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THE INFLUENCE OF PREDATOR-PREY RELATIONSHIPS ON WILDLIFE PASSAGE EVALUATION

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Abstract: The influence of predator-prey systems and interactions on wildlife passage use by mammals has received little attention to date. Predator-prey systems vary throughout the world and across regions. Europe and North America are characterised largely by predator-prey systems in which predator and prey have co-evolved. However, large predators are absent from many areas, enabling prey species (e.g., ungulates) to range in predator-free environments. In mainland Australia, the main predator species are evolutionary novel and have not co-evolved with native prey. These fundamental differences in predator-prey systems potentially influence species' behavior and, it is argued, species' response to passage environments. Predator-prey systems also operate at different spatial scales. The spatial distribution of large mammals is influenced by regional scale predator-prey interactions that potentially influence the species encountering passages. Medium-sized and small mammals tend to operate at more refined geographical scales and passage avoidance or acceptance may be more influenced by localised predator-prey interactions and in response to the passage structure. Biotic interactions at passage approaches and within passage confines potentially influence the successful transit of the passage.

This paper examines the documented and potential influence of predator-prey interactions on wildlife passage use by mammals, and passage effects on predator and prey interactions. It considers predator-prey relationships relative to various spatial scales and takes into account biotic interactions that may occur at passage sites. The potential influences of relaxed selection and co-evolution of predator and prey on predator-prey systems and mammalian responses to passage environments are particularly addressed. It is concluded that extrapolation of management recommendations resulting from passage studies under different predator-prey systems need to be treated cautiously. The influence of predator-prey interactions on passage response by mammalian fauna appears to have been underestimated in passage studies to date and warrants further scientific investigation.

Introduction

The creation and operation of road and railway corridors are known to have adverse effects on wildlife populations through direct habitat loss, fragmentation and barrier effects, and through road and rail-kill (Andrews 1990; Bennett 1991, 1999; Forman et al. 2003). To address these impacts to wildlife, and to maintain connectivity across the landscape, wildlife passages (fauna tunnels, bridges, overpasses and modified culverts) are often proposed in association with new road or railway corridors (Ballon 1985; Gossem et al. 2001) or are retrofitted to ameliorate existing areas of high human safety risk or wildlife impact (Singer and Doherty 1985; Mansergh and Scotts 1989; Roof and Wooding 1996).

Many early wildlife passage studies focused on single-species evaluations (Reed et al. 1975; Reed 1981; Schaal et al. 1985; Singer and Doherty 1985; Mansergh and Scotts 1989). While several of these studies demonstrated improvement in road permeability and alleviation of population stresses for wildlife [e.g., mountain goats (*Oreamnus americanus*), Singer and Doherty 1985; mountain pygmy possum (*Burramys parvus*), Mansergh and Scotts 1989], single-species evaluations fail to consider the cascading effects (positive and negative) on non-target species (Clevenger and Waltho 2000). In contrast, many multi-species evaluations have tended to examine the variety of species using passages and their frequency of movement but often without testing hypotheses or without local abundance or density information (Camby and Maizeret 1985; Hunt et al. 1987; Fehlberg 1994; Foster and Humphrey 1995; Nieuwenhuizen and van Apeldoorn 1995; Norman et al. 1998; Veenbaas and Brandjes 1999). In the absence of this information, such examinations provide little or no ecological context for species' use or passage effectiveness.

More recently, emphasis has been placed on multi-species evaluations and testing the performance of various wildlife passage and habitat attributes in influencing passage use by particular species or taxonomic groups (Yanes et al. 1995; Rodríguez et al. 1996; Rosell et al. 1997; Clevenger 1998; Clevenger and Waltho 1999, 2000; Clevenger et al. 2001). These studies have begun to reveal differences in predator and prey species' responses to different passage structural and habitat variables. However, little attention has been afforded to how fauna use of wildlife passages influences, or is influenced by, other ecological processes, such as predator-prey relationships (Little et al. 2002).

The study of wildlife passages is shifting from the consideration of ameliorating site specific road and rail impacts to examining how wildlife passages function in terms of providing regional connectivity in the landscape and sustaining wildlife communities (Bennett 1999; Clevenger and Waltho 2000; Forman et al. 2003). Animal individuals do not operate in isolation but form part of a complex set of ecological interactions that operate at multiple scales (Lord and Norton 1990; Gehring and Swihart 2003). Predator-prey systems may become destabilised through fragmentation and habitat modification (Cole 1987; Karieva 1987; Donovan et

al. 1997; Collinge 1998). For example, in the absence of predators, prey populations such as ungulates may be unable to sustain an equilibrium with their food resources (Sæther 1997; Ripple and Larson 2000; Ripple et al. 2001). The absence of large predators can also lead to mesopredator release and have adverse flow-on effects to smaller species of prey (Terborgh and Winter 1980; Soulé et al. 1988). Hence, in order to sustain ecological integrity and processes, it is necessary for wildlife passages to sustain predator-prey relationships in the landscape. However, predator-prey interactions may also influence passage acceptance or avoidance by mammals, which in turn can have flow-on effects (positive and negative) to metapopulations.

This paper provides a review of how passage use by mammals is influenced by predator-prey systems and relationships. It also considers how passage structures in turn may affect predator and prey interactions, and thus have flow-on effects back to the predator-prey systems operating in the landscape. Consideration is given to both regional and local effects. International differences in predator-prey systems and species' composition are considered with examples being drawn from Europe, North America and Australia. Areas for future research are identified and implications for wildlife passage evaluation and management provided.

Literature Review

I conducted a literature survey in April 2003 using BIOSIS (Biological Abstracts). A search was conducted 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 conferences on wildlife ecology and transportation (Evink et al. 1996, 1998, 1999) and the *2001 Proceedings of the International Conference on Ecology and Transportation* (CTE 2002) (Papers printed solely as abstracts in CTE 2002 have not been considered due to limited information on methods and results.) The available literature was then examined for evidence of predator-prey influences on wildlife passage use by mammals and any information on the effect of passages on predator-prey interactions. As a number of wildlife passage evaluations are provided in internal departmental reports and post-graduate theses not readily available to the public, this paper largely considers the published material that is available. The focus of this paper is also limited to spatial influences of predator-prey relationships on wildlife passage evaluation.

International Differences in Predator-Prey Composition

To date, little attention has been afforded the international differences in predator-prey systems and wildlife community characteristics and, therefore, the different ecological role played by wildlife passages in different countries and continents. Europe, North America, and Australia have major differences in the composition and distribution of their largest predator and prey species, and this potentially influences their predator-prey systems and mammalian interactions.

In Europe, mammalian predator and prey species have generally co-evolved, although larger predators are rare or absent from many areas. The largest carnivores are gray wolves (*Canis lupus*) and brown bears (*Ursus arctos*). These species occur in discrete populations. The brown bear mainly occurs in Northern Scandinavia adjoining Russia, although remnant populations exist in the Iberian Peninsula, Central Italy, and South-Eastern Europe (Macdonald and Barrett 1993). Wolves occur in Eastern Europe but only have relict populations in Italy, France, Spain, Portugal and Sardinia (Macdonald and Barrett 1993). Lynx (*Lynx lynx*) are scattered throughout Scandinavia but occur only in isolated pockets in other parts of Europe, while Iberian lynx (*L. pardina*) only occurs in isolated pockets in the Iberian Peninsula (Macdonald and Barrett 1993; Palomares et al. 2000). In contrast, ungulates such as wild boar (*Sus scrofa*), red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) are widespread throughout Europe (Macdonald and Barrett 1993). The absence of large predators from many areas has resulted in many ungulate populations existing in predator-free environments (Sæther 1997). Consequently, European passage studies sometimes record use by ungulates coinciding with use by medium and small predator species (Ballon 1985; Nieuwenhuizen and van Apeldoorn 1995; Rosell et al. 1997).

Like Europe, mammalian predator and prey species in continental North America have generally co-evolved, although larger predators are rare or absent from many areas. In the contiguous United States and Mexico, for example, grizzly bears (*Ursus arctos*) and wolves are currently absent from 99 percent of their original range and this has freed many large herbivores (e.g., ungulates) from natural predation (Berger 1998). Rare carnivores in North America for which conservation efforts are in place include grizzly bear, black bear (*U. americanus*), gray wolf, wolverine (*Gulo gulo*), Canadian lynx (*Lynx canadensis*), fisher (*Martes pennanti*) cougar (*Puma concolor*), Florida panther (*P. c. coryi*), and ocelot (*Leopardus pardalis*) (Beier 1995; Foster and Humphrey 1995; Ruediger 1998; Tewes and Hughes 2001).

In mainland Australia, the main predators are evolutionary novel and include the dingo (*Canis lupus dingo*), dog (*C. l. familiaris*), red fox (*Vulpes vulpes*) and cat (*Felis catus*). The dingo is believed introduced from Asia about 3,500 – 4,000 years ago, dogs and cats shortly after European settlement (about 210 years ago), while the red fox was introduced about 140 years ago (Short et al. 2002). Medium-sized and small native carnivores [Tasmanian devil (*Sarcophilus laniarius*), <8kg; tiger quoll (*Dasyurus maculata*), <7kg; eastern quoll (*D. viverrinus*), 1.3kg] exist in Tasmania; however, all but the tiger quoll are believed extinct on the mainland. Dingos, dogs, foxes and cats are known to predate native macropods, such as kangaroos and wallabies and small native mammals (Triggs et al. 1984; Banks 2001; Short et al. 2003). Both the fox and cat have been implicated in the extinction of many ground-dwelling native mammals over the past 130 years (Short et al. 2002).

The implications of the above differences in predator-prey systems and their potential implication for wildlife passage studies can be summarised as follows:

1. In North America and Europe, the use of passages by predators (particularly large carnivores) is seen as a positive environmental outcome; whereas, in Australia, passage effectiveness is potentially compromised by high levels of introduced predator use.
2. Many areas of Europe and North America, have free-ranging large herbivores (e.g. ungulates) occurring in the absence of large predators. Relaxation of anti-predatory behavior may influence prey response to roads and passages.
3. Europe and North America are characterised by prey which, for the most part, have co-evolved with their predators. In Australia, the main predator species (cat, dog, fox) have not co-evolved. The absence of co-evolution appears to influence prey perception of predation risk (Banks 1998; Short et al. 2002) and may influence prey response to passages (Little et al. 2002).

Predator-Prey Relationships and Passage Effects

Do Wildlife Passages Service Species Equally?

In order to examine whether wildlife passage use is influenced by predator-prey interactions, it is first necessary to examine those studies that have examined and tested the response of predator and prey species and taxonomic groups to passage structures. A number of recent multi-species evaluation studies have examined multiple structures and tested whether wildlife passages service species equally by examining the frequency of use by species and taxonomic groups taking into account local abundance information (Yanes et al. 1995; Rodríguez et al. 1996; Clevenger and Waltho 1999, 2000; Clevenger et al. 2001). Two studies (Rosell et al. 1997; Clevenger 1998) have also examined equal use based on presence/absence of taxonomic groups, thereby omitting any influence from population densities or seasonal changes in behavior. These studies have found that passages do not service all species equally and that different passage attributes affect different species' groups in different ways.

Regional Predator-Prey Interactions and Connectivity

The interaction between an animal and a passage will depend on the interaction between regional and local scale influences operating to bring the animal into contact with the road (Opdam 1997; Barnum 2001), the ecological effects of the road operating as a repellent (or in some cases as an attractant) (Getz et al. 1978; Adams and Geis 1983; Forman and Deblinger 2000), and the response of the animal to the passage structure (Clevenger and Waltho 2000; Barnum 2001; Forman et al. 2003).

Large predators are known to be particularly susceptible to road effects and have received particular attention in wildlife passage studies because of their dependence on regional landscapes (Land and Lotz 1996; Ruediger 1998; Clevenger and Waltho 2000; Gloyne and Clevenger 2001). In terms of predator-prey relationships at a regional level, predators may align their territories with prey availability (Forbes and Therberge 1995; Gloyne and Clevenger 2001), seek out new territories when dispersing (Beier 1995; Sweanor et al. 2000), or extend foraging beyond their territories for prey (Forbes and Therberge 1995; Kunkel et al. 1999). In response to predators, prey can adopt a range of anti-predatory behaviors to minimise predation risk. This includes predator avoidance strategies that spatially separate prey from their predators. For example, in England, hedgehogs (*Erinaceus europaeus*) are known to use residential and urban environments to avoid badgers (*Meles meles*) (Doncaster 1994) while in North America, white-tailed deer (*Odocoileus virginianus*) are known to survive population declines by keeping to the periphery of wolf territories (Hoskinson and Mech 1976; Mech 1977). Therefore, passage acceptance or avoidance by mammals may be influenced by regional predator-prey interactions, such as the spatial segregation of predator and prey as well as local interactions at passage approaches (figure 1).

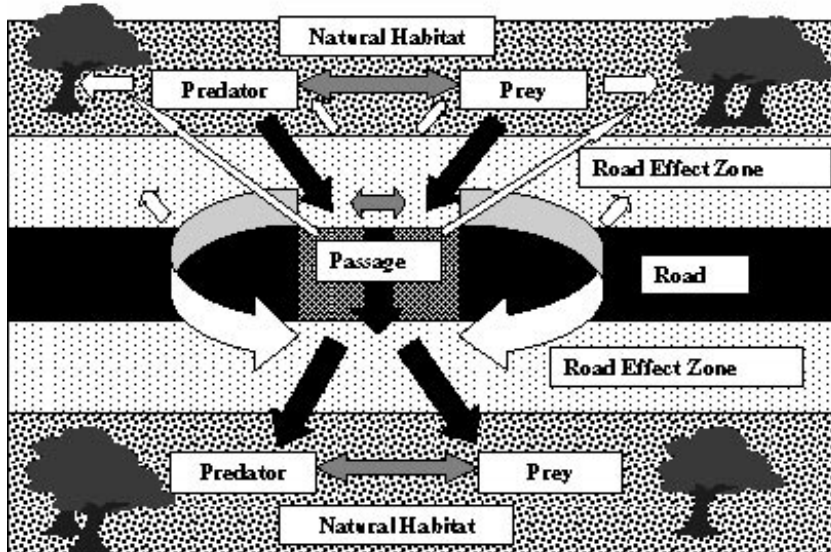


Fig. 1. Predator-prey interactions with respect to passages. Grey arrows indicate predator-prey interactions; white arrows indicate avoidance; black arrows indicate interactions bringing animals to passages and flow-on effects.

The potential influence of regional predator-prey interactions on predator and prey responses to wildlife passages has been considered in four passage studies (Foster and Humphrey 1995; Clevenger 1998; Clevenger and Waltho 2000; Gloyne and Clevenger 2001). The studies by Clevenger and others examined passages along the Trans-Canada Highway in Banff National Park, Alberta, Canada, while the study by Foster and Humphrey was conducted in Florida, U.S.A.

In his study of winter passage use by large mammals in 11 wildlife underpasses, Clevenger (1998) found that both large carnivores [wolves, coyotes (*Canis latrans*), cougars, black bears and grizzly bears] and ungulates [deer (*Odocoileus sp.*) and elk (*Cervus elaphus*)] were using underpass structures but showed different passage preferences. Ungulates used passages in areas of human activity whereas large carnivores were under-utilising or avoiding them. The difference in passage use was attributed to large predators avoiding areas of human occupation and the fact that elk (which accounted for 75% of the ungulate data) were seeking out wolf-free zones as refugia from predation. Clevenger and Waltho (2000) also found differences in predator-prey responses following 35 months of monitoring 11 underpasses. Carnivores had a tendency to use underpasses close to drainage systems whereas ungulates tended to avoid them. The authors argued that the inverse relationship between carnivores and ungulates with respect to drainage may have reflected predator-prey interactions rather than resulting from any direct effect of landscape attributes on underpass use. In their study of four underpasses in Florida, Foster and Humphrey (1995) observed the lowest recordings of deer in an underpass frequented by humans, bobcats and Florida panther, whereas panthers were lowest in the passage most used by deer. The authors commented that inter-specific interactions may have led to deer avoiding passages used by humans, bobcats and panthers.

In contrast, in their study of 22 wildlife crossing structures (open span bridge underpasses, culverts, and overpasses) by cougar and its prey species [mule deer (*Odocoileus hemionus*) and white-tailed deer], Gloyne and Clevenger (2001) found a significant positive correlation between passages made by cougar through wildlife crossing structures and those made by the ungulates. This was attributed to cougar selecting home ranges based on deer presence, an important factor influencing cougar diet. Thus, the authors were able to demonstrate road permeability through the provision and acceptance of passages by cougar and deer, and connectivity in relation to cougar habitat based on continued access to prey. The study also found cougars preferring open-span bridge underpasses and cougar use being greatest in winter, reflecting seasonal variations in cougar and ungulate distribution.

The above studies demonstrate the need for regional connectivity between predator and prey species if predators are to have access to prey resources and if prey populations are to be able to sustain themselves through predator avoidance. However, regional connectivity for wildlife populations and predator-prey processes can also be influenced by localised predator and prey responses to passage structures. In Colorado, U.S.A., Barnum (2001) and Henke et al. (2001) examined passage use in comparison to road crossings at grade.

Both studies found passage use by predators (particularly felids and mustelids); whereas, ungulates avoided beneath-grade structures. However, large carnivore species have also been reported avoiding passage structures (e.g., wolves, Pacquet and Callaghan 1996, Kohn et al. 1999; coyote, Henke et al. 2001, Tigas et al. 2002; black bear, Roof and Wooding 1996; Singleton and Lehmkuhl 1999). Ungulates have also been reported acting hesitant towards, or avoiding, below-grade passage structures (Reed et al. 1975; Olbrich 1984; Schaal et al. 1985; Rodríguez et al. 1996; Rosell et al. 1997; Austin and Garland 2001; Henke et al. 2001; Barnum 2001) but appear to accept overpasses (Nieuwenhuizen and van Apeldoorn 1995; Berris 1997).

If a road acts as a barrier for movement of a species and that species also avoids passage environments, then this can lead to crowding effects, inter- and intra-specific competition for resources, genetic homogeneity, and greater susceptibility of populations to predation, stochastic processes and certain catastrophic events (Simberloff and Cox 1987; Collinge 1998; Lidicker 1999). Similarly, if passages provide connectivity for some species and not others, then this can disrupt predator-prey processes and have flow-on effects to predator and prey populations. Scientific testing of the reasons for avoidance and its ecological consequences has received little attention to date and requires further scientific investigation.

Local Predator-Prey Interactions and Connectivity

Different sized mammals perceive their environment at different spatial scales (Gehring and Swihart 2003). Species-specific responses to fragmentation are related to inter-specific differences in the perception of landscape structure and the degree of fragmentation (Lord and Norton 1990, Gehring and Swihart 2003). It stands to reason then that the perception of fragmentation and the opportunity it may provide for predator foraging, and its propensity to present a predation risk for a prey species, must therefore also be related to scale. Thus, different species are likely to respond differently to various habitat attributes due, at least in part, to their influence on predation risk and opportunity for foraging. The proximity and structure of habitat adjacent to passages may therefore influence predator or prey response at passage approaches.

Passage design may also influence predation risk. Wide, open passages have the advantage of enabling large prey species to detect predators early (Little et al. 2002); however, open areas may present a predation risk to small mammals (Hunt et al. 1987; Rodríguez et al. 1996). Culverts and passages with smaller cross-sections have the advantage of providing protection from aerial predators (Rodríguez et al. 1996). However, long, narrow passages may present a higher predation risk from terrestrial predators due to limited escape opportunity should an encounter take place (Little et al. 2002).

Localised habitat, passage and road structural variables may be particularly important for small and medium-sized mammals with smaller territories (Yanes et al. 1995; Rodríguez et al. 1996; Clevenger and Waltho 1999; Clevenger et al. 2001; Cain et al. 2003). While small mammals have been reported using larger passage structures (e.g. Ballon, 1985; Nieuwenhuizen and van Apeldoorn 1995; Norman et al. 1998), the response of small and medium-sized mammals has largely been tested in studies of culverts (Yanes et al. 1995; Rodríguez et al. 1996; Clevenger and Waltho 1999; Clevenger et al. 2001).

In Spain, both Yanes et al. (1995) and Rodríguez et al. (1996) each examined 17 passages (mainly culverts) and found that small mammals constituted the majority of crossings (77% and 55.6%, respectively) whereas medium-sized wild carnivores showed relatively low rates of crossing (4% and 25.2%, respectively). Yanes et al. (1995) found that small mammals avoided long culverts and preferred culverts that had greater openness and surrounded by more complex vegetation structure. While carnivore use was low, the authors commented that one tunnel serviced all genet (*Genetta genetta*) and almost half the wildcat (*Felis sylvestrus*) crossings. In contrast, Rodríguez et al. (1996) found that small mammals preferred border rather than scrubland and farmland habitat and showed significant preferences for culverts with small entrances (less than or equal to 2m width); whereas, carnivores preferred culvert structures and significantly preferred scrubland with crossing rates being six times higher than border habitat and 20 times higher than in farmland. Rosell et al. (1997) also found that carnivores selected structures within a short distance of forest or shrub vegetation although individual carnivore species tended to respond to different habitat and structural attributes. Small mammals favoured passages with a natural substratum and which had their entrance at the same level as surroundings. The studies by Yanes et al. (1995) and Rosell et al. (1997) made little comment regarding predator-prey interactions; however, Rodríguez et al. (1996) considered that small mammals may have preferred narrower passages due to predation risk.

Studies in Banff have also revealed differences in predator and prey use of culverts (Clevenger and Waltho 1999; Clevenger et al. 2001). In three months of winter monitoring of 24 culverts, Clevenger and Waltho (1999) found that carnivores [weasels (*Mustela sp.*) and American martens (*Martes americana*)] used more passages and used them more frequently than small mammals [snowshoe hares (*Lepus americanus*), red

squirrels (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*), voles (Arvicolinae) and shrews (*Sorex sp.*). Weasels were present in 19 (79%) of the culverts while voles and red squirrels were only present in three and four of the culverts, respectively, although deer mice were recorded in 14 (58%) passages. Conversely, small mammals were more prevalent on transects outside the culverts (red squirrels and hares accounted for 50% of all species detections in adjacent transects while weasels and martens comprised 38%). The authors also observed that voles used the fewest number of culverts yet meadow voles (*Microtus pennsylvanicus*) and red-backed voles (*Clethrionomys gapperi*) were the dominant species in the road corridor. Clevenger et al. (2001) also found differences between predator and prey use of 36 culverts. The authors found that weasels (*Mustela erminea* and *M. frenata*) and deer mice used the culverts most frequently whereas red squirrels and snowshoe hares were the most common in adjacent habitats. In both studies, the authors commented that the inverse relationship between predator and prey was noteworthy.

While the influence of habitat and passage structural attributes on passage response by mammals has yet to be tested in Australia, in their study of fauna tunnels and culverts in New South Wales, Hunt et al. (1987) observed that feral predators predominated at the recently-established tunnels which lacked vegetative cover; whereas, small mammals were absent from these structures. Conversely, small mammals predominated in established culverts which had cover near passage entrances and where predator use was much lower. However, more recent studies (Norman et al. 1998; Taylor and Goldingay *in press*) have found low levels of passage use by feral predators.

It has been suggested that small mammal preference to smaller passages with lower openness may be related to predation risk which may be potentially greater in larger passages than smaller ones (Hunt et al. 1987; Rodríguez et al. 1996; Clevenger and Waltho 1999; Clevenger et al. 2001). However, predominant use by predators may also lead to prey avoidance even of small passages (Clevenger and Waltho 1999; Clevenger et al. 2001). In terms of predator behavior, cover near passage entrances may favour use by native carnivore species (Rodríguez et al. 1996, 1997; Clevenger et al. 2001; Cain et al. 2003). However, in Australia, it has been suggested that feral predators may focus their activities on tunnels which lack vegetative cover (Hunt et al. 1987).

Importantly, the above studies have found that rather than providing regional connectivity, the main species using culverts tend to have small home ranges. Culverts, therefore, appear to service their own unique subpopulations (Yanes et al. 1995; Clevenger and Waltho 1999; Clevenger et al. 2001). For example, Clevenger and Waltho (1999) noted that individual ranges for red squirrel and deer mice were at least an order or two magnitude less than the spatial scale of the 24 culverts (range = 55km). Given the decreased territorial range of these animals, it is possible that these smaller passages may be more important as habitat and be used more regularly by individuals. It is possible then that smaller passages may be more potentially prone to biotic interactions at passage entrances and within passage sites than larger underpasses. Also, while several of the above studies made observations regarding predator and prey responses, none actually correlated predator and prey use to each other, nor tested the reasons for the avoidance or attraction responses encountered. Therefore, the degree to which predator and prey interactions may be influencing passage use can only be inferred and may be masked by responses to the road, passage and habitat attributes.

Scent-Marking

It has been proposed that predator scent may be the means through which prey can detect predators and avoid encounters at passage sites (Doncaster 1999; Clevenger and Waltho 1999; Clevenger et al. 2001; Little et al. 2002). Scent marking of passage entrances by predators has been reported in three recent studies (Clevenger and Waltho 1999; Mathiasen and Madsen 2000; Clevenger et al. 2001); however, only one study (Mathiasen and Madsen 2000) has quantified scent marking by predators. In their study of a single 155m-long fauna underpass in Denmark, Mathiasen and Madsen (2000) recorded frequent use by red foxes, badgers, stone martens (*Martes foina*) and roe deer. The authors recorded territorial marking at the passage entrance by fox (13 times of 122 passages), badgers (4 of 16 passages) and stone martens (6 of 18 passages). Interestingly, the passage marking coincided with observations of prey avoidance. The observations of roe deer were from a single male when eight other deer were observed in the area. Brown hares (*Lepus europaeus*) were observed entering the underpass twice, but on both occasions, they showed reluctant behavior, and exited rapidly (Mathiasen and Madsen 2000).

In their examination of culverts in Banff, Clevenger and Waltho (1999) and Clevenger et al. (2001) observed scent marking by American marten and weasels as a common occurrence (Clevenger and Waltho 1999; Clevenger et al. 2001). These studies also found small carnivores (weasels and martens) predominating within the culverts which coincided with prey (snowshoe hares, red squirrels, voles) avoidance of the passages. Both studies commented that the inverse relationship between predator and prey was noteworthy.

Within-Passage Effects

Passage Occupation

Little information exists regarding the use of passages by species' individuals for purposes other than transit and how this may inhibit movement by other animals. In Texas, USA, bobcats (*Lynx rufus*) have been observed using culverts as day-beds to rest during hot summer days (Hewitt et al. 1998; Tewes and Hughes 2001). Cain et al. (2003) comment that bobcats in Texas used culverts for purposes such as resting, hunting and thermoregulation. In the Netherlands, Douwel (1997) noted the use of purpose-built badger pipes by badgers as setts. Such resident occupation by predators may deter prey species from using the passages. However, such occupation may also deter other carnivores from using passages. For example, Tewes and Hughes (2001) suggested that culvert occupation by antagonists or competitors of ocelots [e.g., bobcats, coyotes, skunks (*Mephitis mephitis*) and rattlesnakes (*Crotalus atrox*)] could function as a barrier to ocelot passage and that scent marking by coyotes or bobcats could deter ocelot use of culverts. In their study of an underpass in Denmark, Mathiasen and Madsen (2000) attributed the presence of other mammals as a possible source of avoidance in the few instances that approaching carnivores (red foxes, badgers, stone martens) failed to enter the passage. The degree to which passage dominance by individuals or species inhibits movement by other animals has been little studied and warrants further investigation.

Wildlife Passages as Prey-Traps

Several papers have suggested the possibility of wildlife passages acting as 'prey-traps' with prey species being effectively funnelled into areas of high concentration (Hunt et al. 1987; Reading 1989; Norman et al. 1998). The issue of whether wildlife passages act as prey-traps was subject to a recent review (Little et al. 2002). The authors found only one confirmed report of passages increasing predation risk, an instance where a purpose-built tunnel, designed to facilitate the movement of the mountain pygmy-possum through road-fragmented habitat, was intruded by a red fox (Little et al. 2002 cit I. Mansergh, personal communication). The authors concluded that evidence of the existence of prey-traps was scant, largely anecdotal and tended to indicate infrequent opportunism rather than recurring patterns of predation. However, they also noted that the conclusions need to be treated cautiously due to the absence of scientific studies examining whether predator density and behavior are influenced by passage presence and whether passages act as prey-traps.

Prey Perception of Predators

The acceptance or avoidance of wildlife passages by prey species may be influenced by predation risk (Doncaster 1999; Clevenger and Waltho 1999; Little et al. 2002). Predation risk in turn is influenced by how a prey species perceives a predator. Prey perception of predators may be influenced by relaxed selection and whether the predator and prey species have co-evolved (Banks 1998; Berger 1998; Blumstein et al. 2000; Short et al. 2002). These influences have direct implications for predator-prey systems and may affect predator-prey interactions at all scales.

Relaxed Selection

Isolation of a prey species from its predator may occur naturally or result from human-induced effects, such as fragmentation (Berger 1998). When a prey species becomes isolated from its predator, it can exhibit a relaxation in its anti-predatory behavior (Berger 1998; Bøving and Post 1997; Blumstein et al. 2000). For example, wolves are known predators of caribou (*Rangifer tarandus*) (Seip 1991; Bøving and Post 1997). However, female caribou in predator-free Greenland display greater predation-vulnerable postures and behaviors (such as lying down flat, foraging in smaller groups and displaying less vigilance during feeding) than caribou in Alaska (Bøving and Post 1997). In Florida, where road mortality constitutes 75-80 percent of Key deer (*Odocoileus virginianus clavium*) deaths, Key deer neither migrate seasonally or form large groups and are more solitary than northern white-tailed deer (Hardin et al. 1976, Calvo and Silvy 1996). It has been suggested that the lack of predators and different competitive and selective pressures may have resulted in these behavioral differences (Calvo and Silvy 1996).

No study appears to have yet examined whether the effect of relaxed selection influences prey response to passage environments. If passages present a predation risk to prey, then it is possible that inhibition towards a passage structure may be reduced under relaxed selection or a prey species may be more willing to accept a passage with lower openness in predator-free environments than would otherwise occur. In this context, caution needs to be exercised if extrapolating passage structure recommendations for prey from studies undertaken under different predation pressures or risk, particularly if extrapolating passage structural designs for prey based on predator-free environments. In situations where predators exist and prey species are found to be avoiding wildlife passages, comparative studies with areas where relaxed selection has occurred may assist in determining whether, and the degree to which, prey avoidance of passages may be due to perceived predation risk or other factors (e.g., road or passage structural characteristics). Such studies may also assist

in determining whether predation risk influences the length of time it takes for prey species to become accustomed to using a passage environment.

Co-Evolution of Predator and Prey

In situations where prey species are present with their predators, the influence of co-evolution between predator and prey may influence passage use by prey species (Little et al. 2002).

In Australia, introduced predators (cat, dog, fox) are known to utilise roads for foraging and movement (Bennett 1991; May and Norton 1996; Meek and Saunders 2000). For example, in their study of red foxes in coastal New South Wales, Meek and Saunders (2000) observed that foxes were recorded on or beside a road on 33 percent of sampling occasions. Foxes, dogs, and cats have also been recorded using wildlife tunnels and culverts for movement (Hunt et al. 1987; Norman et al. 1998; Taylor and Goldingay *in press*), although no data exists regarding their frequency of use relative to their local abundance.

While prey may exhibit antipredatory defences towards evolutionary novel predators (Banks 2001), a number of papers suggest the susceptibility of native prey due to the absence of co-evolution between predator and prey (Banks 1998; Little et al. 2002, Short et al. 2002). There is some evidence that prey may not be able to detect predators from olfactory cues if the predator and prey species have not co-evolved (Dickman 1992, 1993; Banks 1998). In Australia, for example, small mammals, such as native bush rats (*Rattus fuscipes*) and brown antechinus (*Antechinus stuartii*), show no response to fox odor despite these species co-existing with the fox for more than 140 years (Banks 1998). Surplus killing events in Australia by foxes has also been related to ineffective anti-predator defences by prey species when encountering a novel and highly effective predator to which they had no previous exposure (Short et al. 2002).

The absence of co-evolution between predators and prey has a number of potential consequences for prey in relation to wildlife passages, particularly in Australia where introduced predator predominate. At a wider regional scale, increased landscape connectivity through the use of passages may have the negative consequence of increasing connectivity for introduced predators (and increase survivorship by decreasing the opportunity for mortality from vehicular collisions), thereby increasing the exposure of native prey species to predation. At a more localised scale, the absence of co-evolution may result in prey species being less likely to avoid wildlife passages used by predators even if their entrances are scent marked. While this may have the unintended advantage of increasing the propensity of wildlife passages to connect native prey populations in spite of the potential presence and use by predators, it also has the disadvantage that wildlife passages may have a greater propensity to act as prey-traps if prey are unable to recognise predator scent (Little et al. 2002). If the aim is to sustain regional populations of native prey species, clearly the aim should be to reduce introduced predator use of passages as much as possible. Passage systems in Australia may therefore need to focus on strategically placing passages in habitats and areas where feral predators are absent or low in number, or consider supplementary predator control programs.

In the case of North America and Europe where the main predators and prey have co-evolved, prey may more readily exhibit predator avoidance behavior and be able to detect predator scent (Muller-Schwarze 1972; Gorman 1984; Jedrzejewski et al. 1993; Parsons and Bondrup-Nielsen 1996). At a regional scale, such avoidance strategies may be reflected in spatial segregation between predators and their prey (Hoskinson and Mech 1976; Mech 1977; Doncaster 1994; Clevenger 1998). At a local scale, in the vicinity of passages, prey may be more able to avoid passages scent marked by their predators (Clevenger and Waltho 1999, 2000; Doncaster 1999, Clevenger et al. 2001), and the prey-trap phenomenon may be less likely to occur. However, while predator avoidance may safeguard prey from predation, predator use of passages may create a biotic barrier inhibiting the movement of prey and potentially reducing connectivity, particularly if wildlife exclusion fencing is used to prevent crossing at grade (Bergers and Nieuwenhuizen 1999; Doncaster 1999). Further research is required to test whether use of passages and scent marking at passage entrances by predators influences prey avoidance and, if so, whether the duration of any repellence is short lived (Little et al. 2002; Parsons and Bondrup-Nielsen 1996).

Discussion

Fundamental differences exist in the predator-prey systems of Europe, North America and Australia. The potential of wildlife passages in influencing and eliciting predator-prey responses is therefore different between these continents. North America and Europe are characterised generally as co-evolved predator and prey species although large predators are absent from many areas enabling populations of large free-ranging herbivores (e.g., ungulates) to exist under relaxed selection. In contrast, Australia's largest and predominant predators are introduced species which are widespread. In light of these differences, the context for evaluating wildlife passage success differs between continents. For example, use of passages by large predators in North

America is seen a positive management outcome (Foster and Humphrey 1995; Reudiger 1998; Gloyne and Clevenger 2001); whereas, use by predators in Australia is viewed as an environmental problem (Hunt et al. 1987; Norman et al. 1998; Little et al. 2002). The response of prey to a passage structure under relaxed selection may also be different to that where predators are present. The differences in predator-prey systems and differing criteria for measuring success has important implications in determining conservation priorities, appropriate passage location and design, management, and evaluation. Therefore, caution needs to be exercised when extrapolating passage evaluations and management recommendations between countries and under different predator-prey systems.

The absence of predators and relaxation of anti-predatory behavior by prey, and the presence or absence of co-evolution between predator and prey, has the potential to influence predator and, more particularly, prey behavior at all scales. These influences therefore potentially affect predator-prey relationships at a landscape and regional level influencing the spatial distribution of predator and prey species, at a local level influencing mammalian response at passage approaches, and at the passage itself. They therefore have the propensity to affect the response of predator and prey to one another and influence mammalian interactions with passage environments.

Recent passage studies are revealing that predator and prey species are responding to different passage structural and habitat attributes (Rodríguez et al. 1996; Rosell et al. 1997; Clevenger 1998; Clevenger and Waltho 1999, 2000; Clevenger et al. 2001). However, despite the increasing recognition that predator and prey species and groups may respond differently to passage structures, passage evaluation studies examining multiple structures have been reluctant to consider whether differences are occurring because of predator-prey responses to one another. Future passage studies would benefit by correlating predator and prey use and testing whether predator-prey interactions are directly influencing predator and prey use of passages. Such correlation would help determine the degree to which predator and prey are using the same or different passages and the degree to which this may be a response to passage structure or habitat preferences, human influences, or directly as a result of predator-prey interactions. To date only one published passage study has directly correlated predator and prey use of passages (Gloyne and Clevenger 2001).

Wildlife passage studies to date have tended to give little appreciation to the different spatial scales of predator-prey interactions and how this may influence passage use. Increasingly, there is a need for passage systems to provide landscape connectivity if wildlife populations and ecological processes such as predator-prey interactions are to remain stable. Passage systems need to provide permeability for large, dispersing animals dependant on regional landscapes if metapopulations are to survive (Beier 1995; Opdam 1990, 1997). They also need to ensure that rare predators have access to their prey (Gloyne and Clevenger 2001). However, equally, they need to be sufficiently permeable to allow spatial separation of predator and prey in order for prey populations to be sustained. Spatial differences between large predator and prey species have been observed in a number of passage studies to date (Foster and Humphrey 1995; Clevenger 1998; Clevenger and Waltho 2000). Regional landscape connectivity has also been demonstrated by providing access for cougar to its prey (Gloyne and Clevenger 2001). However, the above trends indicate the need for passage systems to be positioned relative to both predator and prey species' ranges if regional predator-prey relationships and processes are to be sustained.

At smaller, more localised scales, there may be more complex interactions between predators, prey and passages. Large carnivores such as bears and cougars are known to avoid roads and areas of human activity (van Dyke et al. 1986; McLellan and Shackleton 1988; Sweanor et al. 2000). The loss or absence of predators from fragments can change the abundance and ecological impacts on prey species, which in turn can have major effects on the structure of animal and plant communities in isolates (Terborgh and Winter 1980; Soulé et al. 1988; Ripple and Larson 2000; Ripple et al. 2001). The loss or absence of predators may in turn result in an increased abundance of mesopredators which in turn may have negative consequences on small mammals and other species (Terborgh and Winter 1980, Soulé et al. 1988). Whether such changes in animal community structure may also influence, or be reflected in, predator and prey use of passages, has yet to be examined.

While smaller passages (e.g., culverts) may sometimes service wide-ranging animals, smaller passages are more likely to be used by smaller-ranging species and therefore service localised subpopulations on either side of a road (Yanes et al. 1995; Clevenger and Waltho 1999; Clevenger et al. 2001). It is possible, then, that smaller passages, such as culverts, may play a larger role in defining the territories of smaller species and be used more frequently than larger underpasses. If smaller ranging carnivorous species adopt passages as part of their territories (as may be evidenced by scent marking), then avoidance strategies by small mammals may render the passage ineffective for small mammal transit. As small mammals are particularly prone to road barrier effects (Oxley et al. 1974; Swihart and Slade 1984; Burnett 1992; Goosem 2001), this could potentially

create crowding effects placing pressure on small mammal populations and making them more susceptible to predation, stochastic processes and certain catastrophic events (Simberloff and Cox 1987; Collinge 1998; Lidicker 1999; Short et al. 2002). This emphasises the need for multiple structures, possibly of varying size, in order to sustain connectivity for local subpopulations of prey species.

Biotic interactions within the passage environment itself (such as predation, territoriality, avoidance, and competition) may also influence use (Foster and Humphrey 1995; Tewes and Hughes 2001; Little et al. 2002). There is a need for passage studies to focus on the biotic interactions that occur at passage entrances and within passages to test whether this influences predator and prey acceptance or avoidance of wildlife passages. The employment of predator scent experiments at passage entrances to test the effect on prey (and predator) species would be particularly useful in this regard (Doncaster 1999; Little et al. 2002).

Future passage evaluations would benefit by identifying the predator-prey systems existing in the locality and considering the role of wildlife passages within this context. Evaluations would also benefit by examining the role and net effect of the wildlife passage system across the landscape. Is there a net benefit of the passage system to the ecology of the area? Does the passage system maintain regional connectivity for predator and prey species? Is the stability of predator-prey relationships maintained? In this regard, the net benefit of the passage system needs to be evaluated taking into account positive outcomes (e.g., reduced mortality from roadkill, facilitated movement, overcoming of barrier effects, genetic exchange, improved population viability, maintenance of native predator access to prey) and any negative effects (potential increased predation risk, prey avoidance, biotic barriers, flow-on effects to predator and prey species from increased connectivity).

The points canvassed in this paper need to be treated cautiously as there is currently very limited scientific testing of road and passage effects on predator-prey relationships and the influence of these relationships on wildlife passage use by mammals. The possibilities discussed here should be used to help guide future hypotheses for further testing.

Implications for Management

The following management and research recommendations are suggested:

1. Extrapolation of passage recommendations to mammals existing under different predator-prey systems needs to be treated cautiously.
2. To capture community-level movements and crossings, structures should be spatially extensive and frequent, and relevant to predator and prey habitat and territories. It is important to have at least one passage or culvert within an individual's home range (Gerlach and Musolf, 2000; Clevenger et al. 2001).
3. The possibility that biological barriers may inhibit movement supports the development of more than one passage at critical crossing points (Tewes and Hughes 2001). Ideally, there should be a mixed size class of passages provided to help ensure that use by predators does not preclude use by prey (Little et al. 2002).
4. Vegetative cover should be considered at passage entrances and interconnect with other adjacent habitat as this enhances passage use by native carnivores (Rodríguez et al. 1996, 1997) and prey species (Hunt et al. 1987; Clevenger and Waltho 1999; Clevenger et al. 2001; Goossem 2001) but tends to preclude use by feral predators (Hunt et al. 1987; Norman et al. 1998).
5. In Australia, wildlife passage strategies may need to focus on where and where not to place passages so that areas with high densities of feral predators can be avoided.
6. Monitoring through the use of video and trip cameras at passage entrances would assist in determining biotic interactions and predator and prey behavior at passage approaches (e.g., scent marking, predator or prey avoidance, potential use of entrances as prey-traps).
7. Use of wildlife exclusion fencing should be treated cautiously. Where predator and prey species have co-evolved, frequent use and scent marking by predators may preclude use by prey species. Fencing together with biotic interactions at passage sites may create barriers for prey movement (Bergers and Nieuwenhuizen 1999; Doncaster 1999).
8. Sampling a limited number of passages may indicate passage avoidance when, in fact, species may be utilising other passages due to predator-prey avoidance or in response to passage habitat or structural attributes. Researchers need to be cautious when basing conclusions on limited sampling.
9. Future research examining predator and prey responses to passages needs to correlate and examine possible predator-prey interaction effects.
10. Further research is required in order to examine whether predator scent influences prey (and predator) avoidance of passages, the duration of any effect, and whether co-evolution of predator and prey influences the perception of olfactory cues.

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