. (1996) found that that human use of the passages and the proximity of the passages to the nearest house did not influence the use of the passages by carnivores or small mammals. However, further examination of the responses of fox and wildcat revealed that both species preferably used passages in habitats with cover and a low degree of human disturbance (Rodríguez et al., 1997)

In their study of wildlife passages in Banff, Clevenger and Waltho (2000) found that the most significant attributes influencing large carnivore use of wildlife underpasses were related to human activity, while in general landscape and structural variables were less important. In contrast, ungulates were more influenced by structural and landscape factors than human activity. In the presence of human activity, therefore, native predator species were less likely to use underpasses than their potential prey species. However, Gloyne and Clevenger (2001) found no correlation between cougar and human use of passages in Banff National Park. In light of the above, in instances where predator and prey species have co-evolved, it appears that passage use by some predator species may be more susceptible to human activity than other species.

The effect of human activity on predator and prey use of passages in Australia, where introduced predators (cat, dog, fox) predominate, has yet to be examined. However, we hypothesize that for introduced predator species, the influence of human activity could be less marked and may even be positively related with predator presence given that such predators are often closely associated with areas of human habitation and disturbance (Dickman, 1993; May and Norton, 1996).

6. Discussion

The issue of passages acting as prey-traps only becomes a relevant consideration if passages designed for prey are exploited by predators. The evidence suggests that passages are rarely exploited as prey-traps. Most studies make no report of predation in and around passage sites. We could only find a single instance where there was direct evidence of a wildlife passage increasing predation risk, and this single example stemmed from passage design. There is currently no evidence of recurring patterns of predation at passage sites. There is also no evidence of prey populations being adversely affected by passages being exploited as prey-traps. However, these observations need to be treated cautiously as no studies have yet specifically examined predation rates in or near passage sites compared with areas away from passage locations.

Wildlife use of passages appears to be related to individual species' preferences to habitat type and passage structure, and larger scale predator–prey interactions occurring in the habitats bisected by road or rail corridors, rather than being influenced by predation from passages acting as prey-traps. Additionally there is some evidence to suggest that where predator and prey species have co-evolved, predator avoidance may occur with some prey species avoiding predator scent. However, predator–prey avoidance mechanisms may not be as prevalent in countries like Australia where the main predators have been introduced and therefore not co-evolved with native prey species. Future experimental studies need to test whether prey species avoid passages used by their predators. Passage studies would also benefit by examining the correlation between predator and prey use of passages.

Future passage studies would benefit from reporting the presence or absence of carrion, animal remains and other anecdotal evidence that may suggest predation within the vicinity of passages. There is also a need for future research examining predator activity and predation rates at passages sites. Radio-tracking predators that have passage sites overlapping within their home range would be particularly useful in this regard.

We believe there is a need for future research to focus on evidence for predator-caused mortality associated with passage structures. Such research needs to provide a population and ecological context for potential impacts on prey species. In terms of providing a relative ecological context, consideration would need to be given to the impacts road-kill and road barrier effects on prey species and potential beneficial effects presented by wildlife passages. We believe that there are five key areas where research needs to focus:

1. Whether the presence of passages increases predation risk to prey species.
2. Whether any increased predator-induced mortality at passage sites affects the local population viability of the prey species.
3. Whether the increase in prey supply at passage sites increases the survivorship and density of the predators, and hence has broader flow-on impacts on the viability of the local population of the prey.
4. Whether the relative size of any predator-caused impact is greater than the reduction in prey viability caused by traffic-induced mortality in a comparable situation in which no passages were established.
5. Whether the relative size of any predator-caused impact is greater than the reduction in prey viability caused by isolation or barrier effects of the road in a comparable situation in which no passages were established.

We also consider that passage studies need to increase their focus on possible predator–prey interactions. This includes consideration of passage use in response to possible large-scale predator avoidance mechanisms in terms of the prey community structure as well as considering possible temporal variations in prey use of passages. The possible influence of predator–prey interactions on passage use by wildlife appears to have been underestimated in passage studies to date.

6.1. Implications for passage design

Protecting prey species from possible predation in wildlife passage environments presents a challenging task for transport designers as most passages are designed to provide for the movement of all species. There is some evidence that predator and prey species prefer passages in different habitats (Hunt et al., 1987; Yanes et al., 1995; Rodríguez et al., 1996, 1997; Clevenger and Waltho, 2000) or prefer different passage dimensions (Hunt et al., 1987; Yanes et al., 1995; Rodríguez et al., 1996; Clevenger and Waltho, 1999, 2000; Clevenger et al., 2001). In this regard, transport designers could consider providing a range of passages in different habitat types rather than necessarily relying on one large passage at one location to service all groups. The provision of a variety of passage types (to match prey species' sizes) at a particular location may also assist prey species (particularly small mammals) avoid predation. For larger prey species (e.g. elk, deer) passages could be designed to minimise predation risk by providing short, wide, and high passages (i.e. high openness ratios) which give prey a greater opportunity to detect predators.

In countries like Australia, where feral predators predominate, passages can be designed to discourage use by feral predators. In this regard, vegetation cover at passage entrances appears to make passages more attractive to native prey species and less attractive to feral predators (Hunt et al., 1987; Finegan, 1997). Predator-proof grilles can be used at passage entrances to favour small mammals and preclude predators (Mansergh and Broome, 1995), however, this may also preclude use by larger native prey species (e.g. macropods). Predator-control programs such as baiting could also be employed around passage sites to maximise prey viability, although impacts to non-target species would need to be considered (NPWS, 2001).

7. Suggestions for future research

No study to date has tested whether wildlife passages increase predation risk or whether prey species avoid passages frequented by their predators. Here we provide a framework around which two future studies could focus.

Hypothesis 1. The presence of wildlife passages increases predation risk.

If a single passage is to be evaluated, a suitable design would be a before–after, control–impact experiment with replicated control sites (Underwood, 1992). To determine predator–prey responses, sampling could utilize a combination of live trapping (mark–recapture) and telemetry of both predator and prey species, but with particular emphasis on radio-tracking predator species.

Hypothesis 2. Prey species avoid passages containing the scent of their predators.

For this experiment, a before–after, control–impact design could be employed using existing passages with the treatment being the introduction of predator scent. Sampling could again use a combination of mark–recapture and telemetry methods applied to prey species. Behavioural studies would assist in determining prey response to predator odour. Such an experiment would need to clearly isolate predator cues and possible alarm signals produced by prey conspecifics (Kats and Dill, 1998; Blumstein et al., 2000).

These types of studies (Hypothesis 1 and 2) would lead to a better understanding of predator–prey interactions at passage sites and assist in improving the evaluation and effectiveness of wildlife passages for prey species.

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