Acta Chiropterologica, 21(2): 321–329, 2019
PL ISSN 1508-1109 © Museum and Institute of Zoology PAS
doi: 10.3161/15081109ACC2019.21.2.007

More traffic, less bat activity: the relationship between overnight traffic volumes and *Chalinolobus tuberculatus* activity along New Zealand highways

Kerry M. Borkin[1, 2, 3], Des H. V. Smith[1], William B. Shaw[1], and Joanna C. McQueen[1]

[1]*Wildland Consultants Ltd, PO Box 7137, Te Ngae, Rotorua 3042, New Zealand*
[2]*Present address: Department of Conservation, PO Box 1146, Rotorua 3040, New Zealand*
[3]*Corresponding author: E-mail: kborkin@doc.govt.nz*

Despite a growing body of evidence worldwide that bats are affected by roads, there has been little research into the effects of traffic volume on bat activity. In New Zealand, there is considerable uncertainty over whether, or to what extent, roads affect New Zealand's endemic bat populations, and this has resulted in uncertainty during the planning and consent phases of road development projects. This research investigated whether *Chalinolobus tuberculatus* (long-tailed bat) activity correlates with night-time traffic volume on New Zealand's highways. Bat activity was monitored at 57 traffic monitoring sites throughout New Zealand using pairs of bat detectors, with one placed beside the highway (highway) and one placed ≥ 200 metres from the highway (distant). Generalised linear mixed effects models were used to investigate the relationship between bat detections, position in relation to the highway, and various measures of traffic volume. The model that best explained the variation in bat detections was the interaction effect between bat detector position (highway, distant) and night-time traffic volume (volume). Outputs from this model show a negative relationship between bat activity and night-time traffic volume for highway bat detector units, while distant bat detector units had no discernible relationship with night-time traffic volume. These results indicate that night-time traffic volume affects the use of roads by bats, i.e. when overnight traffic increased, the probability of detecting bats decreased. Whether or to what extent this will affect the long-term viability of New Zealand's *C. tuberculatus* populations is a high priority for further investigation.

Key words: acoustic monitoring, detection rates, *Chalinolobus tuberculatus*, long-tailed bat, traffic volume, roads

Introduction

There is a growing body of evidence that bats are affected by the construction and operation of roads (Altringham and Kerth, 2016). Effects include deaths due to collisions between vehicles and bats (Lesiński *et al.*, 2010; Iković *et al.*, 2014); loss of habitat available for bats to roost within, forage and commute along (Altringham and Kerth, 2016); fragmentation of populations (because roads act as barriers — Bennett *et al.*, 2013); and increased disturbance by noise (West, 2016) and light (Stone *et al.*, 2009; Smith *et al.*, 2017). In some cases these effects appear to be species-specific (Kitzes and Merenlender, 2014) and habitat-specific (Pourshoushtari *et al.*, 2018). However, there has been little investigation into whether these impacts vary with traffic volume. We used *Chalinolobus tuberculatus*, (the New Zealand long-tailed bat) a vespertilionid, as a model species to investigate the effects of overnight traffic volume on bats.

Chalinolobus tuberculatus is an edge-adapted species (O'Donnell, 2000; O'Donnell *et al.*, 2006; Borkin and Parsons, 2009) considered to be vulnerable to extinction; classified as Threatened-Nationally Critical by the Department of Conservation (New Zealand Government) and the International Union for Conservation of Nature (O'Donnell, 2008; O'Donnell *et al.*, 2018). These bats are central-place foragers, and as such their distribution is limited by the need to return to a roost each day (Daniel and Williams, 1984; Sedgeley and O'Donnell, 1999, 2004; Borkin and Parsons, 2011*a*, 2011*b*). In the past, they have been thought to be relatively resilient to landscape changes because of their presence in a diverse range of habitats, including indigenous forest, exotic plantation forests (Borkin and Parsons, 2010), agricultural areas (Sedgeley and O'Donnell, 2004), and on the edges of urban areas (Dekrout *et al.*, 2014). However, there is now concern about the veracity of this assumption, with long-tailed bats recorded at lower rates where the density of roads, street lights, and housing is higher (Le Roux and Le Roux, 2012). Bat records have also been shown to decline with distance from forested areas (Smuts-Kennedy, 1994), and *C. tuberculatus* have been injured and killed, at least occasionally, when their roosts have been felled (Borkin and Parsons, 2010) or they have been hit by vehicles (Moore, 2001).

Chalinolobus tuberculatus are known to commute and forage along remote forestry roads and roads that bisect their habitat in national parks (O'Donnell, 2000; Borkin and Parsons, 2009). D. S. Le Roux (in litt.) provided some evidence that activity of *C. tuberculatus* reduces with proximity to roads, and this is supported by overseas' research which has found that activity of other bat species declines closer to roads (Berthinussen and Altringham, 2012; Kitzes and Merenlender, 2014). If roads are acting as barriers to bat movement, then they could be resulting in the fragmentation of bat populations. However, it remains unknown what factors associated with roads may limit bat activity. Traffic volume could be an important consideration; particularly given that traffic volumes have increased in many parts of the world over the past few decades (van der Ree *et al*., 2011), including New Zealand.

The aim of this study was to investigate the relationship between *C. tuberculatus* activity and traffic volumes along roads and highways in New Zealand. Given that long-tailed bats are known to forage along forest edges, including quiet sections of forest roads and private roads (O'Donnell, 2000; O'Donnell *et al*., 2006; Borkin and Parsons, 2009), road impacts may be related to traffic volume rather than the presence of a road. If traffic levels are affecting bat behaviour, then observations of bat activity will decline with increasing traffic volume. This research objective is particularly relevant given that traffic volumes in New Zealand have increased by 75% since records began in 1989 (Wen, 2015).

Materials and Methods

Traffic Volumes and Bat Activity

This research was undertaken within the austral summer and autumn between December 2015 and April 2016. Bat activity was measured by identifying bat calls recorded using automated bat detectors. Wildlife Acoustics SMZC Zero Crossing bat recorders (ZC units) used in this study have been estimated to detect bats, at 40 kHz, the peak amplitude of long-tailed bat calls, up to 38 metres from the units (I. Agranat, unpublished data).

Site Selection

We measured bat activity by locations along New Zealand's State Highways that are: (1) within known or potential long-tailed bat habitat and (2) sites where traffic volume is monitored by the New Zealand Transport Agency (Wen, 2015).

At each monitoring site, ZC bat detector units were put out in pairs, with one unit placed at the edge of the 'highway' along a forest edge, line of trees, or other linear landscape feature, while the other was placed alongside another piece of forest edge or linear landscape feature that was ≥ 200 metres 'distant' from the road. We chose this distance because Berthinussen and Altringham (2012) found that noise pollution due to roads appeared to reduce to near ambient levels at around 200 metres, and Altringham and Kerth's (2016) review of the effects of roads on bats considered that the effects of light pollution from road lighting and vehicle lights would only operate over relatively short distances. Side roads were not used for the partner ZC unit unless it was a forestry road. This is because forestry roads are usually closed to vehicles at night and bat activity along this edge would therefore not be affected by traffic at night, or only very occasionally. At some traffic monitoring sites only one pair of ZC units was deployed, while at other sites, where habitat extent allowed, more than one pair of ZC units were deployed. Where two or more pairs of ZC units were deployed along the same section of road, pairs were placed ≥ 250 metres apart (Fig. 1). This distance was chosen to ensure that bats were not simultaneously recorded at two pairs of sites, and so that between-pair distances were greater than within-pair distances.

ZC units were set to 'record at night' mode — from sunset to sunrise — for two entire nights. MetService (New Zealand weather forecasting service) weather forecasts were used to ensure that the ZC units were not used during periods of rain. Sunset and sunrise times were recorded automatically by the units. ZC unit location, distance to the road edge, and distance to the pair partner were recorded using a hand-held GPS unit. All ZC units were within two metres of the ground.

Bat Passes

A long-tailed bat pass was defined as a series of two or more calls, each with peak amplitude at or around 40 kHz, separated from other calls by a period of silence lasting at least one second (Thomas, 1988). Calls of New Zealand bats are readily distinguishable from other nocturnal sounds also recorded on bat recorders, including insects, birds, wind, and rain.

Bat calls were identified using Kaleidoscope Version 3.1.5 (Wildlife Acoustics Inc). Recordings were processed and converted from Zero Crossing file format to an audible.wav file format. Identification of calls was undertaken manually by viewing a spectrogram and/or listening to the .wav file of each recording. Call shapes (or wave forms) were defined as pulses on the spectrogram, or clicks on the corresponding audible .wav file, each with a peak amplitude at or around 40 kHz. The number of bat passes per night was tallied for each ZC unit at each site.

Traffic Volume Data

Data on traffic volume were provided by the New Zealand Transport Agency. This data was used to establish three bat activity covariates: 1) Day-time traffic volume. For day-time traffic volume we used a metric called Annual Average Daily Traffic (AADT) volume (Wen, 2015). The most recent year this was available for was 2014. These data were assumed to correlate with the traffic volumes over the study period; 2) Percentage heavy traffic volume. Percentage heavy traffic (Heavy) is an estimate of the proportion of the AADT which is deemed to comprise a heavy vehicle, i.e. greater than 3.5 tonnes for the current year (Wen, 2015). This was also available for the 2014 calendar year. These data were assumed to correlate with the traffic volumes over the study period; 3) Night-time traffic volume. A standard 'average overnight traffic per night' was determined by summing traffic that passed the count site location between 20:00 hours and 06:00 hours over seven nights during the traffic monitoring period and then calculating its mean. The seven-day traffic monitoring period utilised was closest by date to the period over which bat monitoring took place, unless traffic monitoring was continuous and the first seven days of the same month was then used. The period from 20:00 hours to 06:00 hours was chosen because this encompassed sunset times for most of the locations sampled over the summer and autumn monitoring period. These data were available for 2015–2016.

Data Analyses

Bat detection data were analysed using generalised linear mixed-effects models using the package lme4 (Bates *et al*,. 2015) in R (Ihaka and Gentleman, 1996). Models included two nested random effects: 1) transport monitoring site, and 2) bat monitoring site, i.e. each ZC pair. Initial modelling attempts assumed a negative-binomial distribution, but several models failed to converge, so a binomial distribution was used, by

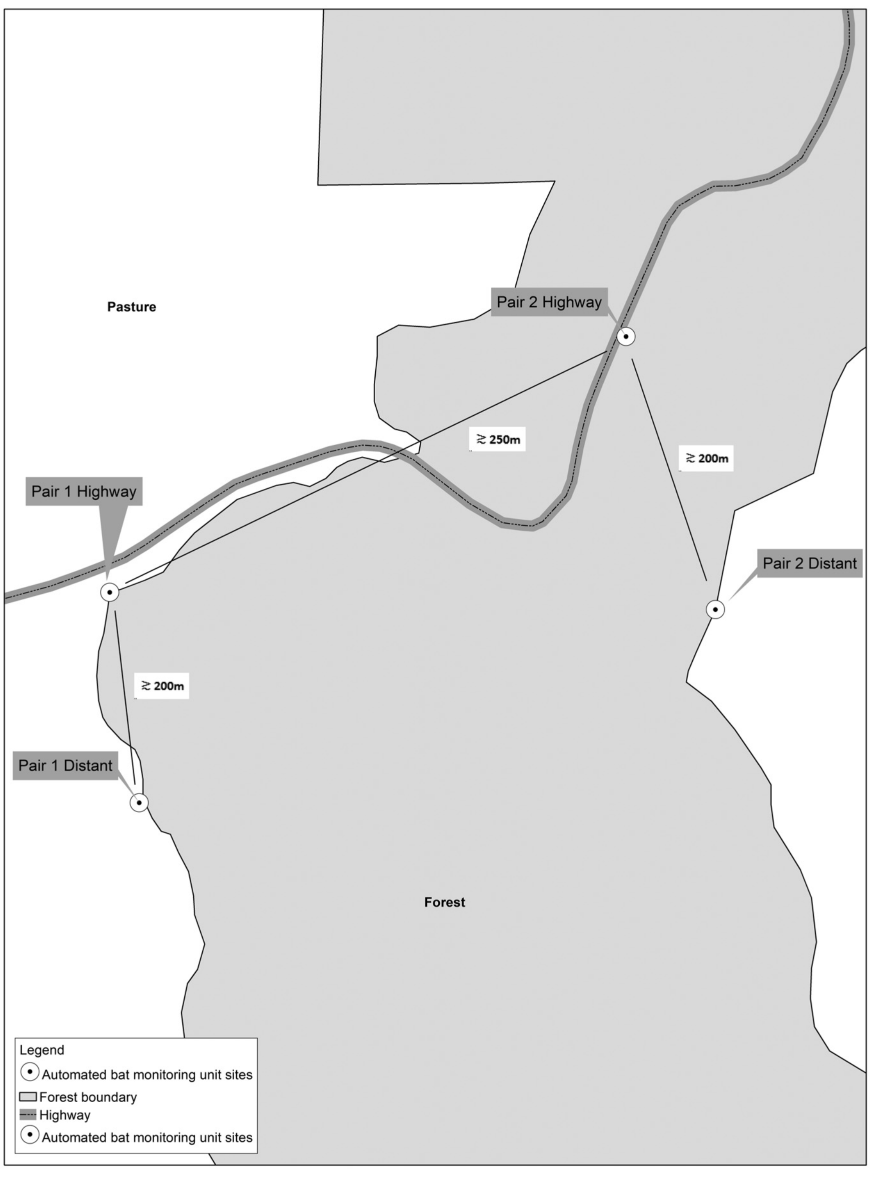

FIG. 1. Schematic diagram of bat monitoring sites along highways. All bat monitoring sites were established at locations where traffic volumes are being monitored by the New Zealand Transport Agency. At some traffic monitoring sites only one pair of bat detectors was established but, at other sites, when habitat extent allowed, more than one pair was established

simplifying the data to be either no bats (0) detected or one bat (1) detected. With the exception of % heavy traffic, data on traffic volume was log transformed.

Only sites where bats were detected at least once were modelled. This was done because we were not confident that sites where bats were not detected were occupied by bats. Addition of sites where bats were not detected, and may not have been present, leads to zero inflation in the data, and provides no additional information on the specific hypotheses that we are trying to address. We also removed one further bat monitoring site because the paired ZC units were 1.5 km apart and this was not consistent with our overall study design.

We ran models with the following fixed effects, all of which had the presence and absence of bats (BP) as the dependent variable: BP~Intercept (intercept only, no predictor), BP~Position (highway versus distant — categorical covariate), BP~Day traffic (day-time traffic volume), BP~Night traffic (night-time traffic volume), BP~Heavy (% heavy traffic), BP~Position*Day traffic (interaction), BP~Position*Night traffic (interaction), BP~Position*Heavy (interaction). All of these models had the random effect bat monitoring site nested within the random effect transport monitoring site. The models were ranked using AIC and Akaike Weights (Burnham and Anderson, 2002). The model with the smallest AIC value is considered to be the most parsimonious in the model set given the data and the number of parameters. Akaike Weights are the probability that a model is the best model in that model set (Burnham and Anderson, 2002). The intercept model is a 'null model', essentially modelling nothing, and any models that are ranked below it are considered to be uninformative.

Used Abbreviations and Acronyms

AADT — Annual Average Daily Traffic volume; AIC — Akaike information criterion; BP — presence or absence of bats; ZC — Wildlife Acoustics SMZC Zero Crossing Bat Recorders; FC — Frequency Compression Automated Bat Monitoring units produced by the New Zealand Department of Conservation; NZ Transport Agency — New Zealand Transport Agency; R — Programme used to analyse and model data; SMZC — Song Meter Zero Crossing.

Results

Between December 2015 and April 2016, 57 traffic monitoring sites were sampled across both the North and South Islands of New Zealand (Fig. 2). Within these traffic monitoring sites, a total of 108 bat monitoring sites (paired ZC units) were deployed. *Chalinolobus tuberculatus* was the only bat species detected during this study.

When bat monitoring sites where no bats were detected were removed, data remained for 39 traffic monitoring sites and 56 bat monitoring sites. Distant ZC units averaged 291 metres from the roads (± 10.75 SE), while the average highway ZC unit was 18 metres from the roads (± 1.95 SE). The sum of bat detections was 760 for distant ZC units (mean 6.6, range = 0–90) and 518 for highway ZC units ($\bar{x}$ = 4.5, range = 0–64). The median number of bat passes for distant ZC units was 1 and for highway ZC units it was 0.

For the generalised linear mixed effects models, the top model in the model set was the interaction effect between position (highway ZC, distant ZC) and night-time traffic volume, with an Akaike weight of 0.95 (Table 1). The interaction effect in this model was statistically significant ($Z = -2.89$, $P = 0.0037$). The second and third ranked models, both with Akaike weights of 0.02, were the interactions between position and % heavy traffic, and position. Position was the highest ranked individual covariate model (i.e. model without an interaction effect). This model predicts that bats are more likely to be detected at distant ZC units compared with highway ZC units (odds ratio for the highway = 0.49, odds ratio for distant = 1.76). The interaction effect between position and day-time traffic volume failed to converge.

For the top model, the coefficient describing the relationship between distant sites and night-time traffic volume was 0.05 with a SE of 0.21, indicating there was not a strong relationship between distant ZC units and night-time traffic volumes. However, the coefficient describing the relationship between highway ZC units and night-time traffic volumes was -0.73 with a SE of 0.25 (CV = 34%) indicating a negative relationship between bat detections

Table 1. Models of bat activity and traffic volume ranked using AIC. The model Position*Day traffic failed to converge, so is not presented in this table

Model	*k* (Fixed effects)	AIC	Delta AIC	Akaike weight
Position*Night traffic	4	297.30	0.00	0.95
Position*Heavy	4	304.69	7.39	0.02
Position	2	305.44	8.14	0.02
Day traffic	2	307.76	10.46	0.01
Heavy	2	307.95	10.65	0.00
Night traffic	2	308.37	11.07	0.00
Intercept	1	309.63	12.33	0.00

and night-time traffic volumes. We used the 'predict' function in R to get the predicted probabilities for each site and plotted them against night-time traffic volumes (Fig. 3). Bat activity along highways can be high when traffic rates are low (close to zero), but this activity declines rapidly as traffic rates reach ≥ 1,000 vehicles per night (Fig. 3A). In contrast, at distant sites there is no clear relationship between bat activity and night-time traffic volumes (Fig. 3B).

Discussion

Bat Responses to Traffic Volumes

The top model from our analysis predicts that, for paired monitoring devices, with one near the highway and one 200 metres or more from the highway, the distant monitoring device is more likely to detect long-tailed bats than the monitoring device near the highway. It also predicts that bat activity

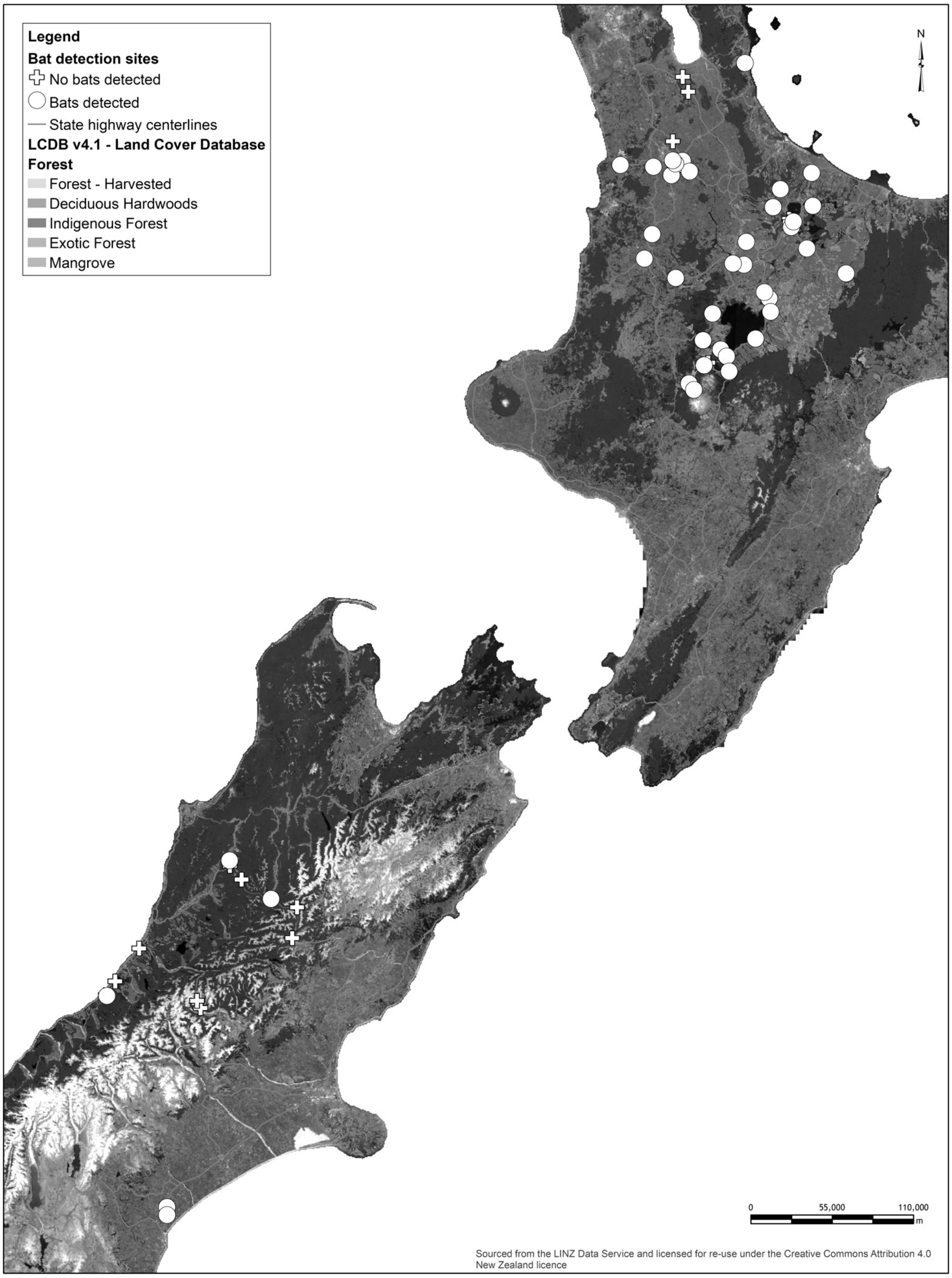

FIG. 2. Locations of bat monitoring sites used in this study

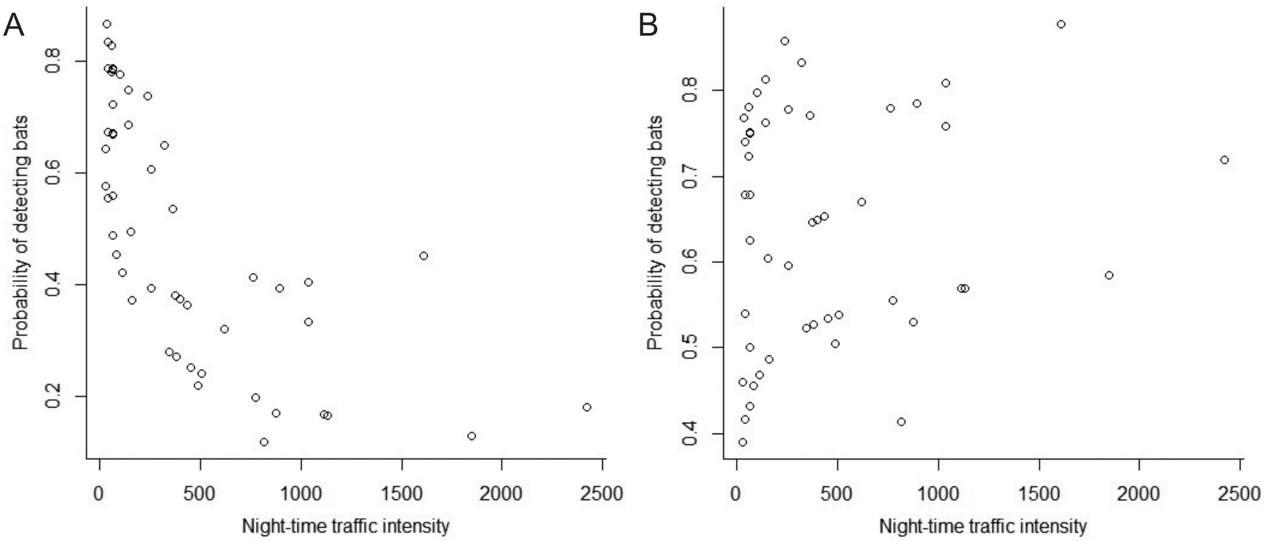

FIG. 3. Predicted probabilities from the top model plotted against night-time traffic volume for A — bat detectors closely adjacent to highways and B — bat detectors 200 metres or more from highways (distant). Night-time traffic volume is the number of vehicles using a highway between 20:00 hours and 06:00 hours

along highways will be negatively correlated with night-time traffic volume, while bat activity 200 metres away appears to be unaffected.

Our study aimed to monitor as many sites as possible with varying traffic volume. Consequently, we did not investigate how varying distance from the highway correlates with bat activity, but instead used distance as a categorical covariate (beside highway; ca. 200 metres distant from the highway). Our results show that *C. tuberculatus* activity can be high along roads with low night-time traffic volumes, but this activity can decrease to very low levels along roads with high night-time traffic volumes. Modelling of foraging activity by *Myotis sodalis* has predicted that when daily traffic volumes greater than 200 vehicles/5 min occurred a road acted as a barrier to bats (Bennett *et al.*, 2013). Bennett *et al.* (2013) found that when traffic volumes were low, roads acted as filters. That is, bat-vehicle encounters prevented bats from crossing a road but they were still able to cross the road eventually. Roads became a barrier to movement at higher traffic volumes, when bats were unable to cross the roads (Bennett *et al.*, 2013).

Establishing whether, or to what extent, this observed decline in bat activity is related to impacts on bat survival and population viability was beyond the scope of this study, but is an important next step. Forman *et al*. (2002) showed that collisions between many wildlife species and vehicles increase with increased traffic volume, vehicle speed, and proximity to wildlife corridors and habitat. However, to date, no research has specifically investigated the relationship between bat mortality rates due to roadkills and traffic volumes (Altringham and Kerth, 2016), although Fensome and Mathews (2016) commented that casualty rates appear to be higher along roads with higher traffic volumes than along low volume roads. However, if long-tailed bats respond to a threat by moving away from it at speed, then roads with high traffic volumes may be acting as substantial barriers (cf. Jacobson *et al.*, 2016).

Possible Behavioural Reasons for Declining Bat Activity at High Traffic Volumes

While traffic volumes may have direct impacts on long-tailed bat survival, it may also affect their behaviour, which may result in indirect effects. The following paragraphs consider possible mechanisms for this effect. Determination of the causal mechanisms that explain the reduction in *C. tuberculatus* activity along New Zealand highways is an important priority.

Overseas studies suggest that the effects of roads on bats may depend on the habitat preferences of the individual species (Kerth and Melber, 2009) and their tolerance of light (Lacoeuilhe *et al*., 2014) and noise (Schaub *et al*., 2008; Bennett and Zurcher, 2013). It appears that, in general, roads may be more of a barrier to bats which largely or only forage within or in very close proximity to taller vegetation, such as New Zealand's *Mystacina tuberculata* (lesser short-tailed bat), than those species which forage in open areas or edges such as *C. tuberculatus* (cf. Kerth and Melber, 2009). However, roads with low traffic volumes can act as positive filters to bat movement while high traffic roads are barriers to their movement (Abbott *et al*., 2012; Bennett *et al*., 2013). Zurcher *et al*. (2010) suggested that bats perceive vehicles as a threat and may exhibit predator avoidance behaviour in response to their presence, e.g. changing direction quickly in response to an approaching vehicle. The only study of *C. tuberculatus* that has investigated their relationship with noise suggests that they can become habituated to it, although this study only addressed aircraft noise (Le Roux and Waas, 2012). Effects of anthropogenic noise, such as traffic noise, on New Zealand's other extant bat species — *M. tuberculata* — may differ from those on *C. tuberculatus*. This is because, whilst foraging on the ground *M. tuberculata* appear to locate their prey by listening for prey-generated noises (Jones *et al*., 2003). *Antrozous pallidus* also listens for prey-generated noise whilst foraging, and has been shown to take longer to find prey in the presence of anthropogenic noise (Bunkley and Barber, 2015). Whether *C. tuberculatus* also listen for the invertebrates they depredate has not been investigated.

Edges are profitable foraging areas for *C. tuberculatus* due to the relatively high abundance of invertebrates (Pawson *et al*., 2008), protection from wind (Davies-Colley *et al*., 2000), and ease of navigation (Kalcounis-Rueppell *et al*., 2013). However, it is possible that roadside sites may become relatively unprofitable foraging areas, because foraging may need to be interrupted by the need to avoid vehicles (Zurcher *et al*., 2010; Bennett and Zurcher, 2013), and invertebrates may be affected by vehicle noise and associated light (Morley *et al*., 2014). In Europe, *Myotis daubentonii* is thought to reduce their foraging activity due to the need to avoid traffic (Luo *et al*., 2015). Modelling of foraging activity by the *Myotis sodalis* also found that foraging success was lower alongside busier roads (Bennett *et al*., 2013).

The impact of increased light associated with increased traffic rates on *C. tuberculatus* is difficult to predict without further research. This is because overseas research has shown that bats can be grouped into two groups: those that avoid artificial light and those that may be attracted to light for foraging opportunities (Lacoeuilhe *et al*., 2014). In the UK, Stone *et al.* (2009) found that *Rhinolophus hipposideros* avoided light. In Canada, however, Furlonger *et al*. (1987) observed that other bat species forage around street lights.

Lack of response of long-tailed bats at sites distant from a road to traffic volumes could be related to a reduction in traffic noise and light. The rate at which bats turn away from vehicles is thought to be related to both the noise at the location where they encounter the vehicle and the noise of the vehicle itself (Bennett and Zurcher, 2013). Bennett and Zurcher (2013) attributed increases in avoidance behaviour by bats to the disturbance threshold (a noise threshold above which bats would be more likely to reverse their route and avoid vehicles) for each particular species. They found that *M. sodalis* had a threshold of approximately 88 dBA, although this could vary between species. Research in New Zealand has found that noise produced by heavy traffic is regularly equivalent to or in excess of this threshold, although it can vary dependent on both road surface and location (Divett and Cenek, 2008). Consequently, it is possible that increased traffic volume results in higher road noise, causing bat activity near to a road to decrease. Importantly for this research, Bonsen *et al*. (2015) found that all traffic noise above 5 kHz was lost within the first 150 m from a road. This frequency does not overlap with the peak amplitude of *C. tuberculatus* echolocation calls, so traffic noise at distant sites may not affect their echolocation. The effects of light are also likely to reduce within short distances from roads (Altringham and Kerth, 2016).

We found that *C. tuberculatus* activity along New Zealand's highways is negatively correlated with night-time traffic volume. The extent to which this is driven by behaviour versus mortality is unknown, but bat activity at adjacent paired sites, ≥ 200 metres from highways, showed no relationship with night-time traffic volume. Whether, or to what extent, reductions in bat activity along highways affects the long-term viability of *C. tuberculatus* populations is a high priority for assessment. If busy highways are acting as barriers to *C. tuberculatus* populations then they may be fragmenting landscapes and resulting in bat populations becoming isolated. A further important priority is to establish the mechanisms that underpin why bat activity is lower in high traffic areas. Understanding this will help with the development of effective mitigation methods.

Acknowledgements

Field assistance was provided by Richard Gillies, Cory Toth, Brian Patrick, and Bruce Mackay of Wildland Consultants.

Richard Gillies assisted with data entry, and bat pass identification. David Greig and Carol Bannock (NZ Transport Agency) provided input and guidance and supplied the bat detectors. Bevan Percival (NZ Transport Agency) provided the traffic volume data. Colin O'Donnell (Department of Conservation) provided input into the research objectives and design. Other members of the project Steering Group are thanked for project approval and guidance: Brad Moore, Therese Balvert, Rachel Kelleher, Peter Simcock, and Tony Denton. Professors John Altringham and Darryl Jones are thanked for their peer review of this manuscript.

This research was funded and supported by the New Zealand Transport Agency. The 'steering group' for this research, which was part of a wider research programme, comprised of representatives from the New Zealand Department of Conservation; New Zealand Transport Agency (NZTA); and two territorial authorities, Hamilton City Council and Waikato Regional Council. Colin O'Donnell (bat ecologist, Department of Conservation) provided input regarding study design; NZTA and the Steering Committee played no part in the collection, analysis, and interpretation of data; in the writing of the report; and in the decision to submit the paper for publication, however permission has been given to do so.

Literature Cited

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

Altringham, J., and G. Kerth. 2016. Bats and roads. Pp. 35–62, *in* Bats in the Anthropocene: conservation of bats in a changing World (C. C. Voigt and T. Kingston, eds.). Springer, New York, 606 pp.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software, 67: 1–48.

Bennett, V. J., and A. A. Zurcher. 2013. When corridors collide: road-related disturbance in commuting bats. Journal of Wildlife Management, 77: 93–101.

Bennett, V. J., D. W. Sparks, and P. A. Zollner. 2013. Modeling the indirect effects of road networks on the foraging activities of bats. Landscape Ecology, 28: 979–991.

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

Bonsen, G., B. S. Law, and D. Ramp. 2015. Foraging strategies determine the effect of traffic noise on bats. Acta Chiropterologica, 17: 347–357.

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

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

Bunkley, J. P., and J. R. Barber. 2015. Noise reduces foraging efficiency in pallid bats (*Antrozous pallidus*). Ethology, 121: 1–6.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer Verlag, New York, xxv + 488 pp.

Daniel, M. J., and G. R. Williams. 1984. A survey of the distribution, seasonal activity and roost sites of New Zealand bats. New Zealand Journal of Ecology, 7: 9–25.

Davies-Colley, R. J., G. W. Payne, and M. van Elswijk. 2000. Microclimate gradients across a forest edge. New Zealand Journal of Ecology, 24: 111–121.

Dekrout, A. S., B. D. Clarkson, and S. Parsons. 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.

Divett, T., and P. Cenek. 2008. Quantification of noise and vibration effects arising from higher mass limits for heavy vehicles. Report produced by OPUS International Consultants Ltd for the Ministry of Transport, Wellington, New Zealand, 28 pp.

Fensome, A. G., and F. Mathews. 2016. Roads and bats: a meta-analysis and review of the evidence on vehicle collisions and barrier effects. Mammal Review, 46: 311–323.

Forman, R. T. T., D. Sperling, J. Bissonette,, A. Anthony, P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. L. France, C. R. Goldman, *et al*. 2002. Road ecology: science and solutions. Island Press, Washington, 504 pp.

Furlonger, C. L., H. J. Dewar, and M. B. Fenton. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology, 65: 284–288.

Ihaka, R., and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics, 5: 299–314.

Iković, V., M. Đurović, and P. Presetnik. 2014. First data on bat traffic casualties in Montenegro. Vespertilio, 17: 89–94.

Jacobson, S. L., L. L. Bliss-Ketchum, C. E. de Rivera, and W. P. Smit. 2016. A behaviour-based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere, 7: e01345.

Jones, G., P. I. Webb, J. A. Sedgeley, and C. F. J. O'Donnell. 2003. Mysterious *Mystacina*: how the New Zealand short-tailed bat (*Mystacina tuberculata*) locates insect prey. Journal of Experimental Biology, 206: 4209–4216.

Kalcounis-Rueppell, M. C., K. M. Briones, J. A. Homyack, R. Petric, M. M. Marshall, and D. A. Miller. 2013. Hard forest edges act as conduits, not filters, for bats. Wildlife Society Bulletin, 37: 571–576.

Kerth, G., and M. Melber. 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., and A. Merenlender. 2014. Large roads reduce bat activity across multiple species. PLoS ONE, 9: e96341.

Lacoeuilhe, A., N. Machon, J.-F. Julien, A. Le Bocq, and C. Kerbiriou. 2014. The influence of low intensities of light pollution on bat communities in a semi-natural context. PLoS ONE, 9: e103042.

Luo, J., B. M. Siemers, and K. Koselj. 2015. How anthropogenic noise affects foraging. Global Change Biology, 21: 3278–3289.

Le Roux, D. S., and N. S. Le Roux. 2012. Hamilton City bat survey 2011–2012. Report prepared by Kessels & Associates Ltd for Project Echo. Available at http://www.waikatoregion.govt.nz/assets/PageFiles/26132/2193861_Hamilton_Citywide_Bat_Survey_Report_2011_2012.pdf.

Le Roux, D. S., and J. R. Waas. 2012. Do long-tailed bats alter their evening activity in response to aircraft noise? Acta Chiropterologica, 14: 111–120.

Lesiński, G., A. Sikora, and A. Olszewski. 2010. Bat casualties on a road crossing a mosaic landscape. European Journal of Wildlife Research, 57: 217–223.

Moore, G. E. 2001. Use of Kinleith Forest by native New Zealand bats and effects of forestry. M.Sci. Thesis. Massey University, Palmerston North, New Zealand, 255 pp.

Morley, E. L., G. Jones, and A. N. Radford. 2014. The importance of invertebrates when considering the impacts of anthropogenic noise. Proceedings of the Royal Society, 281B: 20132683.

O'Donnell, C. F. J. 2000. 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, C. 2008. *Chalinolobus tuberculatus*. The IUCN Red List of Threatened Species 2008:e.T4425A10881758. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T4425A10881758.en. Downloaded on 21 February 2019.

O'Donnell, C. F. J., J. E. Christie, and W. Simpson. 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, C. F. J., K. M. Borkin, J. E. Christie, B. Lloyd, S. Parsons, and R. A. Hitchmough. 2018. Conservation status of New Zealand bats, 2017. New Zealand Threat Classification Series 21. Department of Conservation, Wellington, New Zealand, 4 pp.

Pawson, S. M., E. G. Brockerhoff, E. D. Meenken, and R. K. Didham. 2008. Non-native plantation forests as alternative habitat for native forest beetles in a heavily modified landscape. Biodiversity Conservation, 17: 1127–1148.

Pourshoushtari, R. D., B. P. Pauli, P. A. Zollner, and G. S. Haulton. 2018. Road and habitat interact to influence selection and avoidance behavior of bats in Indiana. Northeastern Naturalist, 25: 236–247.

Schaub, A., J. Ostwald, and B. M. Siemers. 2008. Foraging bats avoid noise. Journal of Experimental Biology, 211: 3174–3180.

Sedgeley, J. A., and C. F. J. O'Donnell. 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, J. A., and C. F. J. O'Donnell. 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.

Smith, D., K. Borkin, C. Jones, S. Lindberg, F. Davies, and G. Eccles. 2017. Effects of land transport activities on New Zealand's endemic bat populations: reviews of ecological and regulatory literature. NZ Transport Agency Research Report, 623: 249 pp.

Smuts-Kennedy, C. 1994. A survey of long-tailed bats (*Chalinolobus tuberculatus*) at Paradise. Diploma in Wildlife Management Thesis, University of Otago, Dunedin, New Zealand.

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

Thomas, D. W. 1988. The distribution of bats in different ages of Douglas-fir forests. Journal of Wildlife Management, 52: 619–626.

van der Ree, R., J. A. G. Jaeger, E. A. van der Grift, and A. P. Clevenger. 2011. Effects of roads and traffic on wildlife populations and landscape function: road ecology is moving towards larger scales. Ecology and Society, 16: 48.

Wen, G. 2015. State highway traffic booklet 2010–2014. New Zealand Transport Agency, New Zealand, 95 pp.

West, E. W. 2016. Technical guidance for assessment and mitigation of the effects of traffic noise and road construction noise on bats. Report No. CTHWANP-RT-15-306.04.1. Prepared for the Division of Environmental Analysis, California Department of Transportation, Sacramento, CA, 354 pp. Available at http://website.dot.ca.gov/env/noise/docs/noise-effects-on-bats-jul2016.pdf.

Zurcher, A. A., D. W. Sparks, and V. J. Bennett. 2010. Why the bat did not cross the road? Acta Chiropterologica, 12: 337–340.

Received 17 July 2019, accepted 22 October 2019

Associate Editor: Wiesław Bogdanowicz