NEW ZEALAND JOURNAL OF ECOLOGY

Roads and wildlife: the need for evidence-based decisions; New Zealand bats as a case study

Chris Jones[1]* , Kerry Borkin[2] and Des Smith[3]

[1]Manaaki Whenua − Landcare Research, PO Box 69040, Lincoln 7640, New Zealand
[2]Wildland Consultants Ltd, PO Box 7137, Te Ngae, Rotorua 3042, New Zealand
[3]Wildland Consultants Ltd, PO Box 9276, Tower Junction, Christchurch 8149, New Zealand
*Author for correspondence (Email: jonesc@landcareresearch.co.nz)

Abstract: Roads and associated land transport activities can affect a wide range of indigenous terrestrial vertebrate species. National legislation, particularly the Resource Management Act 1991, requires that developers 'avoid, remedy or mitigate' the adverse environmental effects of their activities. How these effects are identified and managed in New Zealand varies because regulators and land transport contractors deal with these issues on a case-by-case basis. In recent years, the effects of new road projects on long-tailed bats (*Chalinolobus tuberculatus*) have been receiving attention. In this review, we summarise evidence on likely road infrastructure impacts on bat populations and the efficacy of mitigation approaches, used both internationally and in New Zealand. Our findings indicate that most mitigation methods have little, if any, scientific evidence of their effectiveness. We recommend that such evidence is essential to guide investment in mitigating road effects on bats in New Zealand. Given that such evidence is rare, future investment should be guided by an adaptive management framework that is justified by strong, inferential, evidence-based logic, and accompanied by robust, appropriately designed monitoring planned, in advance, to allow an objective assessment of a method's effectiveness in mitigating an impact. Because such monitoring may be beyond what a single development project can realistically achieve, we suggest the development of a collaborative funding model for supporting the testing and development of mitigation methods. This work is likely to have a significant influence on the future planning and design of road infrastructure projects to minimise the impacts on bats and, more generally, on any native wildlife populations under threat from infrastructure development.

Keywords: adaptive management, *Chalinolobus tuberculatus*, infrastructure, mitigation, *Mystacina tuberculata*, threats

Introduction

Until relatively recently the discipline of road ecology was a minor, applied aspect of ecological and transportation research (Coffin 2007). Early studies focused on wildlife−vehicle collision rates, but as road networks and traffic volumes have increased there has been an increasing awareness of their wider environmental effects and impacts on wildlife populations and ecosystems (van der Ree et al. 2011, 2015). Effective management of the impacts of road infrastructure on wildlife populations requires a balance between often competing social, economic and environmental pressures (Roberts & Sjölund 2015). New Zealand has a fleet of almost 5.1 million registered vehicles (February 2018 figures; MOT 2018), and is ranked in the top 10 nations globally for per capita vehicle use (OICA 2016). With 11 000 km of State highways and 83 000 km of local roads, New Zealand has one of the highest available lengths of road per head of population in the world (NZTA 2016). Over the past two decades the number of vehicle-free households in New Zealand has decreased, while the number owning more than one vehicle has increased (StatsNZ 2015). Approximately 70% of all freight in New Zealand is transported by road.

Two decades ago a national review of potential road impacts on ecological values identified priorities for managing these impacts, including the need to appraise the quality and quantity of ecological impact assessments, and to conduct research into mitigating the fragmentation of natural habitats by road networks (Spellerberg & Morrison 1998). The identification and management of the ecological effects of road development and use in New Zealand varies by project because, until recently (see Smith et al. 2017, Appendix D), there have been no national protocols to guide the process. Regulators and land transport operators deal with ecological issues on a case-by-case basis, resulting in a range of ecological outcomes and costs.

When a road is planned, a series of consents and other permissions from local and national authorities must be obtained before construction can commence. The consenting process is guided by three pieces of legislation. First, the

Resource Management Act 1991 (RMA) addresses the sustainable management of natural and physical resources. Approvals to undertake activities under the RMA are referred to as resource consents. Local authorities use a series of regional and district plans to guide implementation of the RMA and approval of resource consents. To obtain a resource consent, an Assessment of Environmental Effects (AEE) is required; this AEE includes a consideration of whether the actual and potential adverse effects of the proposed development or activity can be avoided, remedied or mitigated. If a planned activity is likely to have anything other than minor environmental effects, the authority will notify the general public of the application, which allows interested parties to make a submission on the application. These submissions can result in a hearing, where affected parties may present evidence against or in support of the application. The eventual decision of the consenting authority may be appealed, in which case the application may be considered by the Environment Court. In the case of a large development, such as the construction of a new road, the consenting and appeal process is likely to be long and complex, with significant financial costs. The draft National Policy Statement on Indigenous Biodiversity (NPSIB; Biodiversity Collaborative Group 2018) further places the emphasis on consenting authorities to 'address measures to … offset or compensate for adverse effects' in addition to the RMA's avoid-remedy-mitigate hierarchy.

Second, where proposed projects are likely to affect Crown conservation estate, the Department of Conservation (DOC) will issue a concession under the Conservation Act 1987 if it is satisfied that habitats and species will be protected sufficiently.

Third, any land transport project that involves disturbance or risk of death to endemic wildlife requires an authorisation under the Wildlife Act 1953, which is also administered by DOC. Assessments are required to gain approval for these permits. There is no specified method for undertaking an assessment, but liaison with DOC staff is required. Conditions may be imposed directly by DOC via the authorisation permit. As such, a different and possibly more stringent set of conditions may result from those that were determined for a project during the RMA consenting process.

In recent years, the effect of road projects on endemic long-tailed bats (*Chalinolobus tuberculatus*) has become topical, due to road projects (e.g. sections of the Waikato Expressway in the central North Island) in areas that still retain remnant bat populations in fragmented habitats. A lack of empirical evidence of the impacts of roads on New Zealand bat populations can lead to strongly conflicting opinions, leading in turn to a prolonged consenting process. This absence of clear, robust evidence has resulted in a range of management conditions being imposed on road developments, with little certainty around the outcomes for bat populations.

In an attempt to address this uncertainty, we review current global knowledge of the impacts of roads on bats and of the measures used to mitigate those impacts, both overseas and in New Zealand. Although we focus on mitigation, we acknowledge that avoidance of any impact is likely to lead to the best outcome for at-risk populations. Similarly, we acknowledge the emergence of ecological compensation as a management option in the NPSIB, but there is significant doubt that this approach is practical for a number of reasons, particularly the time-lag between impact and compensatory ecological response, or whether compensation for ecological loss, e.g. through methods such as pest control, can be maintained in perpetuity (Maron et al. 2010, 2012). Throughout this paper

we consider mitigation of impacts at the population level to define effectiveness. We conclude with recommendations for priority actions to fill vital knowledge gaps and emphasise the need for management decisions to be evidence-based (Pullin & Knight 2009). Although we focus on the mitigation of road impacts on indigenous bat populations, the core principles outlined in this review apply to populations of any terrestrial vertebrate species facing similar issues.

Bats: a brief overview of ecology, life history and population dynamics

Although it is likely that only two species of bat survive in New Zealand, bats represent one of the most diverse groups of mammals globally. The taxonomic order Chiroptera contains over 1300 living species divided into 2019 families (Roskov et al. 2018). These include the large fruit-eating bats of the Old World tropics and the smaller and frequently (but not exclusively) insectivorous bats ('microbats') that navigate and locate prey using echolocation (high-pitched sonar). The remainder of this review focuses on the small echolocating bat families, for two reasons: (i) most research in Europe and North America on road impacts focuses on these species; and (ii) both New Zealand species of bats belong to this group. New Zealand has two known extant species of bat: the long-tailed bat and lesser short-tailed bat (*Mystacina tuberculata*), both of which are considered of conservation concern (O'Donnell et al. 2018), primarily from the effects of habitat fragmentation and predation by introduced mammals. Key information on both species is summarised in Table 1, and we direct the reader to O'Donnell (2005) and Lloyd (2005) for more detailed accounts.

Bats' life histories conform to a general pattern, with interspecific variations. The following summary is based on a range of sources and is intended as a generalisation to illustrate where characteristics of bat ecology and behaviour place them at risk from road and infrastructure developments (UK Highways Agency 2008; SÉTRA 2009; Stone et al. 2013; for more detail see Altringham 2011).

During winter in temperate zones, including New Zealand, when insects and other foods are in short supply, bats may hibernate; i.e. they enter extended periods of torpor (minimal activity and low metabolic rate) in quiet, humid sites with low, constant temperatures, emerging occasionally on milder evenings when insects are active. Bat roost choice varies with their reproductive state. Consequently, in winter when females are neither pregnant nor lactating and males are not making sperm, they use cooler roosting sites, while in summer, when breeding female bats require warmth to enhance both the growth of their foetus *in utero* and milk production, they live communally in warmer roosts, often accompanied by non-breeding females. During the summer months the males are generally solitary, living apart from the females in separate roosts. Females frequently continue to use communal roosts that are separate from the males when pregnant and lactating.

Bats spend the daylight hours resting inside a roost emerging to feed at, or soon after, dusk. The timing of their emergence from the roost is critical, as delayed emergence will reduce the amount of time available to forage at the time when the abundance of crepuscular insects is at its greatest.

Both sexes share breeding roosts and swarming sites in the autumn in order to mate. Female gestation is temporarily halted, by delaying fertilisation (through storage of sperm) or by halting the development of the embryo, until the next

Table 1. Summary of key ecological and life-history information for extant New Zealand bat species. Data from Lloyd 2005, O'Donnell 2005, O'Donnell et al. 2006, and O'Donnell et al. 2018, unless cited otherwise. Note that behaviour and life-history traits may vary between populations.

	Long-tailed bat (*Chalinolobus tuberculatus*)	Lesser short-tailed bat (*Mystacina tuberculata*)
Status	Threatened: Nationally Critical	Threatened: Nationally Vulnerable (northern sub-species) At Risk: Declining (central sub-species) At Risk: Recovering (southern sub-species)
Distribution	Wide, patchy distribution − North Island. Few isolated populations on west coast of South Island. Declining nationally compared with historical records.	Discrete known populations generally associated with old-growth indigenous forests: the majority in the North Island; also Eglinton Valley (South Island), Murchison Mountains, and Whenua Hou / Codfish Island. Core ranges of all populations are in indigenous forests. Range restricted and has declined compared to historical records.
Habitat	Generally considered an edge-adapted species. Largest populations in mature, unmodified indigenous forest. Known to roost in indigenous forest, exotic plantations, modified landscapes − use edges and gaps to move/forage. Activity highest along edges such as riparian zones, cliff edges and other linear landscape features. Several known populations in urban/peri-urban areas (e.g. Hamilton, Temuka, Auckland)	Generally considered a forest interior species. Largest populations in mature, unmodified lowland indigenous forest. Appear to require old, large tree stands for roosts. Activity highest in forest interior. May forage in habitats adjacent to indigenous forest, including exotic plantation forest, but generally avoid open/edge habitats except for commuting between forest patches.
Home range size	Median estimates (Eglinton Valley, indigenous forest): • males: 1589 ha • females: 1361 ha (post-lactation); 360 ha (lactation) • juveniles >2 weeks independent; 2006 ha Ranges appear smaller in peri-urban habitat (Dekrout 2009). Concentrate activity in small core areas.	In Eglinton Valley (indigenous forest): range 130−6220 ha; median 480 ha. Ranges smaller in mixed-habitat mosaic (Toth et al. 2015). Concentrate activity in small core areas.
Life-history	Insectivorous. Mate late summer/autumn; pregnancy delayed until spring. Births: November to mid-December. Dates vary between populations. Females produce one young per year after 2−3 years old in native forest; may breed earlier in other habitats. Single young born mid-December. Adult survival in South Island indigenous forest variable; inversely proportional to introduced predator abundance. Form distinct social groups, which have distinct roosting areas; foraging areas that overlap between social groups.	Primarily insectivorous, but also eat nectar, pollen and fruit. Mate late summer; pregnancy delayed until spring. Single young born mid-December−mid-January. Around 80% of mature females breed annually − likely to vary according to local conditions.
Foraging habit	Wing morphology typical of aerial-hawking, moderate/fast-flying species. Primarily forages (highest activity rates) in forest edge/gap habitats; activity is relatively high over water bodies. Observed flying 3–60 m above ground (Borkin 2010).	Wing morphology suggests gleaning-hawking habit. Activity rates highest in forest interiors; mixed foraging strategy, some hawking, but mainly gleaning and terrestrial hunting for invertebrates using passive listening. Commute at high speed between forest canopy layer and understory, but reported as foraging within 2 m of the forest floor (Lloyd 2001). Capable of high manoeuvrability in cluttered environments.
Emergence	From up to 1 hour before to 30 min after sunset; influenced by temperature, humidity, invertebrate activity and light.	Only at full darkness; return to day roosts 30 min before dawn twilight.
Roosting	Roost in a range of habitats, most well-insulated roosts in indigenous forest (Sedgeley & O'Donnell 2004). Utilise cavities, peeling bark, fissures, and splits in trunk/limbs of usually large, old trees. Fewer cavities are available in many exotic tree species. May use rock cavities/fissures. Shift roosts frequently where sufficient available sites; in other habitats roost occupancy times are longer and roost switching less frequent.	In habitat mosaics, active in range of habitats, but generally roosts in old-growth forests. Primarily small cavities in trunks of large, mature trees, but use variety of similar spaces. May have 20−30 colonial roosts within 10 000−13 000 ha of forest. Visit roosts intermittently during the night. In summer, whole colonial groups move every few days between roosts, km apart.

spring. During spring and summer female bats gather into maternity roosts for a period of at least 12 weeks to give birth and rear their young. Usually only one pup is born annually and remains under close care for 4–6 weeks until it is old enough to fly and hunt independently (Mitchell-Jones 2004). During breeding, the females need to hunt intensively and generally return to the roost several times a night to feed their young.

Once the pups are independent, the communal group may break up and the bats move to other roosts. Bats may gather from a wide area to form maternity roosts, so any disturbance or destruction of these roosts can affect bats over a large spatial scale (Mitchell-Jones 2004). The same maternity roosts may be used every summer, as bats have a strong tradition of returning to the same site year after year.

Individual bats use the same routes (commuting corridors, flight paths or fly-ways) regularly for commuting between roosts and foraging areas. Alteration of routes can cause increased energy costs to bats in finding, possibly longer, alternative routes to feeding areas and therefore reduced foraging time.

A bat's wing shape influences its manoeuvrability and, in combination with its call characteristics, the type of prey hunted and habitat in which it forages (Norberg & Rayner 1987). Some bats ('gleaning' foragers) with wider, more rounded wings are better able to fly in cluttered environments, such as forest interiors, taking prey from vegetation, while other 'aerial hawking' species (including New Zealand's long-tailed bats) with narrower, more pointed wings forage on flying insects in open, uncluttered spaces. Another group of species, including New Zealand's short-tailed bats, use a combination of both strategies.

Many species of small echo-locating bats are at risk of extinction globally (Mickleburgh et al. 2002), with the primary threats being habitat degradation and loss, human hunting, and the impacts of introduced predators. Studies of the factors likely to predict extinction risk have identified restricted geographic range and wing shape (Jones et al. 2003; Safi & Kerth 2004). Gleaning bats are generally at higher risk of extinction because their survival is linked more critically to the existence of suitable habitat and because their wing shapes are not adapted to long-distance migratory flights. More recently, Sagot and Chaverri (2015) have linked roost specialisation to extinction risk, with those bat species able to use a greater range of roost types predicted to be at lower risk.

Bats' life histories are typical of larger, more 'K-selected' species with delayed maturity, high annual adult survival, and slow reproductive rates. Consideration of the relative contribution of demographic rates to population growth can help to identify the most critical processes to protect when managing impacts on a population. Understanding these rates can allow managers to identify and prioritise the management of those rates most likely to achieve a desired conservation or control outcome (Dixon et al. 1996). Thus, for bats, management interventions aimed at maintaining high survival rates of adult female bats will have the greatest effect on maintaining population growth (Pryde et al. 2005; O'Shea et al. 2011; O'Donnell et al. 2017). The key messages about managing bat populations are as follows:

- If a population is small, it is likely to be very vulnerable to chance catastrophic impacts and other small-population effects (e.g. Allee effects).
- Growth of all populations will be most sensitive to reduced breeding-age female survival. Given that even a healthy bat population is likely to grow slowly (~1–5% annually, *ibid.*) any impact on adult survival should be regarded as a threat to population viability.
- Because adult female survival is the most important contributing parameter to population growth, larger populations are likely to be less vulnerable to short-term reductions in reproductive output, although longer-term impacts will restrict population growth.

In the following sections we describe the effects of roads on bats and the methods employed internationally and in New Zealand to mitigate these effects. Other than in cases where habitat clearance leads to a catastrophic level of mortality, most of the effects and mitigations described can be viewed in terms of their effects on a population's vital demographic rates, as outlined above.

Effects of roads on bats

Habitat loss

When roads and their associated infrastructure are built and maintained bat populations may suffer loss of essential habitat. The UK Highways Agency (2008) summarised these effects as 'the permanent direct loss of bat habitats, such as roosts, foraging areas and landscape features used for commuting.' The direct effects of habitat loss will depend on the particular bat species' requirements and the type of habitat removed. For example, if wetlands are removed, it will affect wetland-foraging bat species. Loss of foraging habitat means that individual bats may need to increase their home range to compensate, which, in turn, increases the energy cost of foraging. At some point, a threshold of habitat loss will be unsustainable for individuals, leading to reduced survival rates and reproductive outputs. Loss of roosts is likely to be critical to bat populations given the important roles they play in breeding. In particular, it will be critical when roosts are occupied by females and dependent young, but loss of hibernation roosts will also be highly detrimental because of long-term fidelity to roost sites. Impacts of roost loss will become more pronounced when roosts are restricted to certain rare habitat types. Habitat around roosts is also critical to their continued use; Davidson-Watts (2007) found *Pipistrellus* species selected roost sites primarily due to the presence of suitable surrounding habitats.

Roost loss can force bats to expend excess energy in finding and/or commuting to new roosts, and replacement roosts may be of sub-optimal quality (e.g. reduced thermal insulation; O'Donnell & Sedgeley 2006), leading, via lower survival and reproductive rates, to smaller populations (Brigham & Fenton 1986; Borkin et al. 2011).

For many bat species, older trees have much greater value as roost sites, so their loss can have a disproportionately greater impact than that of younger trees (Burgar et al. 2015). Direct mortality from the felling of roost trees is also a significant risk when forest areas are cleared for development, meaning that torpid bats and pregnant or nursing females and their dependent young are likely to be at the greatest risk because of their limited ability to escape (Borkin & Parsons 2010). The risk of this loss to populations will vary seasonally, but to a small population or social group of bats the loss of one or more communal roosts may have dire consequences for long-term viability, particularly if those roosts contain significant proportions of the population's breeding adult females.

Habitat modified by noise

Remaining habitat adjacent to roads may be changed by the presence of the road, its associated infrastructure and the vehicles using it. Bats depend heavily on hearing to navigate and detect prey and several studies have identified the negative effects of noise on bats. Schaub et al. (2008) showed that simulated traffic noise levels deterred greater mouse-eared bats (*Myotis myotis*), which detect prey by 'passive listening', from foraging effectively; and Siemers and Schaub (2011) described a decline in the speed and success of foraging by the same species with increasing road noise.

The frequency at which commuting bats changed their flight path to avoid roads increased with road noise levels, with an apparent threshold of 88 dB (Bennett & Zurcher 2013). The same study also showed that bats avoided roads at locations where noise levels were greatest. By looking at the

effects of noise on different aspects of the foraging behaviour of echolocating Daubenton's bats (*Myotis daubentonii*), Luo et al. (2015) suggested that their observed reduction in foraging efficiency was due to the fact that although bats could still detect prey, they avoided loud ambient noise levels.

Habitat modified by light

Increased levels of illumination from artificial light sources on and around roads have also been identified as likely to affect bats' nocturnal behaviour patterns. More light-tolerant bats may be attracted to aggregations of insect prey around white street lights (Blake et al. 1994; Rydell & Racey 1995). Evidence of the negative effects of lighting was first provided by Kuijper et al. (2008), who compared pond bats' (*Myotis dasycneme*) commuting behaviour under dark and illuminated conditions. Light had two main effects: it reduced the number of 'feeding buzzes' (characteristic echolocation sounds produced when attacking prey) by 60%, despite insect abundance increasing; it also induced bats to turn away from their normal commuting route, even at relatively low illumination levels. Stone et al. (2009) described marked reductions in slow-flying bats' normal use of hedgerows illuminated with high-pressure sodium lights compared to unlit hedgerows. Bats also delayed their normal activity under lit conditions. These behaviours are likely to have two effects on individual fitness: alteration of commuting routes creates increased energy demands; and both altered commuting behaviour and delayed emergence serve to reduce the time available to forage.

A similar effect was found for slow-flying species when both light-emitting diode (LED) and metal halide street lights were trialled, although no effect was detected on the commuting behaviour of faster-flying species (Stone et al. 2012, 2015). Matthews et al. (2015) found that increased activity at street lamps was only significant when tree cover was also present. Therefore, lighting effects on bats are likely to vary by species and according to local habitat. Fast-flying species may be attracted to the increased foraging opportunities presented by insects around street lights, but this behaviour may also increase the risk of motor vehicle collisions, particularly to juveniles that may not have learned avoidance behaviours (Stone et al. 2015). Slower-flying, clutter-adapted species are more likely to avoid artificial lighting, possibly to reduce predation risk. However, in Hamilton, New Zealand, Dekrout (2009) found a negative relationship between density of street lights and the activity of long-tailed bats, which are an aerial hawking species.

Habitat change through creation of edges

Road construction creates new edges in what was previously contiguous habitat. The associated reduction in cover, shade and humidity and increased light, wind and exposure, can have mixed effects depending on individual species' requirements. North American aerial hawking species were much more active along managed pine plantation edges than in forest interiors, while gleaning, clutter-adapted *Myotis* species avoided edges (Morris et al. 2010). In a related study, bats were recorded as flying predominantly parallel to the forest edge, with few feeding 'buzzes' recorded, suggesting that the edges were being used as linear landscape elements to facilitate commuting (Kalcounis-Rueppell et al. 2013). In contrast, Jantzen and Fenton (2013) found edge use to be similar across bats of all foraging types, although the most clutter-adapted species of those studied had significantly lower levels of activity outside of the forest than species classified as 'edge' or 'open' foragers.

Mortality through vehicle collisions

Where commuting or foraging bats cross roads, they risk collision with vehicles. In New Zealand, there have been reports of long-tailed bat collisions with vehicles (e.g. Moore 2001) but data are sparse. The relative abundances of different species in the habitats surrounding roads will be reflected in road-kill statistics, but species' behaviour also has an influence. Slow, low-flying, gleaning species may show disproportionately high mortality rates, whereas fast, high-flying species are relatively rarely encountered (Lesinski 2007, 2008). Where a road crosses a commuting route, casualties are also likely to be higher, and even high-flying species may be guided into traffic (Lesinski et al. 2011). Peak mortality occurs during periods of migration to different seasonal roosts, and during the dispersal of newly independent young (Gaisler et al. 2009; Russell et al. 2009; Semrl et al. 2012).

Characteristics of both the road and the surrounding landscape can influence the risk of road mortality to bats. In Austria, Gaisler et al. (2009) noted that significantly more bat carcasses were detected where a road ran between two lakes over which the bats foraged than along other stretches. In Poland, twice as many road-kills were recorded on one stretch of a road than at another bordering the same forest, but 10 km away (Lesinski et al. 2011). The authors suggested that commuting bats were 'funnelled' by forest lanes onto the road, but vehicle numbers and speed were also key factors. Similarly, Medinas et al. (2013) found that landscape features were the most important of a range of factors in predicting bat road casualty rates: more road-kills occurred where roads crossed high-use habitats such as dense woodland, water bodies and riparian zones. They also recorded higher mortality rates of female bats in early summer, corresponding to the energy-demanding late pregnancy and lactation periods of the life cycle, when females must forage more frequently, but are likely to fly more slowly and with reduced manoeuvrability.

In considering road mortality data as an indicator of population impacts, two important points must be considered. Firstly, surveys are likely to underestimate true mortality rates significantly because of difficulties in detecting small road-killed bat carcasses (Slater 2002; Santos et al. 2011; Teixeira et al. 2013). Second, although road mortality has the potential to contribute to population change, this effect cannot be inferred reliably without knowledge of the proportion of the population affected, the demographic classes (sex, age, reproductive status) to which they belong, and the relative impact of this mortality in the context of the population's other vital demographic processes.

Effects of roads on bat behaviour

In addition to direct mortality effects, roads affect the behaviour of commuting and foraging bats, although different species can have quite different responses. Kerth and Melber (2009) radio-tracked individuals of two species of bat near a motorway during foraging and seasonal roost switching. An aerial hawking species that characteristically flew in open spaces crossed the motorway readily during both periods, but a gleaning species rarely crossed the motorway, and when it did, individuals used an underpass. This avoidance was in spite of the motorway lying within the species' normal commuting range. As well as avoiding crossing the motorway, bats of the gleaning species had smaller than normal foraging ranges.

Road avoidance behaviour may be due, in part, to the deterrent effect of traffic for some species: around twice as

many commuting *Myotis* bats in the USA reversed their course away from a road crossing their commuting route when traffic was present compared to when it was absent (Zurcher et al. 2010). One possible explanation for this effect is the avoidance of noise, described above. Characteristics of habitats adjacent to the road also influence bat behaviour; bats' typical use of linear landscape elements to navigate across a landscape can lead them onto roads, but they may be more reluctant to cross the road because it creates a break in the linear landscape element (Russell et al. 2009; Abbott et al. 2012a; Bennet & Zurcher 2013).

Either because of direct mortality or behavioural avoidance of the road due to light, noise or traffic movement, roads can be barriers to bats' foraging, commuting and migration. This barrier effect can have impacts on the populations of bats in an area. In a transect-based study in the north of England, total bat activity and the diversity of recorded species declined dramatically with proximity to a motorway, particularly in areas of lower canopy cover (Berthinussen & Altringham 2012b). Recent studies have confirmed these findings: in northern California, Kitzes and Merenlender (2014) found total bat activity to be reduced by about half adjacent to a road compared with 300 m away. This effect was greater on cooler nights, suggesting that habitat alteration may play a part in driving the observed behaviour. A survey of five British roads undertaken as part of the development of generic methodologies showed declines in both bat activity and diversity with increasing proximity to the roads (Berthinussen & Altringham 2015). Similarly, long-tailed bat activity near New Zealand highways declined as overnight traffic intensity increased, but no effects were detected at paired monitoring points 200 m from the road (Smith et al. 2017, Appendix C). Given that long-tailed bats in New Zealand are distributed patchily across a landscape, local populations may be maintained by immigration from other patches. Barrier effects of roads are likely to interfere with this process, making small, isolated sub-populations more vulnerable to local impacts.

Vulnerability of New Zealand bat species to development
When the life history characteristics of each New Zealand bat species are considered, their specific vulnerabilities to road, and other infrastructure, development becomes apparent (See Table 1 for a summary of life history characteristics). Both long-tailed bats and lesser short-tailed bats have their largest populations in areas of mature, unmodified, indigenous forest, and home ranges are smaller in modified landscapes (Dekrout 2009; Toth et al. 2015) and after trees have been felled (Borkin & Parsons 2014). Roosts that are available outside of unlogged indigenous forest are less well-insulated than those chosen by long-tailed bats in indigenous forests (Sedgeley & O'Donnell 2004). Consequently, there may be increased costs of reproduction and reduced likelihood of survival for populations in modified, or otherwise fragmented, landscapes compared to those in indigenous forests. Short-tailed bats are particularly likely to be vulnerable to roads where they fragment indigenous forest due to their apparent dependence on these forests for roosts and a preference for foraging within forest interiors (as measured by activity rates; O'Donnell et al. 2006). Long-tailed bats may be more resilient to development than short-tailed bats because they appear less dependent on unmodified indigenous forest (due to their wide distribution throughout New Zealand; O'Donnell 2005), and are thought to be more flexible with their roost choice, as well as being edge-adapted (O'Donnell et al. 2006). However, evidence is

emerging of long-tailed bat activity rates being lower along busy roads than on other edges (Smith et al. 2017, Appendix C), and where light levels are highest (Le Roux & Le Roux 2012). Crewther and Parsons' (2016) development of a habitat suitability model for long-tailed bats in Auckland also found that distance to roads and population density were important factors in predicting the presence of long-tailed bats. Their model suggested that long-tailed bats are less likely to be present close to roads and where population density is high. This suggests that long-tailed bats are unlikely to be resilient to road projects.

Mitigation of road effects on bats (i): international approaches and evidence

In response to identifying the threats presented to bats by roads and their associated infrastructure, a range of mitigation approaches have been developed, primarily in Europe. Here we review published evidence regarding bat behaviour in relation to mitigation structures to determine their effectiveness. Most attempts to mitigate impacts have been based on incorporating structures into road design to facilitate safe movements across the road.

Under-road structures
Bats' use of under-road structures as crossings was first recorded in a series of observational studies in central Europe (Bach et al. 2004). At around the same time a new highway scheme in Wales incorporated two culverts at pre-existing bat crossing points specifically to facilitate safe crossing of the new road by bats. Although use was low during the road's construction, bats of a number of species used the culverts increasingly following the road's opening, although some were observed to alter their behaviour away from more well-lit areas near the culverts (Wray et al. 2006). Kerth and Melber's (2009) study of the effects of a motorway on bats' behaviour revealed that a variety of bat species used underpasses to cross safely, but that encounters were dominated by characteristically low-flying, gleaning species.

Research has also focused on the characteristics of crossing structures that might influence their use by bats. Use of 54 culverts under Dutch roads was dominated by low-flying, gleaning bat species, and by over-water foragers where the culvert carried a water flow (Boonman 2011). Bats used all culverts of cross-sectional area greater than 4 m^2, and use increased with cross-sectional area above that threshold. Gleaning species were the only bats to use narrow drainage pipes to traverse a road in Ireland, but a greater variety of bats used a large underpass nearby (Abbot et al. 2012b). In both the Irish and Dutch studies, the height of the underpass was the most important component of cross-sectional area in determining bat use.

Bats' use of three underpasses in the north of England varied with the underpasses' location (Berthinussen & Altringham 2012a). At one underpass, sited on a pre-road construction commuting route, the majority (96%) of observed bats used it to cross the road; at two others (not aligned to commuting routes), more bats crossed over the road at traffic height than used them, despite landscaping attempts to divert their flight paths towards the underpasses. A subsequent study of three more underpasses by the same authors showed up to two-thirds of observed bats using the structures at two underpasses,

and the vast majority at the third underpass (Berthinussen & Altringham 2015). The most used underpass was the widest and highest, and maintained a pre-existing commuting route. The other two, smaller, lesser-used underpasses maintained some characteristics of the original flight paths.

Over-road structures

Because of bats' tendency to use linear landscape elements as commuting routes, over-road mitigation structures have been used to attempt to take advantage of this behaviour in guiding bats above the traffic flow. Perhaps the most commonly used is the bat-bridge, or gantry, which consists of a series of horizontal wires strung over a road with mesh or plastic spheres attached to the wires to increase their echolocation profile. Despite their extensive use and high cost (~$NZ280 000 each; http://news.bbc.co.uk/2/hi/uk_news/england/cornwall/8320610.stm; accessed 29/10/15) , there appears to be little evidence of their effectiveness being used in deciding to employ them, other than assumptions based on what was known about bats' behaviour.

In the first robust assessment of their usefulness, Berthinussen and Altringham (2012a) compared the proportions of observed bats using four gantries with those crossing the road at unsafe heights, and found that the majority of bats at all sites avoided using the gantries, even one that had been in place for 9 years prior to the survey. Most bats crossed the roads at pre-existing commuting routes at heights that placed them in danger of vehicle collision. In a subsequent study at three more gantry sites, one of which was yet to be completed by having wires attached, bats' use of the gantries was negligible and most crossed roads at unsafe heights nearby (Berthinussen & Altringham 2015).

The overwhelming conclusion is that bat gantries are ineffective at guiding bats across roads at safe heights. Similarly, we could find no evidence of the effectiveness of vegetated 'hop-overs,' where high vegetation is planted or manipulated to provide continuous habitat over a road. O'Connor and Green (2011) reported that around half of bats observed crossing a road in the UK used a hop-over at a 'safe' height, but no comparison data were available to evaluate either before/after use or the proportion of all bats crossing safely.

Other studies have recorded or investigated bats' use of other over-road structures, including minor road- and foot-bridges and purpose-built 'green bridges'. Few bats were recorded using overbridges spanning motorways relative to crossing the motorways at other sites or using underpasses, in two separate studies (Bach et al. 2004; Abbott et al. 2012a). Berthinussen and Altringham (2015), in developing their survey design, also recorded minimal use of a minor-road-carrying overbridge with no vegetation and no connectivity to linear habitat features. The same authors also looked at two over-road structures designed specifically to help wildlife cross major roads. These structures were an 'environmental overbridge' with high sides and a row of planted vegetation, over which 80% of observed bats crossed; and a 'green bridge', described as 'a relatively wide, substantial structure and although it carries a paved minor road, it is well vegetated with dense and continuous mature trees and shrubs along each side that are well connected with treelines and surrounding woodland'. Ninety-seven percent of observed bats used this structure to cross the road. Other features of the bridge, including its connectivity to pre-existing habitat on both sides and its placement at commuting height may have influenced its effectiveness. Similarly, a diverse range of microbat species were more active over a vegetated overbridge compared with adjacent cleared road edges in Queensland, Australia, suggesting that this approach may be effective in providing habitat connectivity in fragmented landscapes (McGregor et al. 2017).

Artificial roost boxes

Although not specific to road effects, the provision of artificial roost boxes has been used internationally with the aim of providing additional, or replacement, potential roosts and enhancing biodiversity in a variety of habitats (Brittingham & Williams 2000; Smith & Agnew 2002; Ciechanowski 2005; Bender 2009). However, there are few published studies documenting their efficacy (Hayes & Loeb 2007) and, of those studies, there are suggestions that the effect may be low (Griffiths et al. 2017, 2018).

There is some overseas evidence to suggest that, in areas where natural roosts are limited in number, bat uptake of roost boxes may be higher (Smith & Agnew 2002; Ciechanowski 2005). Roost boxes may also be more effective when placed near the roosts they aim to replace (White 2004) and when their aspect orientation is considered in relation to sunlight (Dillingham et al. 2003). However, they should be considered only a temporary solution for areas undergoing restoration and that currently have few suitable roost trees. It is generally recommended that long-term strategies instead focus on providing natural roosting structures (Hayes & Loeb 2007; Popa-Lisseanu et al. 2009; Griffiths et al. 2018). Artificial roost boxes are far less efficient at buffering and delaying temperature fluctuations than natural cavities, and therefore bats are likely to prefer natural cavities where available (De Bruyn et al. 2003). In a survey of building permits (derogation licences) in England for projects that might result in roost loss, Stone et al. (2013) noted that most proposed mitigation methods were based on anecdotal evidence of their effectiveness, and that post-development monitoring data were inadequate to tell whether or not the mitigation attempts had been effective. As with other types of mitigation, we caution that evidence of some use does not translate to effectiveness in mitigating an impact at the population level.

Lighting regimes

There have been no published studies of the effectiveness of different lighting regimes in reducing impacts on bats at roads. Stone et al. (2015) made a series of recommendations to minimise impacts, including: interconnected light-exclusion zones along known flight-lines; dimming or switching off lights during critical bat movement periods, reducing overall light intensity (although species-specific thresholds are unknown); and avoiding using lights with short-wavelength (blue to ultra-violet) outputs, to which bats and some insects may be more sensitive. More recently, Rowse et al. (2016) detected no difference in aerial-hawking species' activity between low pressure sodium (LPS) and newer light-emitting diode (LED) street lights, although slow-flying, gleaning species were rarely encountered under either lighting regime.

Mitigation of road effects on bats (ii): approaches used in New Zealand

In this section we review the evidence for mitigating road impacts on bats in New Zealand. In doing so we address the following key questions:
- What has been done to mitigate/compensate for road impacts on bats in New Zealand?

- What was the logic or justification for what was done?
- What monitoring of these mitigation efforts has taken place?
- Is there evidence that this mitigation worked?

Overview of mitigation

The use of mitigation approaches in managing threats to New Zealand bats from infrastructure projects has been limited until recent years. Current research into long-tailed bat ecology in and around the Waikato region, as well as the establishment of Project Echo (a multi-agency initiative that aims to increase awareness of bats) in 2010, has highlighted bats' presence outside of unlogged native forests (Dekrout 2009; Borkin 2010; Le Roux 2010). These developments have meant that road projects increasingly need to avoid, minimise and mitigate effects on long-tailed bats.

Predator control aimed at improving breeding success and survival of bats, planting of indigenous vegetation to improve foraging habitats, and the provision of interim artificial roost boxes to provide roosts are methods that may improve the likelihood of persistence of long-tailed bats (Pryde et al. 2006). Bat management plans, which may be required by regional councils for resource consents or as part of designation conditions imposed by district councils, have since focused on these as potential mitigation methods. However, the lack of research, and therefore lack of evidence of their effectiveness for New Zealand species, has resulted in sign-off on bat management plans being protracted (and therefore expensive), and remaining contentious even after completion. Protracted consent processes may result in political pressure to make changes to legislation that may not be conservation friendly. For more details on the resource consent conditions imposed on recent road development projects in New Zealand we direct the reader to Smith et al. (2017, Appendix A).

Predator control

Control of introduced predators should be considered a compensatory, or offsetting, tool, not one that mitigates the impacts of infrastructure projects directly, and it is important to note that its effectiveness in this context has never been investigated. New Zealand bats are preyed upon by cats (*Felis catus*; Scrimgeour et al. 2012), brush-tailed possums (*Trichosurus vulpecula*; O'Donnell 2000a), rats (*Rattus* spp.) and stoats (*Mustela erminea*; Pryde et al. 2005; O'Donnell et al. 2010). In years of high rat and stoat abundance in beech forest habitat in the Eglinton Valley (Fiordland National Park), survival of long-tailed bats was low; conversely, when rat and stoat abundance were low, survival rates of long-tailed bats were higher (Pryde et al. 2005). The impact of introduced predators on long-tailed and short-tailed bat populations outside of contiguous beech forest habitat is poorly described; to the authors' knowledge, the only published research that investigates the relationship between predator control and bat survival rates over a longer period than one predator control operation was undertaken in Fiordland beech forest for long-tailed bats (O'Donnell et al. 2017).

Increasing mean survival rates can increase the likelihood of persistence of a population and may reverse declines in populations and the possibility of local extinction due to predation, but long-term population monitoring is required to ensure that predator control is having the desired effect (Pryde et al. 2006; O'Donnell et al. 2017). Monitoring is required because the level to which predator populations must be suppressed for bat recovery to occur has not been established for most predator species, and because there is concern regarding the effects of some toxin-based control methods on bats, particularly short-tailed bats, due to either direct or secondary poisoning (O'Donnell et al. 2011; Dennis & Gartrell 2015).

Predator control that has been implemented to date due to consent condition requirements has been over areas far smaller than bat home ranges and roosting ranges. For example, control of rats and possums occurred over 399 ha of the Taupiri Scientific Reserve in the case of the Huntly Section of the Waikato Expressway (Connolly 2015a, b), where home ranges of juvenile long-tailed bats are likely to be in excess of 1800 ha (juvenile long-tailed bats in North Island exotic forest; Borkin & Parsons 2011a). Areas under predator control along the Cambridge Section of the Waikato Expressway were even smaller (Davies et al. 2013; Matthews 2015). Small areas of predator control are unlikely to protect entire colonies or social groups of long-tailed bats (O'Donnell 2014; O'Donnell et al. 2017). The recommendations made by DOC for the protection of long-tailed bat colonies involve the control of predators over entire forest areas (e.g. a minimum of 1000 ha, but preferably several thousand hectares; O'Donnell 2014), and recent research has shown that predator control that aims to increase survival of long-tailed bats is only effective over areas >3000 ha, when entire roosting areas are included in the controlled area and where a control buffer of sufficient width to prevent reinvasion is maintained (O'Donnell et al. 2017). This large area is needed because long-tailed bat colonies can use many roosts over the course of one year, and only a proportion of these roosts may be protected by small areas of predator control. However, outside of National Parks it is difficult to implement large-scale predator control across non-contiguous habitat, where there are multiple land tenures, which is a huge challenge for using predator control as a compensatory tool.

Acoustic monitoring is a widely used monitoring tool for determining the presence of bats (Ahlen & Baagøe 1999; Furey et al. 2009; Harrison et al. 2012) and examining their activity patterns (Hayes 1997). Acoustic monitoring is possible in New Zealand because the two extant species echolocate (Parsons 1997); i.e. they produce ultrasound or use biosonar, to 'visualize' their environment and navigate through it (Jones & Teeling 2006). Automatic bat monitoring units (ABMs) detect bats' echolocation calls, record these in some form, and, with interpretation from the user, can confirm that a bat has been within the vicinity of the ABM.

Monitoring at the majority of road projects is inadequate to determine effects on population survival because it is based on acoustic monitoring which only records relative changes in levels of activity. Only an extended mark−recapture programme with permanent marking of individual bats would be able to determine changes in survival rates and whether the prescribed predator control is achieving its objectives (O'Donnell 2009). A monitoring programme sufficiently intensive and extensive to determine population level responses may be considered onerous or out of step with what is required in other areas of mitigation.

Tree-felling protocols

Both New Zealand bat species shelter during the day in roosts, which may be in trees or other vegetation, caves, rock crevices or buildings (Daniel & Williams 1983, 1984). Roosts are also used during the night between foraging bouts (O'Donnell 2002). Bats are known to remain within trees when they are

felled, and consequently may be injured or killed when this occurs (Cheeseman 1893; Borkin & Parsons 2010), reducing colony size (Borkin et al. 2011).

In recent years, various regional councils have required projects that cut down trees and other vegetation to undertake intensive monitoring in locations where long-tailed bats have been detected previously to prevent bat injury or mortality (Davies et al. 2013; Connolly 2015a, b). This process is governed by 'tree/vegetation removal protocols' and involve using a professional ecologist to identify potential roosts using a combination of knowledge of features, such as cavities, associated with roosts and automatic bat monitoring units (ABMs). Following this monitoring, tree felling will only take place if the ecologist determines the trees are not being used by bats at that time. If ABM monitoring is equivocal, then an arborist is often required to inspect tree cavities and other potential roost locations within the tree to confirm that these are unoccupied by bats before felling may take place.

These protocols have largely targeted long-tailed bats and, to the authors' knowledge, have not yet been applied to short-tailed bats. They also frequently overlook the use of 'non-tree' vegetation as roosts and do not protect these roosts even though long-tailed bats are known to use dead tree ferns as roosts (Borkin & Parsons 2011b).

To our knowledge, few active bat roosts have been located in the thousands of trees felled using current protocols, and no bats have been located during post-felling inspections. Although implementation of tree removal protocols adds considerable cost to each project, the accuracy of these protocols for identifying bat roosts remains untested. Therefore, the effectiveness of these protocols as a mitigation method remains unknown, and a formal test of the current protocol's ability to detect a roost, where present, is recommended.

Planting vegetation

Maintaining the connectivity of bat populations requires 'functional connectivity' of habitats; that is, individuals must be able to move between resource patches in the landscape (Hale et al. 2012). Critical resources for bats include both roosts and foraging areas. For species such as long-tailed bats, which commute along tree networks and other linear landscape features such as forest and road edges (O'Donnell 2000b; Borkin & Parsons 2009), population connectivity requires maintaining structural connectivity between areas (Hale et al. 2012), and of both roosts and foraging habitat between social groups of bats.

The construction of a road is likely to interrupt population linkages: some recent overseas studies show that at least some bat species will avoid a busy road rather than fly across it (Bennett & Zurcher 2013). The removal of vegetation is also likely to increase fragmentation of long-tailed bat populations because their colony sizes and home ranges are smaller in areas where tree felling has taken place (Borkin et al. 2011; Borkin & Parsons 2014). These impacts increase the risks of colony isolation, loss of genetic diversity, Allee effects, and ultimately local extinction (Meyer et al. 2009).

The planting of vegetation has been recommended as a tool to improve remaining, or replace lost, foraging habitat (Pryde et al. 2006) and maintain connectivity between local bat populations (Matthews 2015). The effectiveness of this approach in the short-to-medium term has not been demonstrated although Borkin (2010) found relatively low use of young native vegetation regenerating areas by long-tailed bats compared to other habitat types. Planting programmes

along the Cambridge and Huntly sections of the Waikato Expressway aim to mitigate some of the effects of road construction on bats (Matthews 2015; Connolly 2015a, b). Some of the species included in the planting plans for each of these sections may form potential roosts in the long term (60−80 years; Tim Martin, Wildland Consultants Ltd, pers. comm.), but they do not address the loss of roosts in the short term.

On the northern side of the Cambridge section the focus of mitigation efforts has been on maintaining as many trees as possible, while on the southern side it has been on establishing fast-growing species to mitigate potential decreases in connectivity between colonies and population fragmentation (Matthews 2015). Monitoring that is planned to take place in both these sections may clarify whether the re-planted areas are still used by bats, but because they focus solely on acoustic monitoring these monitoring programmes will be unable to show whether populations remain sufficiently linked to maintain population processes adequately.

Both New Zealand bat species fly at heights that mean they could be within the path of vehicles, particularly large trucks. Long-tailed bats have been noted flying at 3−60 m above the ground (Borkin 2010). Le Roux et al. (2014) compared detection rates at various heights within one tree stand and detected long-tailed bats most commonly between 4 and 6 m above the ground (relative to ABMs placed 15−30 m above the forest floor, although ABMs were not placed at ground-level). In comparison, Scrimgeour et al. (2013) found that short-tailed bats were detected most frequently at 10−12 m from the forest floor (when compared with ABMs placed at 22.0−25.0 m and 1.5−2.0 m within a podocarp and a beech forest). It has been suggested by Lloyd (2001) that short-tailed bats commonly fly within 2 m of the forest floor. Because of this variability in reported behaviour and the potential for significant barrier and mortality effects at road crossings, we suggest that research is required urgently to investigate bat flight behaviour over and near existing and planned New Zealand roads.

In some cases, specific sites have been identified as important road-crossing points for bats prior to projects beginning (e.g. at Cambridge; Connolly 2013). In one case, within the Cambridge section of the Waikato Expressway, long-tailed bats were observed crossing the road several times in close proximity to a line of tall oak trees perpendicular to the road (Connolly 2013). In response, a vegetated 'hop-over' of tall, fast-growing trees was designed with the aim of encouraging bats to fly high above the traffic and thus avoid collisions (Matthews 2015). Whether monitoring will be undertaken to determine if the use of this site to cross the expressway continues post-construction is unclear, and therefore its effectiveness is likely to remain unknown.

With the aim of reducing the likelihood of bat−vehicle collisions along the extent of the Cambridge section of the Waikato Expressway, the following measures were also recommended:

> Tall planting that is adjacent to the Expressway will be set back from the carriageway as far as possible within the land owned by NZTA to encourage bats to fly further away from the Expressway alignment and thus avoid collisions. A relatively wide verge of low vegetation (grass/ low shrubs) will be maintained adjacent to the carriageway wherever possible to discourage bats from foraging along the roadside (Matthews 2015).

As in the above examples, it is not clear whether any monitoring will be undertaken to determine the effectiveness of this planting strategy in terms of minimising bat−vehicle

collisions once the expressway section is operational. Furthermore, we can find no published evidence of the likely effectiveness of this approach.

Artificial roost boxes

The provision of artificial roost boxes is aimed at mitigating the effects of the loss of natural roosts during road development. Their use was approved in the Bat Management Plan (Enabling Works) for the Cambridge section of the Waikato Expressway (Davies et al. 2013). A later plan suggested that additional roost boxes would not be used as a mitigation tool because a workshop made up of representatives of the contractor and NZTA questioned their effectiveness (Matthews 2015).

There is limited evidence of long-tailed bats using artificial roost boxes. A short-term trial of artificial roost boxes began in 2003 in South Canterbury, to provide potential roosting opportunities for the resident long-tailed bat population, which was in rapid decline (Pryde et al. 2006). Approximately 25% of natural roosts were lost within 4 years of the study because of either natural attrition or tree felling for firewood (Pryde et al. 2006). The remaining roosts were considered poor quality because of their low insulating properties and large entrances, which potentially exposed their inhabitants to unstable microclimates and increased the risk of predation (Sedgeley & O'Donnell 2004). Roost boxes installed in 2003 were used by bats within 2 years and were still in use 5 years after installation. Boxes were used by bats at least occasionally (two bats were found in one box and guano was found in multiple boxes; Colin O'Donnell, DOC, pers. comm., 19 October 2015). Checks since this time have detected no apparent use by bats.

Some roost boxes were no longer available to be used by bats because they were full of nesting materials placed there by rifleman and other bird species, and the long interval between checks may have meant that bat guano had disintegrated (Colin O'Donnell, DOC, pers. comm., 19 October 2015). Recommendations made since this time have suggested that roost boxes require frequent emptying so that they remain available for use by bats (Moira Pryde, DOC, pers. comm., 12 October 2015). If long-tailed bats use roost boxes, it is likely that their use may take some years to be observed (Moira Pryde, pers. comm., DOC, 12 October 2015), as is the case for the Australian congeneric Gould's wattled bat (*Chalinolobus gouldii*; Bender 2009). Recently long-tailed bats have been observed roosting in several artificial bat boxes in Hamilton city, 5 years after their installation (K. Borkin, pers. obs.). It is unknown how soon after their installation use began.

A long-term investigation into the use of artificial roost boxes by long-tailed bats is recommended to address questions regarding bats' use of these structures. Most research into roost use by New Zealand bats has focused on female-dominated maternity colonies (Sedgeley & O'Donnell 1999; Sedgeley 2003). However, such colonies differ from roosts used by male bats (Borkin & Parsons 2011b), and more detailed research into the roosts used by male bats is recommended so that artificial roost boxes can emulate roosts used by males as well as those used by female-dominated maternity colonies.

Lighting regimes

The effect of lighting on New Zealand bats remains little studied, with the majority of work having taken place in urban Hamilton. After undertaking an extensive acoustic monitoring survey, Le Roux and Le Roux (2012) concluded that the effect of lighting and other anthropogenic variables on long-tailed bats was why otherwise suitable habitat remained unused in the city. In particular, lighting appeared to form a barrier to bats' use of some areas of habitat: along the Waikato River corridor little activity was detected downstream of the first major well-lit bridge compared with upstream (Dekrout 2009; Le Roux & Le Roux 2012). In Hamilton, bat activity was correlated negatively with streetlight density (Dekrout et al. 2014) despite anecdotal reports suggesting that long-tailed bats will forage occasionally around or above streetlights (Connolly 2013).

Le Roux and Le Roux (2012) have suggested creating a landscape that is more 'permeable' to bat movement, including the implementation of low-impact road and bridge lighting regimes. Subsequently, recommendations have been made to minimise lighting, and therefore by association night work, where long-tailed bats are present in several component projects of the Waikato Expressway (Davies et al. 2013; Connolly 2015a, b). The effects of lighting on bats were considered in one pedestrian bridge project where it was recommended to minimise light spill and use motion-activated sensors so that lights were only activated when users were approaching and using the bridge to minimise potential effects on long-tailed bats (Turner 2014). To our knowledge, no monitoring of bat activity, behaviour or population rates was recommended, or has taken place, to determine the success of these specific mitigation measures. We support the recommendation of Le Roux and Le Roux (2012) that experimental research is required to better elucidate the effect of light and roads on bat behaviour so that more targeted mitigation and management techniques can be developed.

Assessing the effectiveness of mitigation

Of the approaches used in New Zealand, there is no evidence that any minimise the impacts of roads on bats or help to maintain bat population viability, despite their frequent use in mitigation plans. In many cases, this lack is because research has not taken place to investigate their effectiveness. Similar issues affect the consenting process of other impacted taxonomic groups, such as lizards. To clarify this apparent criticism, it is important to consider what we mean by 'effectiveness'. For example, take a study or survey result describing bats' use of a road-crossing structure. We could interpret this finding as follows: bats use the structure to cross the road, therefore it is reducing road mortality, and therefore it is contributing to population viability. But we should also ask the following questions to be confident of any reported 'success':

- What proportion of the local bat population is using the structure to cross the road safely, and what proportion is avoiding or crossing the road unsafely?
- How does the proportion of bats crossing the road safely compare to pre-road movements?
- By how much was road mortality reduced by the structure?
- Is the remaining road mortality sustainable: how does it affect population viability?

In giving evidence to an enquiry into a British road development project, Altringham (2008) noted, correctly, that it is:

important to distinguish between use and effectiveness. This is linked with the distinction between assessing mitigation at the individual and population levels. Conservation is the protection of species and ecosystems at

the population level: maintaining favourable conservation status means maintaining stable populations. Assessment at the individual level is not a guide to what is happening at the population level.

This is because an individual's behaviour may not always conform to, or represent reliably, the behaviour of most other members of the population. Indeed, caution must be used when extrapolating measures of activity to infer the status of a population. Even if activity or use is maintained at a development site, mechanisms other than 'no effect' may be operating. For example, a consistent post-development level of activity may result from fewer bats being more active, new bats moving into a habitat because mortality of residents has made local resources more available, or a declining population being forced to increase their use of remnant sub-optimal habitat.

Many infrastructure projects in New Zealand that undertake monitoring for bats use acoustic monitoring. This method is a valid way of establishing broad measures of bat activity and identifying, in the first instance, those areas where further survey effort should be targeted. Generally, though, most pre-infrastructure surveys have taken place over short timeframes, and sample sizes have been small, which means that little confidence can be placed in their ability to detect changes in relative activity reliably.

In most situations the ultimate goals of monitoring will be to establish whether land transport activities are having a negative impact on bat population abundance and long-term viability, and whether mitigation measures lead to long-term population sustainability. However, population abundance can be difficult and costly to estimate. Therefore, measures of activity (e.g. numbers of bat passes detected by ABMs) may be relied on, inappropriately, to infer changes in population status. Activity indices are unable to provide a reliable indication of population size or viability simply because it is impossible to tell whether an observed level of activity results from single passes from many bats or multiple passes by few bats.

Furthermore, indices of abundance are commonly flawed because they often rely on both activity (which varies by individual, habit, season, etc.) and an assumption that there is a consistent linear relationship between the index and true abundance, which is rarely the case as it requires the focal species' detectability to remain constant, both spatially and over time (Williams et al. 2002). If this is not the case, differences in index values may be attributable to changes in population size, detectability, or to some combination of the two. Without additional information on how detection probability changes according to variables such as season, habitat, weather or previous experience of the index method, it is impossible to know the relative effect of a change in population size on the measured index value (Williams et al. 2002).

In applied wildlife management, it is unfortunately common for much more time and money to be spent on 'doing things' than on monitoring the effectiveness of those interventions. Although this is understandable given the strong socio-economic drivers behind many development projects, including roads, a lack of robustly designed and sufficient monitoring means there is frequently no evidence to allow management decisions to be made in the planning stage of a project and, later, no evidence that a management intervention has been effective, and therefore cost-effective.

Yoccoz et al. (2001) have suggested that monitoring design should be driven by three simple questions: (1) why monitor? (2) what should be monitored? and (3) how should monitoring be carried out? The answer to the first question depends on the context of the project and the existence of clearly defined SMART (specific, measurable, achievable, relevant and time-bound) goals or outcomes (Doran 1981). Identifying these outcomes should then lead, logically, to the identification of what to monitor (i.e. what will tell you if you have achieved the project's desired outcome?). Identification of the key variables of interest will then guide monitoring requirements, including the choice of the most appropriate methods to be used.

Roedenbeck et al. (2007) noted that studies on the ecological effects of roads are rarely able to make strong inferences, for two main reasons: (1) they are often focused on measuring an inappropriate end point, such as movement rates across roads, rather than the key variable of population persistence; and (2) an absence of monitoring, both before and after a road is built or a mitigation put into place. The authors emphasised that the most robust study design is a before-after-control-impact (BACI) design, in which the before (pre-construction baseline) and after (post-construction) states of a variable are compared, both at an impact site (where an intervention is to take place) and at a control (reference) site.

If a full BACI design is not feasible, power analysis models can demonstrate that simple but replicated before-after comparisons carry greater inferential strength than control-impact comparisons (Roedenbeck et al. 2007). Weaknesses in survey design meant that, of 30 studies of the effectiveness of wildlife road-crossing structures reviewed by Taylor and Goldingay (2010), only one was able to draw robust conclusions about the affected species' population viability. In a review of attempts to mitigate road impacts on European protected species, Ward et al. (2015) noted:

> In the majority of studies in which the benefits of road crossing structures were quantified, we found definitions of effectiveness to be inadequate. Many studies focussed on the use frequency of road crossing structures or changes in the absolute numbers of animals killed without accounting for pre-road movement rates, for changes in road crossing away from structures, for changes in population mortality rates (including within and between ages or sexes) and for population-level benefits.

Other key questions that need to be addressed in the design of a monitoring programme to determine the effects of a road or mitigation intervention on a wildlife population include how long monitoring should be undertaken and its extent (number of sites). The first question can best be answered by thorough consideration of the life history and ecology of the species of interest; for example, a programme aimed at monitoring changes at the population level of slow-breeding, long-lived species such as bats would probably require decades of data to detect a significant change reliably, but one aimed at detecting changes in behaviour or mortality at a road would probably require a shorter duration, defined by predictable seasonal or annual patterns of behaviour and a knowledge of their inherent variability.

Bat activity can vary from day to day and between seasons due to many factors, including climatic conditions (Turbill 2008), reproductive activity (Russ et al. 2003), the distance between roosts and foraging areas (Ciechanowski et al. 2007), and invertebrate availability (O'Donnell 2000b), resulting in wide sample variance and consequently requiring large sample sizes for precise estimates of activity (Hayes 1997). O'Donnell and Langton (2003), when using counts of bat passes along line transects, noted that large sample sizes and/or long monitoring programmes are required to obtain sufficient power to detect

changes in relative abundance, because long-tailed bat activity is inherently variable, even with standardised survey methods. A more recent analysis suggests that monitoring for fewer than 10 years would provide insufficient statistical power to infer changes in populations reliably, particularly small changes (Meyer 2015).

Insufficient or highly variable data may not detect population trends that are actually occurring. Therefore, it is essential that a statistical power analysis be undertaken during the design phase of a monitoring programme. This analysis should demonstrate that the monitoring programme is capable of producing sufficient data to answer questions pertinent to project goals. If sites are sampled inadequately then there is greater probability of incorrect or ambiguous inferences being drawn (Hayes 1997). Because of the inherent spatial and temporal variability in monitoring data, it is important that a power analysis uses, wherever possible, data from a pilot study specific to the population in question.

The use of statistical modelling techniques, particularly those that take into account the probability of detecting bats given they are present, can greatly improve monitoring programmes, along with a well-balanced design and highly standardised sampling (Meyer 2015). Unfortunately, there are no formal guidelines describing sampling effort for acoustic monitoring of New Zealand bats using ABMs (Sedgeley 2012). The development of such guidelines is essential and should be based on power analyses that make use of existing data.

Mitigation of road impacts on wildlife will incur a cost to the agency building the road. The only way to be confident that any investment in mitigation is cost-effective is to monitor the effectiveness of various mitigation strategies in reducing impacts on a population. If monitoring is not designed appropriately to provide the necessary information, it imposes an additional cost from which little benefit is derived, and the uncertainty created by weak monitoring data may lead to drawn-out resource consent decision processes.

Conclusions and recommendations

Outside of National Parks and other large areas of contiguous indigenous habitat, New Zealand bat populations, particularly long-tailed bats, also exist in fragmented habitats. Some populations in these fragmented habitats are likely to be small and therefore particularly vulnerable. In addition to small-population effects, population growth is most strongly influenced by the survival rates of breeding female bats. Because of bats' inherent life-history characteristics, population growth is slow, even under good conditions. Therefore, recovery of populations from significant perturbations is likely to take decades.

The effects of road infrastructure impacts on the viability of bat populations can be inferred from published evidence, but can only be demonstrated by monitoring a population using an appropriate survey design over the time-frame in which a population change can be detected reliably, or in which changes in vital rates can be measured. Individual species' vulnerability and responses to roads vary according to the characteristics of their flight, foraging and ranging behaviours, and any prediction of likely impacts must be based on a thorough understanding of these traits. The design of methods and strategies aimed at mitigating impacts on a local population should be based on a firm understanding of that species' behavioural and life-history traits. If such information is lacking, then collection

of data should be prioritised as part of the monitoring design.

If an impact due to the development of road infrastructure is considered likely – or even a significant risk – to a bat population, the first consideration should be to examine whether that impact can be avoided by shifting the planned footprint of the development. If avoidance is not feasible, mitigation should be considered.

Investment in mitigation of road effects on bats should be based, ideally, on previous evidence of effectiveness. This evidence is rarely available, so investment should be: (i) justified by strong, inferential, evidence-based logic, and (ii) accompanied by robust, appropriately designed monitoring that is planned, in advance, to allow an objective assessment of a method's effectiveness in mitigating an impact.

Such monitoring may be beyond what a single development project can achieve realistically. The most immediate need for individual projects, or groups of linked projects, is to identify localised risks to vital bat population processes and focus on mitigating those risks. For mitigation approaches at road crossings, evidence of use is not evidence of effectiveness, so monitoring should be designed, ideally, to compare crossing safety with pre-road conditions, or to consider relative proportions of safe versus unsafe crossings by bats. The use versus effectiveness logic also applies to other mitigation approaches, such as the installation of artificial roost boxes.

Clearly, some mitigation approaches, such as crossing structures, may be difficult to modify to improve their effectiveness following construction. To overcome this, a centrally coordinated adaptive management process can be used to design new structures based on evidence of the effectiveness of others. The aggregated information from more than one project will be much more powerful and useful than that from a single project.

Population ecology emphasises the importance of maintaining survival rates of breeding adults, particularly females, to maintain bat populations. Given this vulnerability, mitigation must help immediately. Mitigation approaches based on re-vegetation (e.g. planting trees as 'hop-overs') are unproven and are likely to take many years to be effective, if at all. While we cannot discount their usefulness, they are unlikely to mitigate immediate impacts on bat populations. These methods, if used, should form part of a wider long-term strategy that also includes measures to mitigate the immediate impacts. Given that planning for road projects often occurs many years prior to construction beginning, it would be useful to investigate the effectiveness of 'mitigation', including planting, in the years prior to construction occurring. Because of the importance to New Zealand bat populations of maintaining adult survival, we suggest that methods of mitigating flight path severance should be investigated as a priority. Such investigations require knowledge of how (where, when and at what height) bats travel through a landscape in which a road is planned thus allowing identification of a suitable mitigation approach (e.g. whether an under- or over-road structure would be most appropriate). Any structure should seek to maintain existing flight paths (alignment, height). Of the over-road structures considered overseas, vegetated bridges appear to have the greatest potential to mitigate impacts, but further evaluation is needed. Therefore, we recommend that the characteristics of New Zealand bats' flight behaviour be investigated with some urgency, particularly at sites where planned roads are likely to cross existing flight paths.

The loss of an occupied maternity roost due to tree-felling may be catastrophic to a small local bat population, particularly

because of the potential impacts of the loss of breeding-age females. Although current tree (or vegetation)-removal protocols generally prohibit tree removal during winter, or when temperatures are below a threshold (to avoid loss of hibernation roosts and to increase the likelihood of detection of bats during pre-felling monitoring – bats are more likely to be in torpor and less likely to be detected when temperatures are low; Smith et al. 2017), the risk to maternity roosts is often dependent on the ability to detect them in trees prior to felling. This risk remains unquantified because the accuracy of current survey methods remains untested. Therefore, a robust assessment of current protocols and research into roost identification methods are recommended.

The additional cost of mitigation, monitoring and associated research to already-expensive road projects is an international issue. For example, overseas between 7.5% and 10% of road project budgets have been dedicated to mitigating impacts on wildlife (van der Grift et al. 2013). Given the national importance of this issue and the threatened status of many of the wildlife species that are likely to be affected by road developments, we recommend that a collaborative funding model for supporting the testing and development of mitigation methods be developed. This model could include the New Zealand Transport Agency, regulatory authorities, DOC, the road industry and other industries that may benefit from improving the status of biodiversity on their lands.

Research support for individual projects may be available via other sources through collaboration with research providers. This collaboration would spread the costs and support the collection of data consistently across projects, thus facilitating the meta-analysis of data to provide stronger inferences about effectiveness. An alternative approach may be to stipulate the conditions for monitoring the effectiveness of mitigation within contracts. Projects currently suffer the costs of delays due to prolonged litigation during the consent process, often because of debate and uncertainty as to the likely effectiveness of mitigation methodologies, and significant sums are spent on implementing mostly untested mitigation approaches. An investment in developing an evidence-based mitigation strategy, while requiring upfront financial input, is likely to reduce costs and delays in the long term.

Although the primary focus of this review has been on the effects of roads, and their mitigation, on New Zealand bat populations the general principles described above for assessing impacts from a population ecology perspective and thereby prioritising mitigation strategies, can be applied to bats facing the impacts of other types of development (e.g. wind farms, transmission lines or power schemes) and also to any indigenous vertebrate population. An approach that links the mechanism of impacts to effects at the population level by considering effects on vital demographic rates can help guide managers towards solutions that will sustain a whole population. Whatever the potential species-infrastructure conflict, we strongly recommend the following:

- If avoidance is not possible, prioritise mitigation of those impacts considered likely to have the greatest effects on population growth and viability.
- Use robust evidence (not anecdotal or 'accepted', but untested, practice) to identify potential mitigation approaches.
- Prioritise mitigation methods based on:
  (a) Robust scientific evidence of success when used on the species to be protected in similar locations or habitats. Robust evidence should include demonstration of sufficient statistical power and some quantification of effect magnitude.
  (b) Peer-reviewed scientific evidence of successful use on the species to be protected in other location/habitat type(s).
  (c) Peer-reviewed scientific evidence of successful use on related or similar species in other location/habitat type(s).
- If reliable evidence of mitigation is not available, identify likely approaches based on published research and consider trials of those methods. Trials must be designed using the criteria suggested in the previous section above, to allow objective and robust assessment of effectiveness and should consider the caveats also set out in the previous section. Expert thinking could be involved here, particularly if the published literature is lacking, but the key thing is to set up the monitoring appropriately, and spread risk across a number of mitigation options, being prepared to quickly drop/modify options that produce poor results, i.e. an adaptive management framework.
- Establish a robust monitoring programme to evaluate the effectiveness of the mitigation method used.
- Data collected at individual projects should be made publicly-available, so that other similar data sets can be compared in a meta-analytical approach to assess the effectiveness of mitigation methods more generally.

Acknowledgements

References

Abbott IM, Butler F, Harrison S 2012a. When flyways meet highways: the relative permeability of different motorway crossing sites to functionally diverse bat species. Landscape and Urban Planning 106: 293−302.

Abbott IM, Harrison S, Butler F 2012b. Clutter adaptation of bat species predicts their use of under motorway passageways of contrasting sizes: a natural experiment. Journal of Zoology 287: 124−132.

Ahlen I, Baagøøe HJ 1999. Use of ultrasound detectors for bat studies in Europe: experiences from field identification, surveys, and monitoring. Acta Chiropterologica 1: 137−150.

Altringham JD 2008. Bat ecology and mitigation: proof of evidence. Public enquiry into the A350 Westbury Bypass on behalf of the White Horse Alliance. UK, Wiltshire Council. 37 p.

Altringham JD 2011. Bats: from evolution to conservation. Oxford, UK, Oxford University Press. 349 p.

Bach L, Burkhardt P, Limpens HJ 2004. Tunnels as a possibility

to connect bat habitats. Mammalia 68: 411−420.

Bender R 2009. White-striped freetail bats in boxes. The Australasian Bat Society Newsletter 33: 5−7.

Bennett VJ, Zurcher AA 2013. When corridors collide: road-related disturbance in commuting bats. Journal of Wildlife Management 77: 93−101.

Berthinussen A, Altringham J 2012a. Do bat gantries and underpasses help bats cross roads safely? PloS one 7: e38775.

Berthinussen A, Altringham J 2012b. The effect of a major road on bat activity and diversity. Journal of Applied Ecology 49: 82−89.

Berthinussen A, Altringham J 2015. WC1060. Development of a cost-effective method for monitoring the effectiveness of mitigation for bats crossing linear transport infrastructure. Report prepared by the University of Leeds for DEFRA (Department for Environment, Food, and Rural Affairs), England.

Biodiversity Collaborative Group 2018. Report of the Biodiversity Collaborative Group. Biodiversity (Land and Freshwater) Stakeholder Trust, Wellington. 183 p.

Blake D, Hutson AM, Racey PA, Rydell J, Speakman JR 1994. Use of lamplit roads by foraging bats in southern England. Journal of Zoology 234: 453–462.

Boonman M 2011. Factors determining the use of culverts underneath highways and railway tracks by bats in lowland areas. Lutra 54: 3−16.

Borkin KM 2010. Ecology of New Zealand long-tailed bat (*Chalinolobus tuberculatus*) in exotic plantation forest. Unpublished PhD thesis, University of Auckland, Auckland, NZ. 172 p.

Borkin KM, Parsons S 2009. Long-tailed bats' use of a *Pinus radiata* stand in Kinleith Forest: recommendations for monitoring. New Zealand Journal of Forestry 53: 38−43.

Borkin KM, Parsons S 2010. The importance of exotic plantation forest for the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). New Zealand Journal of Zoology 37: 35−51.

Borkin KM, Parsons S 2011a. Home range and habitat selection by a threatened bat in exotic plantation forest. Forest Ecology and Management 262: 845−852.

Borkin KM, Parsons S 2011b. Sex-specific roost selection by bats in clearfell harvested plantation forest: improved knowledge advises management. Acta Chiropterologica 13: 373−383.

Borkin KM, Parsons S 2014. Effects of clear-fell harvest on bat home range. PLoS ONE 9: e86163.

Borkin KM, O'Donnell CFJ, Parsons S 2011. Bat colony size reduction coincides with clear-fell harvest operations and high rates of roost loss in plantation forest. Biodiversity and Conservation 20: 3537−3548.

Brigham RM, Fenton MB 1986. The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64: 1128−1133.

Brittingham MC, Williams LM 2000. Bat boxes as alternative roosts for displaced bat maternity colonies. Wildlife Society Bulletin 28: 197−207.

Burgar JM, Craig MD, Stokes VL 2015. The importance of mature forest as bat roosting habitat within a production landscape. Forest Ecology and Management 356: 112−123.

Cheeseman TF 1893. Notes on the New Zealand bats. Transactions and Proceedings of the New Zealand Institute 26: 218−222.

Ciechanowski M 2005. Utilization of artificial shelters by bats (Chiroptera) in three different types of forest. Folia Zoologica 54: 31−37.

Ciechanowski M, Zajac T, Biłas A, Dunajski R 2007. Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. Canadian Journal of Zoology 85: 1249−1263.

Coffin AW 2007. From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transport Geography 15: 396−406.

Connolly T 2013. Waikato Expressway: Cambridge Section long-tailed bat surveys summer 2012-13: Lloyd Property, Mellow Manor, Karapiro Gully. Report prepared by Opus International Consultants Ltd, Hamilton, New Zealand for New Zealand Transport Agency. Report No.: 2-61647.02/910HR.

Connolly T 2015a. Draft bat management plan part 1 and 2: Waikato Expressway Huntly Section. Contract No.: NZTA 2/09-007/601. Report prepared by Opus International Consultants Ltd, Hamilton, New Zealand, for New Zealand Transport Agency and the Fulton Hogan-HEB Joint Venture.

Connolly T 2015b. Overall ecological management plan Waikato Expressway Huntly Section. Contract No.: NZTA 2/09-007/601. Report prepared by Opus International Consultants Ltd, Hamilton, New Zealand, for New Zealand Transport Agency and the Fulton Hogan-HEB Joint Venture.

Crewther K, Parsons S 2016. Report on modelled distribution of long-tailed bats in the Auckland region. Report prepared for Auckland Council, Auckland, New Zealand.

Daniel MJ, Williams GR 1983. Observations of a cave colony of the long-tailed bat (*Chalinolobus tuberculatus*) in North Island, New Zealand. Mammalia 47: 71−80.

Daniel MJ, Williams GR 1984. A survey of the distribution, seasonal activity and roost sites of New Zealand bats. New Zealand Journal of Ecology 7: 9−25.

Davidson-Watts I 2007. Roost selection, foraging behaviour and habitat use by two cryptic species of pipistrelle bat. Unpublished PhD thesis. University of Bristol, Bristol, UK.

Davies F, Matthews T, Borkin K 2013. Waikato Expressway: Tamahere − Cambridge Section bat management plan (stage one: enabling works). Report prepared by URS and Wildland Consultants Ltd for HEB Construction Ltd.

De Bruyn L, Van Der Wijden B, Verken S, Verhagen R 2003. Tree cavities, microclimate and bats: an experimental study. Proceedings of 3rd International Wildlife Management Congress, 1−5 December 2003, Christchurch, New Zealand. Christchurch, New Zealand, The Wildlife Society, Landcare Research New Zealand Ltd, Australasian Wildlife Management Society.

Dekrout AS 2009. Monitoring New Zealand long-tailed bats (*Chalinolobus tuberculatus*) in urban habitats: ecology, physiology and genetics. Unpublished PhD thesis. University of Auckland, Auckland, NZ. 168 p.

Dekrout AS, Clarkson BD, Parsons S 2014. Temporal and spatial distribution and habitat associations of an urban population of New Zealand long-tailed bats (*Chalinolobus tuberculatus*). New Zealand Journal of Zoology 41: 285−295.

Dennis GC, Gartrell BD 2015. Non-target mortality of New Zealand lesser short-tailed bats (*Mystacina tuberculata*) caused by diphacinone. Journal of Wildlife Diseases 5:

177−186.

Dillingham CP, Cross SP, Dillingham PW 2003. Two environmental factors that influence usage of bat houses in managed forests of Southwest Oregon. Northwestern Naturalist 84: 20−23.

Dixon P, Friday N, Ang P, Heppell S, Kshatriya M 1996. Sensitivity analysis of structured-population models for management and conservation. In: Tuljapurkar S, Caswell H eds. Structured population models in marine, terrestrial and freshwater systems. New York, Chapman and Hall. Pp. 471−513.

Doran GT 1981. There's a SMART way to write management's goals and objectives. Management Review 70: 35−36.

Furey NM, Mackie IJ, Racey PA 2009. The role of ultrasonic bat detectors in improving inventory and monitoring surveys in Vietnamese karst bat assemblages. Current Zoology 55: 327−341.

Gaisler J, Řehák Z, Bartonička T 2009. Bat casualties by road traffic (Brno-Vienna). Acta Theriologica 54: 147−155.

Griffiths SR, Bender R, Godinho LN, Lentini PE, Lumsden LF, Robert KA 2017. Bat boxes are not a silver bullet conservation tool. Mammal Review 4: 261–265.

Griffiths SR, Lentini PE, Semmens K, Watson SJ, Lumsden LF, Robert KA 2018. Chainsaw-carved cavities better mimic the thermal properties of natural tree hollows than nest boxes and log hollows. Forests 9: 235.

Hale JD, Fairbrass AJ, Matthews TJ, Sadler JP 2012. Habitat composition and connectivity predicts bat presence and activity at foraging sites in a large UK conurbation. PLoS ONE 7: e33300.

Harrison ME, Boonman A, Cheyne SM, Husson SJ, Marchant NC, Struebig MJ 2012. Biodiversity monitoring protocols for REDD+: can a one-size-fits-all approach really work? Tropical Conservation Science 5: 1−11.

Hayes JP 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. Journal of Mammalogy 78: 514−524.

Hayes JP, Loeb SC 2007. The influences of forest management on bats in North America. In: Lacki MJ, Hayes JP, Kurta A eds. Bats in forests: conservation and management. Baltimore, MD, The John Hopkins University Press. Pp. 207−235.

Jantzen MK, Fenton MB 2013. The depth of edge influence among insectivorous bats at forest-field interfaces. Canadian Journal of Zoology 91: 287−292.

Jones G, Teeling E 2006. The evolution of echolocation in bats. Trends in Ecology and Evolution 21: 149−156.

Jones KE, Purvis A, Gittleman JL 2003. Biological correlates of extinction risk in bats. The American Naturalist 161: 601−614.

Kalcounis-Rueppell MC, Briones KM, Homyack JA, Petric R, Marshall MM, Miller DA 2013. Hard forest edges act as conduits, not filters, for bats. Wildlife Society Bulletin 37: 571−576.

Kerth G, Melber M 2009. Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. Biological Conservation 142: 270−279.

Kitzes J, Merenlender A 2014. Large roads reduce bat activity across multiple species. PLoS ONE 9: e96341.

Kuijper DP, Schut J, van Dullemen D, Toorman H, Goossens N, Ouwehand J, Limpens HJGA 2008. Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*). Lutra 51: 37−49.

Roskov Y, Abucay L, Orrell T, Nicolson D, Bailly N, Kirk PM, Bourgoin T, DeWalt RE, Decock W, De Wever A, Nieukerken E, van, Zarucchi J, Penev L 2018. Species 2000 & ITIS Catalogue of Life, 2018 Annual Checklist. www.catalogueoflife.org/annual-checklist/2018. Leiden, the Netherlands, Species 2000, Naturalis.

Le Roux DS 2010. Monitoring long-tailed bat (*Chalinolobus tuberculatus*) activity and investigating the effect of aircraft noise on bat behaviour in a modified ecosystem. Unpublished MSc thesis. University of Waikato, Hamilton, NZ. 253 p.

Le Roux DS, Le Roux NN 2012. Hamilton City bat survey 2011–2012. Report prepared by Kessels & Associates Ltd for Project Echo. Hamilton, Project Echo and Kessels & Associates Ltd. 22 p.

Le Roux DS, Le Roux NN, Waas JR 2014. Spatial and temporal variation in long-tailed bat echolocation activity in a New Zealand city. New Zealand Journal of Zoology 41: 21–31.

Lesiński G 2007. Bat road casualties and factors determining their number. Mammalia 20: 138−142.

Lesiński G 2008. Linear landscape elements and bat casualties on roads − an example. Annales Zoologici Fennici 45: 277−280.

Lesiński G, Sikora A, Olszewski A 2011. Bat casualties on a road crossing a mosaic landscape. European Journal of Wildlife Research 57: 217−223.

Lloyd BD 2001. Advances in New Zealand mammalogy 1990–2000: short-tailed bats. Journal of the Royal Society of New Zealand 31: 59−81.

Lloyd DB 2005. Lesser short-tailed bat. In: King CM ed. The handbook of New Zealand mammals. 2nd edn. Melbourne, Australia, Oxford University Press. Pp. 110−126.

Luo J, Siemers BM, Koselj K 2015. How anthropogenic noise affects foraging. Global Change Biology 21: 3278−3289.

Maron M, Dunn PK, McAlpine CA, Apan A 2010. Can offsets really compensate for habitat removal? The case of the endangered red-tailed black-cockatoo. Journal of Applied Ecology 47: 348–355.

Maron M, Hobbs RJ, Moilanen A, Matthews JW, Christie K, Gardner TA, Keith DA, Lindenmayer DB, McAlpine CA 2012. Faustian bargains? Restoration realities in the context of biodiversity offset policies. Biological Conservation 155: 141–148.

Mathews F, Roche N, Aughney T, Jones N, Day J, Baker J, Langton S 2015. Barriers and benefits: implications of artificial night-lighting for the distribution of common bats in Britain and Ireland. Philosophical Transactions of the Royal Society of London B: Biological Sciences 370: 20140124.

Matthews T 2015. Waikato Expressway: Tamahere−Cambridge Section bat management plan (stage two: main works). Report prepared by AECOM for HEB Construction Ltd.

McGregor M, Matthews K, Jones D 2017. Vegetated fauna overpass disguises road presence and facilitates permeability for forest microbats in Brisbane, Australia. Frontiers in Ecology and Evolution 5: 153−162.

Medinas D, Marques JT, Mira A 2013. Assessing road effects on bats: the role of landscape, road features, and bat activity on road-kills. Ecological Research 28: 227−237.

Meyer CFJ 2015. Methodological challenges in monitoring bat population- and assemblage-level changes for anthropogenic impact assessment. Mammalian Biology − Zeitschrift Fur Saugetierkunde 80: 159−169.

Meyer CFJ, Kalko EKV, Kerth G 2009. Small-scale fragmentation effects on local genetic diversity in two

Phyllostomid bats with different dispersal abilities in Panama. Biotropica 41: 95–102.

Mickleburgh SP, Hutson AM, Racey PA 2002. A review of the global conservation status of bats. Oryx 36: 18−34.

Mitchell-Jones AJ 2004. Bat mitigation guidelines. Peterborough, UK, English Nature.

Moore GE 2001. Use of Kinleith Forest by native New Zealand bats and effects of forestry. Unpublished Master of Science thesis. Massey University, Palmerston North, New Zealand. 256 p.

Morris AD, Miller DA, Kalcounis-Rüeppell MC 2010. Use of forest edges by bats in a managed pine forest landscape. Journal of Wildlife Management 74: 26−34.

MOT 2018. Annual fleet statistics 2015. Wellington, NZ, Ministry of Transport. 64 p.

Norberg UM, Rayner JMV 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London, Series B 316: 335−427.

NZTA 2016. Research and data. New Zealand Transport Agency. http://www.nzta.govt.nz/roads-and-rail/research-and-data (accessed 13/12/2016).

O'Connor G, Green R 2011. A review of bat mitigation in relation to highway severance. Contract report from The Halcrow Group Ltd to the UK Highways Agency.

O'Donnell CFJ 2000a. Distribution, status and conservation of long-tailed bat (*Chalinolobus tuberculatus*) communities in Canterbury, New Zealand. Unpublished Report for Environment Canterbury, New Zealand.

O'Donnell CFJ 2000b. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity on the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). New Zealand Journal of Zoology 27: 207−221.

O'Donnell CFJ 2002. Timing of breeding, productivity and survival of long-tailed bats *Chalinolobus tuberculatus* (Chiroptera: Vespertilionidae) in cold-temperate rainforest in New Zealand. Journal of Zoology 257: 311−323.

O'Donnell CFJ 2005. New Zealand long-tailed bat. In: King CM ed. The handbook of New Zealand mammals. 2nd edn. Melbourne, Australia, Oxford University Press. Pp. 98−109.

O'Donnell CFJ 2009. Population dynamics and survivorship in bats. In: Kunz TH, Parsons S eds. Ecological and behavioural methods for the study of bats. 2nd edn. Baltimore, MD, The Johns Hopkins University Press. Pp. 158−176.

O'Donnell CFJ 2014. Setting up a long-tailed bat management prescription at a new site. Advice note DOCDM-1444273. Christchurch, NZ, Department of Conservation.

O'Donnell CFJ, Langton S 2003. Power to detect trends in abundance of long-tailed bats (*Chalinolobus tuberculatus*) using counts on line transects. Science for Conservation 224. Wellington, NZ, Department of Conservation. 19 p.

O'Donnell CFJ, Sedgeley JA 2006. Causes and consequences of tree cavity roosting in a temperate bat, *Chalinolobus tuberculatus*, from New Zealand. In: Zubaid A, McCracken GF, Kunz TH eds. Functional and evolutionary ecology of bats. New York, NY, Oxford University Press. Pp. 308–328.

O'Donnell CFJ, Christie JE, Simpson W 2006. Habitat use and nocturnal activity of lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in temperate rainforest. New Zealand. Journal of Zoology 33: 113–124.

O'Donnell CFJ, Christie JE, Hitchmough RA, Lloyd B, Parsons S 2010. The conservation status of New Zealand bats, 2009. New Zealand Journal of Zoology 37: 297–311.

O'Donnell CFJ, Edmonds H, Hoare JM 2011. Survival of PIT-tagged lesser short-tailed bats (*Mystacina tuberculata*) through a pest control operation using the toxin pindone in bait stations. New Zealand Journal of Ecology 35: 291−295.

O'Donnell CFJ, Pryde MA, van Dam-Bates P, Elliott GP 2017. Controlling invasive predators enhances the long-term survival of endangered New Zealand long-tailed bats (*Chalinolobus tuberculatus*): implications for conservation of bats on oceanic islands. Biological Conservation 214: 156–167.

O'Donnell CFJ, Borkin KM, Christie JE, Lloyd B, Parsons S, Hitchmough RA 2018. Conservation status of New Zealand bats, 2017. New Zealand Threat Classification Series 21. Wellington, NZ, Department of Conservation. 4 p.

O'Shea TJ, Ellison LE, Stanley TR 2011. Adult survival and population growth rate in Colorado big brown bats (*Eptesicus fuscus*). Journal of Mammalogy 92: 433−443.

OICA (Organisation Internationale des Constructeurs d'Automobiles) 2016. World vehicles in use: 2014 figures. http://www.oica.net/category/vehicles-in-use (accessed 16/12/2016).

Parsons S 1997. Identification of New Zealand bats (*Chalinolobus tuberculatus* and *Mystacina tuberculata*) in flight from analysis of echolocation calls by artificial neural networks. Journal of Zoology 253: 447−456.

Popa-Lisseanu AG, Bontadina F, Ibáñez C 2009. Giant noctule bats face conflicting constraints between roosting and foraging in a fragmented and heterogeneous landscape. Journal of Zoology 278: 126−133.

Pryde MA, O'Donnell CFJ, Barker RJ 2005. Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): implications for conservation. Biological Conservation 126: 175−185.

Pryde MA, Lettink M, O'Donnell CFJ 2006. Survivorship in two populations of long-tailed bats (*Chalinolobus tuberculatus*) in New Zealand. New Zealand Journal of Zoology 33: 85−95.

Pullin AS, Knight TM 2009. Doing more good than harm: building an evidence-base for conservation and environmental management. Biological Conservation 142: 931−934.

Roberts K, Sjölund A 2015. Incorporating biodiversity issues into road design. In: van der Ree R, Smith DJ, Grilo C eds. Handbook of road ecology. Chichester, UK, Wiley-Blackwell. Pp. 27–31.

Roedenbeck IA, Fahrig L, Findlay CS, Houlahan JE, Jaeger JA, Klar N, Kramer-Schardt S, Van der Grift EA 2007. The Rauischholzhausen agenda for road ecology. Ecology and Society 12: 11−31.

Rowse EG, Harris S, Jones G 2016. The switch from low-pressure sodium to light-emitting diodes does not affect bat activity at street lights. PLoS ONE 11: e0150884.

Russ JM, Briffa M, Montgomery WI 2003. Seasonal patterns in activity and habitat use by bats (*Pipistrellus* spp. and *Nyctalus leisleri*) in Northern Ireland, determined using a driven transect. Journal of Zoology 259: 289−299.

Russell AL, Butchkoski CM, Saidak L, McCracken GF 2009. Road-killed bats, highway design, and the commuting ecology of bats. Endangered Species Research 8: 49−60.

Rydell J, Racey PA 1995. Street lamps and the feeding ecology

of insectivorous bats. Symposia of the Zoological Society of London 67: 291−307.

Safi K, Kerth G 2004. A comparative analysis of specialization and extinction risk in temperate-zone bats. Conservation Biology 18: 1293−1303.

Sagot M, Chaverri G 2015. Effects of roost specialization on extinction risk in bats. Conservation Biology 29: 1666−1673.

Santos SM, Carvalho F, Mira A 2011. How long do the dead survive on the road? Carcass persistence probability and implications for roadkill monitoring surveys. PLoS ONE 6: e25383.

Schaub A, Ostwald J, Siemers BM 2008. Foraging bats avoid noise. Journal of Experimental Biology 211: 3174−3180.

Scrimgeour J, Beath A, Swanney M 2012. Cat predation of short-tailed bats (*Mystacina tuberculata rhyocobia*) in Rangataua Forest, Mount Ruapehu, Central North Island, New Zealand. New Zealand Journal of Zoology 39: 257−260.

Scrimgeour J, Molles L, Waas JR 2013. Vertical variation in flight activity of the lesser short-tailed bat in podocarp and beech forests, Central North Island, New Zealand. New Zealand Journal of Ecology 37: 193−198.

Sedgeley JA 2003. Roost site selection and roosting behaviour in lesser short-tailed bats (*Mystacina tuberculata*) in comparison with long-tailed bats (*Chalinolobus tuberculatus*) in Nothofagus forest, Fiordland. New Zealand Journal of Zoology 30: 227−241.

Sedgeley JA 2012. Bats: counting away from roosts − automatic bat detectors Version 1.0: Inventory and monitoring toolbox: bats series DOCDM-590733. Christchurch, NZ, Department of Conservation.

Sedgeley JA, O'Donnell CFJ 1999. Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. Biological Conservation 88: 261−276.

Sedgeley JA, O'Donnell CFJ 2004. Roost use by long-tailed bats in South Canterbury: examining predictions of roost-site selection in a highly fragmented landscape. New Zealand Journal of Ecology 28: 1−18.

Semrl M, Presetnik P, Gregorc T 2012. First proper 'after construction' monitoring in Slovenia immediately reveals bats (Chiroptera) as highway casualties. Presentation at 2012 Intra Eco Network Europe International Conference: Safeguarding Ecological Functions Across Transport Infrastructure. October 21–24, Potsdam, Germany. Swedish Biodiversity Centre.

SÉTRA (Service d'études sur les transports, les routes et leurs aménagements) 2009. Bats and road transport infrastructure: threats and preservation measures. Sétra Information notes – Economics Environment Design Serie n° 91 S Sétra ÉTRA CETE de l'Est, CETE Normandie-Centre. [Translated 2011.]

Siemers BM, Schaub A 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. Proceedings of the Royal Society of London B: Biological Sciences 278: 1646–1652.

Slater FM 2002. An assessment of wildlife road casualties – the potential discrepancy between numbers counted and numbers killed. Web Ecology 3: 33–42.

Smith D, Borkin K, Jones C, Lindberg A, Davies F, Eccles G 2017. Effects of land transport activities on New Zealand's endemic bat populations: reviews of ecological

and regulatory literature. New Zealand Transport Agency Research Report 623. Wellington, NZ, New Zealand Transport Agency. 146 p.

Smith GC, Agnew G 2002. The value of 'bat boxes' for attracting hollow-dependent fauna to farm forestry plantations in southeast Queensland. Ecological Management and Restoration 3: 37–46.

Spellerberg IF, Morrison T 1998. The ecological effects of new roads – a literature review. Science for Conservation 84. Wellington, NZ, Department of Conservation. 55 p.

StatsNZ 2015. 2013 Census QuickStats about transport and communications. Statistics New Zealand. http://www.stats.govt.nz/Census/2013-census/profile-and-summary-reports/quickstats-transport-comms/number-motor-vehicles.aspx (accessed 13/12/2016).

Stone EL, Jones G, Harris S 2009. Street lighting disturbs commuting bats. Current Biology 19: 1123–1127.

Stone EL, Jones G, Harris S 2012. Conserving energy at a cost to biodiversity? Impacts of LED lighting on bats. Global Change Biology 18: 2458–2465.

Stone EL, Jones G, Harris S 2013. Mitigating the effect of development on bats in England with derogation licensing. Conservation Biology 27: 1324–1334.

Stone EL, Harris S, Jones G 2015. Impacts of artificial lighting on bats: a review of challenges and solutions. Mammalian Biology-Zeitschrift für Säugetierkunde 80: 213–219.

Stone EL, Wakefield A, Harris S, Jones G 2015. The impacts of new street light technologies: experimentally testing the effects on bats of changing from low-pressure sodium to white metal halide. Philosophical Transactions of the Royal Society of London B: Biological Sciences 370: 20140127.

Taylor BD, Goldingay RL 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. Wildlife Research 37: 320–331.

Teixeria FZ, Coelho AVP, Esperandio IB, Kindel A 2013. Vertebrate road mortality estimates: effects of sampling methods and carcass removal. Biological Conservation 157: 317–323.

Toth CA, Cummings G, Dennis TE, Parsons S 2015. Adoption of alternative habitats by a threatened, 'obligate' forest-dwelling bat in a fragmented landscape. Journal of Mammalogy 96: 927–937.

Turbill C 2008. Winter activity of Australian tree-roosting bats: influence of temperature and climatic patterns. Journal of Zoology 276: 285–290.

Turner R 2014. Alan Turner Memorial Bridge: assessment of effects on native bats. Report prepared by Andrew Stewart, New Zealand for Waikato District Council.

UK Highways Agency 2008. Interim advice note 116/08: nature conservation advice in relation to bats. Available at: http://www.standardsforhighways.co.uk/ha/standards/ians/pdfs/ian116.pdf.

van der Grift EA, van der Ree R, Fahrig L, Findlay S, Houlahan J, Jaeger JA, Klar N, Francisco Madrinan L, Olson L 2013. Evaluating the effectiveness of road mitigation measures. Biodiversity and Conservation 22: 425–448.

van der Ree R, Jaeger JA, van der Grift EA, Clevenger AP 2011. Effects of roads and traffic on wildlife populations and landscape function: road ecology is moving toward larger scales. Ecology and Society 16: 48.

van der Ree R, Smith DJ, Grilo C 2015. The ecological effects of linear infrastructure and traffic: challenges and opportunities of rapid global growth. In: van der Ree

R, Smith DJ, Grilo C eds. Handbook of road ecology. Chichester, UK, Wiley-Blackwell. Pp. 1–9.

Ward AI, Dendy J, Cowan DP 2015. Mitigating impacts of roads on wildlife: an agenda for the conservation of priority European protected species in Great Britain. European Journal of Wildlife Research 61: 199–211.

White EP 2004. Factors affecting bat house occupancy in Colorado. The Southwestern Naturalist 49: 344–349.

Williams BK, Nichols JD, Conroy MJ 2002. Analysis and management of animal populations. San Diego, CA, Academic Press.

Wray S, Reason P, Wells D, Cresswell W, Walker H 2006. Design, installation, and monitoring of safe crossing points for bats on a new highway scheme in Wales. In: Irwin CL, Garrett P, McDermott KP eds. Proceedings of the 2005 International Conference on Ecology and Transportation. Raleigh, NC, Center for Transportation and the Environment, North Carolina State University. Pp. 369–379.

Yoccoz NG, Nichols JD, Boulinier T 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution 16: 446–453.

Zurcher AA, Sparks DW, Bennett VJ 2010. Why did the bat not cross the road? Acta Chiropterologica 12: 337–340.