



RESEARCH

Influence of weather on long-tailed bat detection in a North Island exotic forest

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Abstract: Accurate surveys and monitoring are required to guide the conservation and management of threatened species. Some fauna species are cryptic or difficult to observe because they are nocturnal, mimic other species, conceal themselves, or can be incredibly hard to survey. Emergence and activity of these species may be related to complex environmental cues including weather and atmospheric conditions. The conservation status of New Zealand's long-tailed bat (*Chalinolobus tuberculatus*) is Threatened-Nationally Critical. Occurrence and activity of long-tailed bats is commonly monitored with acoustic bat detectors. However, even in locations where long-tailed bats are known to be present, they may only be detected on a subset of nights meaning that detection with acoustic detectors is imperfect. We analysed long-tailed bat detection data collected in Kinleith Forest, central North Island, New Zealand in 2006 and 2007 using zero-inflated generalised linear (mixed) effect models. We found relationships between bat detection and several environmental variables. Results suggest that bat surveys would be most effective at detecting bats when undertaken one to four hours after sunset, on nights when the temperature at sunset is above 8°C, and preferably when the temperature stays in the 8 and 17°C range during the night. Higher humidity and a light breeze may also be a desirable condition for monitoring. A night that is similar to, or slightly warmer, than recent nights may be favourable. Caution should be taken extrapolating these results to elsewhere because bats in other regions may respond differently to temperatures out of necessity. High site-specific variation in bat counts at higher temperatures and humidity occurred with zero activity often recorded. Therefore, we caution against assuming bats are absent because they have not been detected by surveys undertaken during higher temperatures and humidity conditions unless surveys have been run for multiple nights in suitable conditions.

Keywords: acoustic surveys, *Chalinolobus tuberculatus*, detection rates, echolocation, humidity, New Zealand, survey design, temperature, weather

Introduction

Survey and monitoring of threatened species is a critical requirement to determine whether a species is present at a site and whether management that aims to maintain or increase population size is being effective (Buckland et al. 2000; Legge et al. 2018). Threatened species may be present in low numbers or only present at a sub-set of locations over a wide area so detection of their presence can be difficult (MacKenzie 2005). This can become more challenging when the threatened species is also hard-to-survey because they are cryptic or elusive: they may look similar to other species, be nocturnal, hide from observers either deliberately or because they are ensconced in difficult-to-observe places such as cavities in trees during the day, and they may not emerge from these places daily (McDonald 2010). However, even cryptic species can produce detectable sounds that can be distinguished from those of other species and recording of these sounds can be used to estimate abundance, density, and activity (Marques et al. 2012).

Passive acoustic detectors are being used increasingly to sample the calls of threatened species (Gibb et al. 2018). In recent years, they have been used in a variety of ways to inform conservation managers. For example, they have been used to spatially and temporally model behaviour of a threatened passerine (Metcalf et al. 2019), to better understand distribution of a threatened cryptic wetland bird (Williams et al. 2018a), and to estimate colony sizes of bats as they emerge from caves (Klopper et al. 2016). The use of passive systems that record calls of a threatened species without the need for a person to be standing alongside it interpreting the calls in real time has meant that larger areas can now be surveyed repeatedly and, over far longer periods, cost-effectively (Skalak et al. 2012; Wright et al. 2016). However, for many species, little is understood about how best to target times of year or to design monitoring programmes so that species can be detected or changes in activity observed (Law et al. 2015).

Effectiveness of survey and monitoring efforts can be improved when more is understood about the activity patterns

and detectability of the cryptic species and when monitoring is designed using this knowledge (Williams et al. 2018b). The use of appropriate equipment can further reduce costs and increase the area over which sampling of threatened species can take place (Williams et al. 2018a; Metcalf et al. 2019) when the best period to sample these species is understood. For example, efforts to monitor matuku/Australasian bittern (*Botaurus poiciloptilus*), a threatened cryptic wetland bird, have become more effective since call-rate patterns have been better understood and monitoring has been restricted to a short time period around sunrise (Williams et al. 2018a; Williams, et al. 2018b).

Worldwide, more than one third of all bat species are considered threatened or are data deficient, which is more than other mammals or birds (Frick et al. 2020). Bats often remain unobserved because they are nocturnal, are often hidden from observers during the day as they roost in cavities or under bark of trees or in caves, and may not emerge from these each day (Czenze et al. 2017). Survey and monitoring for bats often uses acoustic detectors that detect bats' echolocation calls (Skalak et al. 2012; Wright et al. 2016). For surveys (or inventory), acoustic detectors should be placed in habitat considered likely to be used by bats (Sedgeley 2012). However, the relationship between bat population size and echolocation call rates (also known as activity rates) is unclear, although it is assumed that declining activity levels should be a warning sign for a decreasing population (Law et al. 2015). This is because one bat can echolocate once or one hundred times at one location. Additionally, emergence and activity patterns can vary considerably between nights and seasons (O'Donnell 2000). This can be due to the combined influences of availability of prey and temperature (O'Donnell 2000), rain (Geipel et al. 2019), stage of the breeding cycle (Borkin 2010), social activity (Hafat et al. 2018), and whether bats even emerge from torpor (a low metabolic state) and are active and able to be detected (Geiser et al. 2011). Also, bats do not always echolocate when flying, particularly when in the presence of conspecifics (Chiu et al. 2008). Understanding drivers of activity will help improve effectiveness of survey programmes by providing direction for operators around when surveys would be more likely to detect bats, if present.

Long-tailed bats (pekapeka *Chalinolobus tuberculatus*) are endemic to New Zealand. They are an edge-adapted species (O'Donnell 2000; O'Donnell et al. 2006; Borkin & Parsons 2009) and classified as Threatened-Nationally Critical by the Department of Conservation (New Zealand government) and "Critically endangered" by the International Union for Conservation of Nature (O'Donnell 2021; O'Donnell et al. 2023). Long-tailed bats are central-place foragers, so their distribution is limited by the need to return to a roost each day (Sedgeley & O'Donnell 1999; Borkin & Parsons 2011). Previous research has found that temperature at least partially drives long-tailed bat activity, with individuals that had transmitters attached not emerging from their roosts when it was below 5°C (O'Donnell 2000; Griffiths 2007), but these studies did not take place over all months of a year.

Acoustic surveys for long-tailed bats vary in duration, often being undertaken for 10 days over periods of fine weather. Data from these surveys usually contains a high frequency of non-detections (zeros) and even at sites where bats are eventually detected there are often several nights where bat passes are not recorded at all. It is therefore difficult to conclude that long-tailed bats are not present at sites with suitable habitat even when not detected during a survey.

Projects, such as road developments, can involve the destruction of habitat that might be suitable for long-tailed bats. Provisions in the Resource Management Act (1991) and the Wildlife Act (1953) requires the presence or absence of species such as long-tailed bats to be determined at such sites before a construction project commences. If long-tailed bats are present, steps to conserve them and maintain their habitat must be incorporated into project planning (Smith et al. 2017). Failure to reliably determine the presence or absence of long-tailed bats can either put the bats at risk, or unnecessarily delay or add expense to some projects. So, it is important for surveys to take place when detection of bats is most likely.

Development of effective survey methods for long-tailed bats requires an understanding of what factors are correlated with emergence from their roosts. O'Donnell (2000) and Griffiths (2007) both identified relationships between long-tailed bat activity and temperature with emergence occurring on warmer nights (Griffiths 2007). However, more specific information on temperature thresholds and whether other variables influence emergence and detection rates would greatly assist in the development of long-tailed bat survey protocols.

The objective of this research was to analyse an existing data set from a central North Island *Pinus radiata* forest, to determine whether weather variables such as temperature, humidity, wind speed, and rain, predict long-tailed bat detection rates. If some of the variables measured do predict bat detections, then analysis may identify favourable conditions for surveys of long-tailed bats.

Methods

Data used for this analysis is from Borkin (2010). This is the first analysis of New Zealand long-tailed bat detections that spans all the months of the year. Data on temperature, relative humidity, rainfall, and wind speed were recorded in the study location and were available for correlation with bat detections. Field design and data collection was aimed at meeting the specific research objectives of Borkin (2010), but the data also provides a useful opportunity to investigate the above objective, although not collected for this purpose.

Study site

Long-tailed bat detections were recorded monthly over a year in three main habitat types: *Pinus radiata* stands, pasture, and native regenerating areas. The monitoring was undertaken within or adjacent to Kinleith Forest (37° 47' S, 175° 53' E), an exotic plantation forest comprising mainly *Pinus radiata* logged at that time using clear fell harvest on a 26–32-year cycle (Ministry of Agriculture and Fisheries 2007). Long-tailed bats roost and forage within this forest (Moore 2001; Borkin & Ludlow 2009). The study area boundaries were the Kopakorahi Stream, the Waikato River, State Highway 1, and Jack Henry Road (Fig. 1).

Data collection

Acoustic monitoring of long-tailed bats was undertaken using Automated Bat Monitoring units (ABMs; New Zealand Department of Conservation Electronics Unit, Wellington, New Zealand 2005) between December 2006 and November 2007. These units contained a heterodyne bat detector and are described in O'Donnell and Sedgeley (1994).

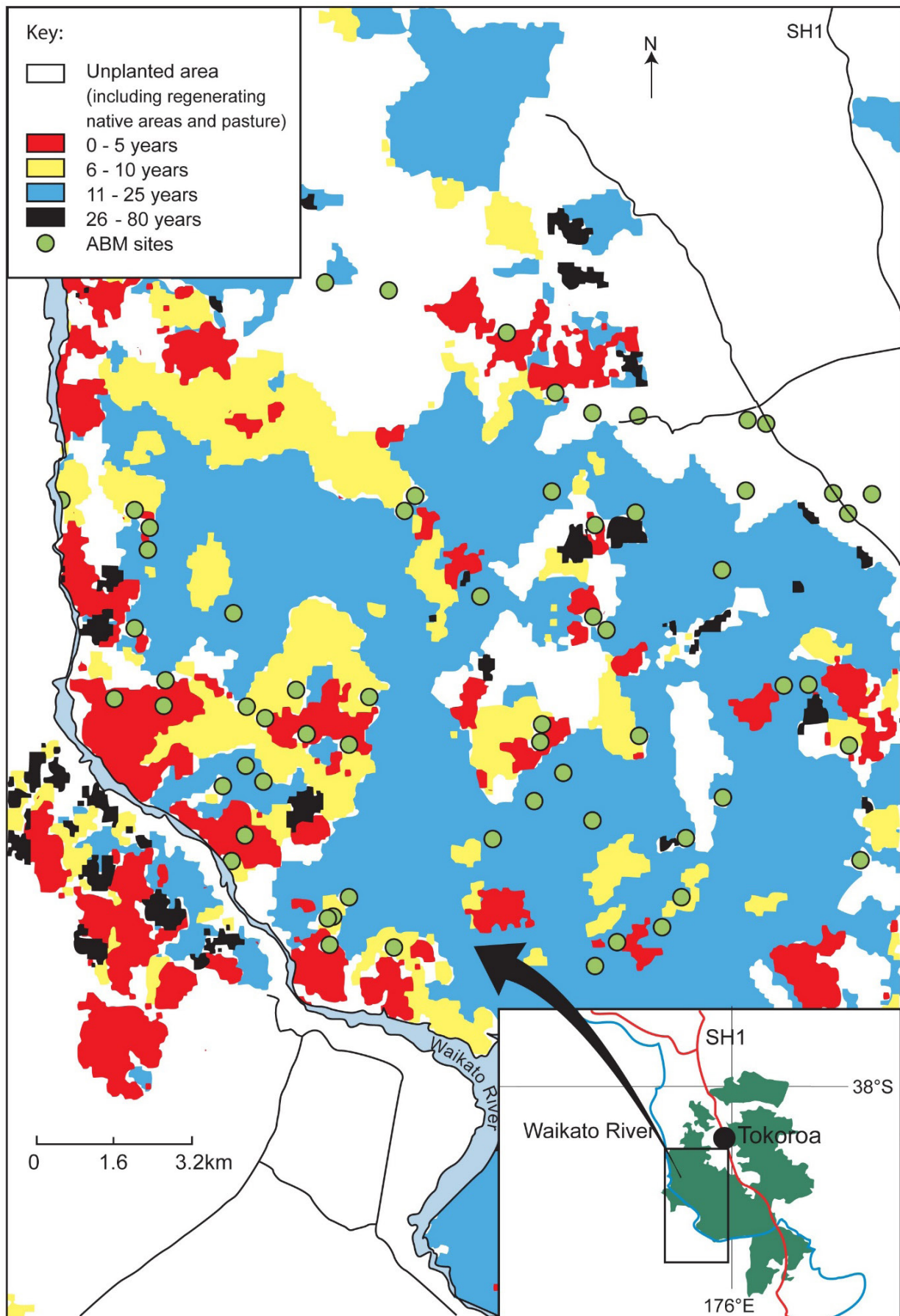


Figure 1. Automated bat monitoring unit (ABM, detector) sites within unplanted, native regenerating and pasture areas, and *P. radiata* age classes (0–5, 6–10, and 11–25 years old) and the extent of these habitats within this area of Kinleith Forest at the time of data collection.

Monitoring took place on the first five fine nights of each month that were suitable for monitoring. Monitoring did not occur on nights when rain was recorded in the first two hours after sunset. If the weather deteriorated sufficiently to disrupt data collection, monitoring was abandoned and repeated on the next available fine night. This field protocol (that omits inclement weather) means that the findings of the analysis carried out here cannot be extrapolated to include very bad weather days such as those with very high windspeeds and/or rainfall.

Monitoring began at sunset and ended at sunrise. Times of sunrise and sunset were based on the closest main centre (Tauranga) published in the New Zealand Nautical Almanac (Land Information New Zealand 2006, 2007). Different sites were monitored for each of the five nights each month; 25 sites in total were surveyed each month, but these were not always the same site. ABMs were allocated randomly to sites. Sites were chosen so that there were equal numbers of ABMs in unplanted, native regenerating and pasture areas, and across three *P. radiata* age classes (0–5, 6–10 and 11–25 years old). The native regenerating areas were young, low stature, islands of mainly modified vegetation in a matrix of *P. radiata* plantation, and largely consisted of kānuka (*Kunzea ericoides*), kōhūhū (*Pittosporum tenuifolium*), *Coprosma* spp., and makomako (*Aristolelia serrata*) with exotic weeds present at most sites and few or no mature trees.

Roads and edges were chosen as sites to place ABMs as long-tailed bats are known to use these more than forest interiors (O'Donnell 2000; Moore 2001; Griffiths 2007; Borkin & Parsons 2009). The microphone in each ABM was oriented parallel to the edge. The direction along the road or edge that the microphone was orientated was determined by tossing a coin. The types of ABMs used in this study can detect long-tailed bats that pass within 50 metres (Parsons 1996). Sites were sufficiently placed so that a long-tailed bat could not be detected simultaneously at multiple sites, so sites were considered independent.

ABMs were set to 40 kHz, which corresponds with the peak energy of long-tailed bats' echolocation calls (Parsons 2001). Calls of the other extant New Zealand bat species, *Mystacina tuberculata*, peak in energy at 28 kHz, and so echolocation calls are easily differentiated (Parsons 2001). Bat activity was quantified as the number of bat passes recorded (Appendix S1 in Supplementary Materials). One bat pass was defined as a sequence of two or more echolocation calls separated from other calls by a period of silence of at least one second (Thomas 1988).

Weather data was supplied by the Rural Fire Protection Authority from a permanent weather station (Athol Base) situated within the area being studied. Data provided for analysis included rainfall (mm), air temperature (°C), relative humidity (%), and wind speed (km h⁻¹), hourly. Maximum overnight temperature, relative humidity, and wind speed, as well as the total overnight rainfall was calculated, in addition to the previous night. Differences between the maximum overnight weather variables and the same variables for the previous night were also calculated.

Data analysis

All analyses were carried out in R version 4.1.2 (R Core Team 2021). Selection of environmental predictor variables is outlined in Appendices S2–S5 in Supplementary Material. We modelled bat passes in response to environmental variables

using zero-inflation models, which reduce problems associated with multiple zero sources (true and non-detection) and resulting overdispersion (Zuur 2009). Zero-inflation models consist of two sequential steps: (1) a zero-inflation sub-model is parameterised to distinguish true zeroes from non-detection zeroes, (2) a count sub-model is calibrated that includes a smaller subset of the zero values. We used this two-step process to build two models at two discrete temporal scales that can be important to bat surveyors. Firstly, we modelled at the scale of whole nights (hereafter: night model), which answers the question “On which night should I survey?”. In the night model the response variable was total bat passes recorded over the course of the night as predicted by weather data at larger scales, such as the total precipitation over the course of the preceding day. Secondly, we modelled at the scale of one hour (hereafter: hour model) which answers the question “At what time of the night should I survey?”. In the hour model the response variable was total bat passes recorded over the course of the hour as predicted by instantaneous weather conditions recorded hourly, such as windspeed. Both response variables and most predictor variables were poorly correlated across the two scales (Pearson's correlation coefficients: bat passes = 0.52, wind speed = 0.41, temperature = 0.83, precipitation = -0.07). We expected that hourly bat behaviour may be modulated seasonally due to life cycle stages. The hour model therefore included only data from December to April and only the first eight hours after sunset.

We built the night model using the package *pscl* version 1.5.5 (Jackman 2020), and modelled hour data in the package *glmmTMB* version 1.1.2.3 (Brooks et al. 2017). We included location as a random effect in the hour model to account for the non-independence of datapoints. All models were fitted with a Poisson distribution and a log link for the count model and a binomial distribution with a logit link for the zero-inflation model. In the case of both the night and hour models, we first calibrated a full additive model version using all uncorrelated predictors in both the zero-inflated and the count sub-models and habitat type (native forest, plantation or pasture) in the zero-inflated sub-model. Some predictors appeared to have quadratic, not linear, relationships with the response variable on visual inspection and were included as such in the model. Next, non-significant terms were dropped sequentially from the model until only significant terms remained in each sub-model. To ensure we had considered the most parsimonious solution, we calibrated several additional simpler model structures. These included structures where quadratic terms and terms with small absolute coefficient estimates were dropped.

All model structures for each data type were compared to one another and to a null model that excluded the zero-inflation portion (Appendices S6–S7). Models were compared using Akaike's Information Criterion (AIC; Sakamoto et al. 1986) and r-squared values where possible using the package *performance* version 0.8.0 (Lüdecke et al. 2021). In addition, we used log likelihood ratio tests in the function *lrtest* in the package *lmtree* version 0.9-39 (Zeileis & Hothorn 2002) as well as the Vuong's non-nested hypothesis test in the *pscl* package (Vuong 1989) for the night models.

Results

Fit models

Night model

The best performing night model ($R^2 = 0.74$) is presented in Fig. 2. The zero-inflation portion of the model was of the form:

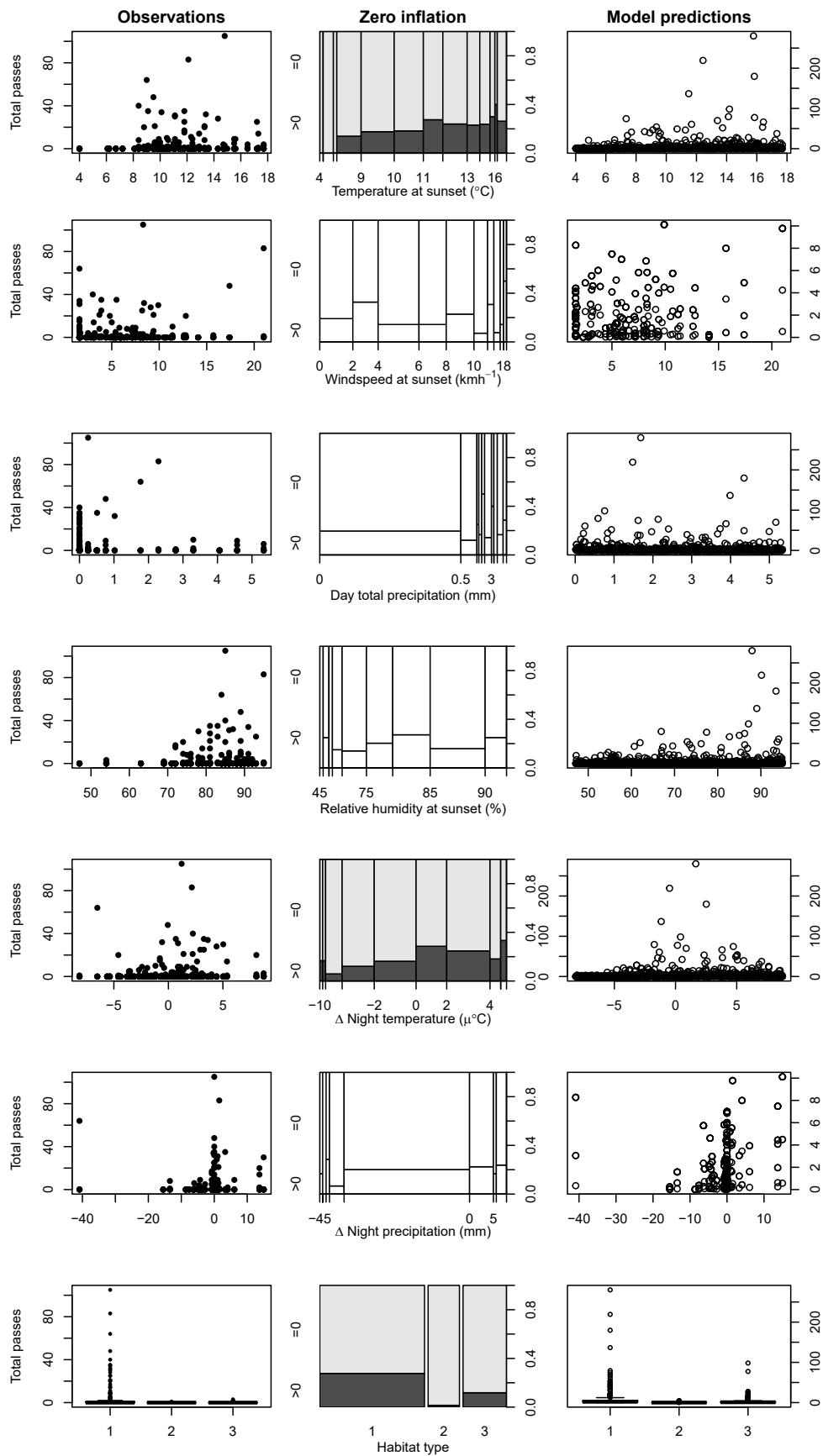


Figure 2. Effect of environmental variables on recorded nightly bat passes. Environmental variables include both absolute measurements, and changes in the variable from the preceding night (denoted by Δ); the full definition of each predictor is provided in the model structure. For each environmental variable, presented from left to right: field observations, zero inflation sub-model results (this graph is presented in white where the variable is not a significant predictor), and count model predictions. Habitat types are (1) plantation forests, (2) pasture, and (3) regenerating native areas.

$$\Sigma passes \sim TSS + T\Delta + Habitat \quad (1)$$

And the count portion of the model was of the form:

$$\Sigma passes \sim poly(TSS) + WSSS + Rain_{\Sigma d} + RHSS + poly(T\Delta) + poly(Rain\Delta) \quad (2)$$

Where (1) $\Sigma passes$ = sum of all bat passes over the night of the observation, (2) TSS = temperature at sunset on the day of the observation, (3) $T\Delta$ = mean temperature on the night of the observation minus mean temperature on the preceding night, (4) $WSSS$ = windspeed at sunset on the day of the observation, (5) $Rain_{\Sigma d}$ = the total precipitation (mm) over the preceding day, (6) $RHSS$ = relative humidity at sunset on the day of the observation, (7) $Rain\Delta$ = total rain on the night of the observation minus total rain on the preceding night, and (8) ‘poly’ indicates a polynomial (quadratic) relationship.

Hour model

The best performing hour model (conditional $R^2 = 0.63$; Fig. 3) had a zero-inflation portion of the form:

$$Passes_h \sim Habitat \quad (3)$$

And the count portion of the model was of the form:

$$Passes_h \sim poly(T_h) + WS_h + poly(H) + 1|Location \quad (4)$$

Where (1) $Passes_h$ = number of bat passes in the hour of the observation, (2) T_h = the temperature recorded at the hour of observation, (3) WS_h = the windspeed at the hour of the observation, (4) H = the number of hours since sunset, (5) $1|Location$ indicates that ABM location was used as a random variable, (6) Estimated parameters, standard errors, and t -values for each model are provided in Appendix S6.

Predictions

Night model

The baseline odds of not detecting bats when bats may really be present (i.e., a false zero) were high. For every night and location with a bat detection 11.7 nights are expected that are false zeros (predictions of odds are presented as exponentiated parameter estimates for the hurdle model).

Rates of detection increased on warmer nights. The odds of non-detection decreased by 0.88 for each 1°C increase in temperature at sunset (-0.13 ± 0.05 (parameter estimate and standard error), $p = 0.01$). False zeroes were particularly likely

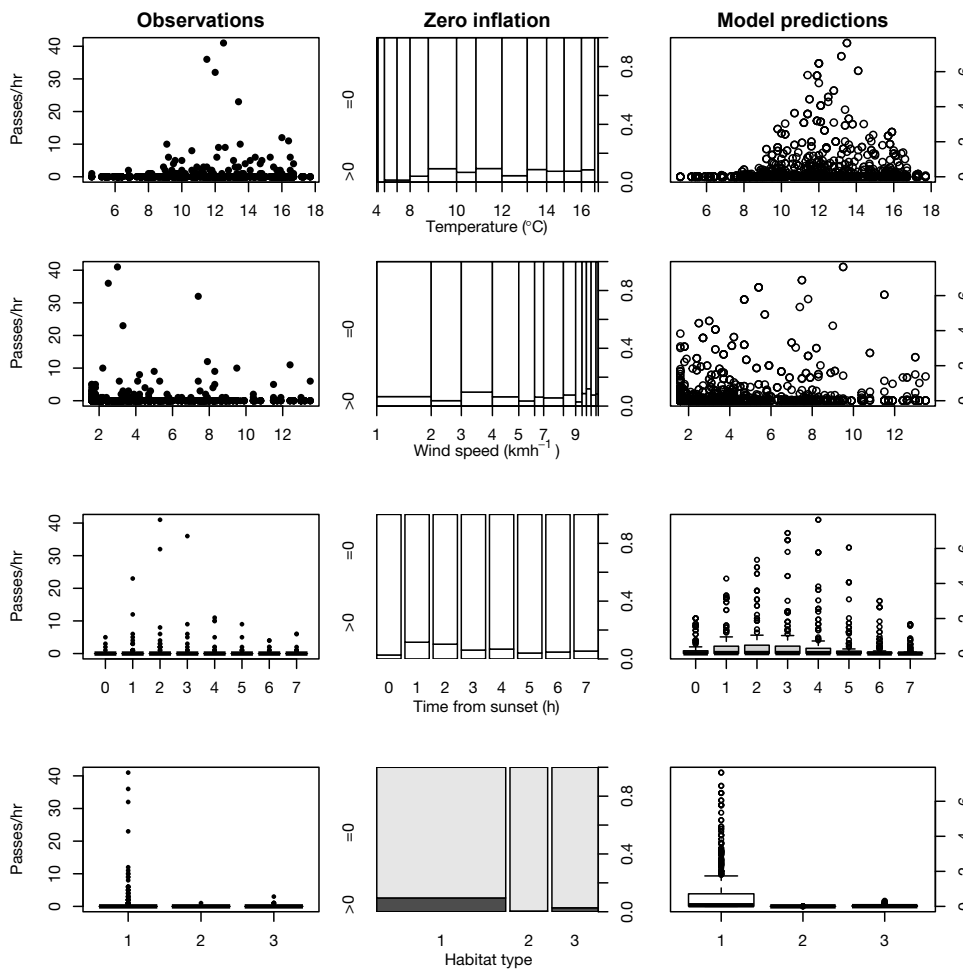


Figure 3. Effect of environmental variables on recorded hourly bat passes. The full definition of each predictor is provided in the model structure. For each environmental variable, presented from left to right: field observations, zero inflation sub-model results (this graph is presented in white where the variable is not a significant predictor), and count model predictions. Habitat types are (1) plantation forests, (2) pasture, and (3) regenerating native areas.

when the temperature was below 8°C. Similarly, chances of detection are increased on nights that are warmer than the preceding night. For every 1°C warmer than the night is than the preceding night the odds of non-detection reduce by 0.91 (-0.09 ± 0.05 , $p = 0.04$).

Habitat has a large impact on non-detections. The chances of false zeros are highest in plantation forest, lower in regenerating native areas, and highly unlikely in pasture. Relative to plantation forest, the odds of a false zero is reduced by 2.98 (1.09 ± 0.36 , $p < 0.01$) and 27.36 (3.31 ± 1.02 , $p < 0.01$), for regenerating native areas and pasture respectively.

Models incorporating polynomial terms have coefficients that are difficult to interpret so polynomial coefficients are not reported here. Instead, we provide a description of relationships. Fewer bat passes were predicted when temperature at sunset was below 8°C or above 14°C (polynomial relationship, $p < 0.01$). Higher windspeeds at sunset had a small positive effect on the number of bat passes predicted over the night (0.03 ± 0.01 , $p < 0.001$) over the range considered. The total rain over the day had a negative relationship with bat pass counts (-0.11 ± 0.04 , $p < 0.01$), although higher relative humidity at sunset was associated with slightly higher bat pass counts (0.03 ± 0.01 , $p < 0.001$). We predict most bat passes on nights with similar or slightly warmer temperatures relative to the preceding night (polynomial relationship, $p < 0.001$); when a night was $> 2^\circ\text{C}$ colder or $> 5^\circ\text{C}$ warmer than the preceding night, fewer bat passes were recorded. Differences in overnight rain relative to the preceding night affected bat pass counts (polynomial relationship, $p < 0.001$), with highest counts when precipitation levels are similar to the preceding night.

Hour model

The baseline odds of bat non-detections in the hour model were much lower. For every hour when bats are detected, 3.9 hours are expected at that same site that are false zeros. This is likely because, as expected, location (i.e. site), which was included as a random effect, explained a substantial amount of variance (4.54; standard deviation = 2.13).

Only habitat type significantly impacted bat non-detection (false zeroes). Bat non-detections were most likely in plantation forest, and significantly less likely in pasture (odds reduce by 15.21; 2.72 ± 1.29 , $p = 0.03$). There was a non-significant reduction in bat non-detection in regenerating native areas relative to plantation forest (0.51 ± 0.62 , $p = 0.41$).

The count sub-model indicated that temperature, wind speed, and hours from sunset determined how many bat passes were recorded (the count sub-model). Bat passes within a given hour were most likely to occur when the temperature was between 8 and 17°C (as a polynomial, $p < 0.001$), with the greatest reductions in bat passes expected when temperatures were very low. Higher windspeeds were associated with slight increases in bat pass numbers (0.09 ± 0.03 , $p < 0.001$) over the range of windspeeds encountered during the survey ($1.6\text{--}29\text{ km h}^{-1}$). Finally, time from sunset determined how many bat passes were detected (as a polynomial, $p < 0.001$), with bat detections peaking two hours after sunset i.e., 120–180 minutes after sunset.

Discussion

Little is known about what drives long-tailed bats to emerge from their roosts and forage at certain sites on certain nights. O'Donnell (2000) and Griffiths (2007) observed that long-

tailed bat emergence and activity was related to temperature with the latter study noting a 5°C threshold below which long-tailed bats would not emerge. Our research provides nuance to the trend identified by previous work that temperature is a key driver of detection rates and expands on the finding by showing that other environmental variables are also important determinants of bat activity patterns.

Our research also reinforces the importance of vegetation—exotic or native—for long-tailed bats. Despite long-tailed bats being observed foraging and commuting over pasture elsewhere (Dekrout 2009), this was the least likely habitat for bats to be detected within in this study, followed by islands of native regenerating areas with few or no mature trees, then plantation forest. Borkin's (2010) analyses of the same data found that most activity in plantation forest was within the oldest stands; typically, the oldest vegetation remaining in the landscape.

On which night should I survey?

We show that bat detection on a given night is most likely when temperature at sunset is above 8°C and on nights that are warmer than the preceding night. Interestingly, temperature at sunset was the only environmental variable considered that determined whether bats were detected on a given night; both the absolute temperature and whether the preceding night was warmer or cooler determined detection rates. However, the number of detections were further explained by relative humidity at sunset, windspeed, and total rainfall overnight relative to the previous day. Nights with very low windspeeds or very high temperatures had fewer bat detections. Although bat activity reduced after rainy days, humid nights had more bat detections. The amount of bat activity also depended on environmental conditions in the context of earlier weather; the highest numbers of detections occurred on nights with similar or slightly warmer temperatures relative to the preceding night and when precipitation levels are similar to the preceding night.

Understanding which nights are likely to be best to survey for bats is crucial if surveys are to be effective at detecting bats where they occur. Surveys that take place during periods when temperatures are low or on nights when the weather is particularly inclement are likely to be less reliable for bat detection, but may still detect bats. In Fiordland long-tailed bats flew in temperatures are cold as -1.5°C (O'Donnell 2000), we detected bats flying on nights with temperatures as low as 8.4°C at sunset when temperatures had dropped as low as 5.6°C during the day. Our dataset avoided particularly inclement weather, but we expect that bats would be detected at lower temperatures. Despite O'Donnell's (2000) comments that previously published studies were incorrect when they suggested that long-tailed bats hibernate for several months over winter (e.g. Daniel & Williams 1981), this continues to be repeated in the unpublished literature and in public talks. We highlight that we, along with other researchers, detected bats each month we collected data (O'Donnell 2000; Griffiths 2007; Borkin & Parsons 2009). We expect that the lower detections found on cooler or more inclement nights reflect a response by bats to the lower availability of invertebrates (O'Donnell 2000; Griffiths 2007), a greater use of torpor (O'Donnell 2000; McNab & O'Donnell 2018), and an earlier return to roosts on nights when temperatures are cooler (Griffiths 2007).

Detection rates of bats are also likely to vary with the location of the caller and habitat. Bats that are closer to detectors are more likely to be recorded (Freeze et al. 2021). When detectors are placed in habitat with high levels of clutter, bats

are less likely to be detected because their calls are blocked, reflected, or distorted by objects between the bat and the detector (Freeze et al. 2021). Given that we chose to place ABMs on roads and edges in all habitat types in our study, we expect this has had little effect on detection variability in our case, apart from along the edges of native regenerating areas which were relatively cluttered compared to other habitat types (Borkin 2010).

The rate at which bat calls attenuate varies with the speed of sound and atmospheric attenuation, so this may affect detection rates, but the exact relationship depends on the frequency at which bats call (Pettersson 2004; Goerlitz 2018). Both the speed of sound and atmospheric attenuation differ with weather conditions, particularly temperature and relative humidity (Pettersson 2004; Goerlitz 2018). Atmospheric attenuation reaches a maximum at high temperatures and low-medium humidities with lower rates at higher relative humidities and lower temperatures (Goerlitz 2018). We suspect that this means that for long-tailed bats, which call at a peak amplitude of 36–40 kHz (O'Donnell & Borkin 2021), detections observed at higher relative humidities, whether these are warm or cool, are an underestimate of the true number of calls made on humid nights. On warmer nights call attenuation is also likely to be high (Goerlitz 2018), and long-tailed bat call rates may be underestimated. We recommend, therefore, that weather variables are considered when attempting to infer changes in activity rates over time and that these are included in modelling or, at the very least, reported.

At what time of the night should I survey?

This work also gives a more granular picture of the time of night when monitoring may be most effective. While bats show diurnal cycles in activity, with activity peaking 120–180 minutes after sunset at our site, environmental variables also play a role. The number of bat detections was highest while the temperature was between 8 and 17°C, and when there was a slight breeze. Based on data collected in Fiordland's Eglinton Valley, where temperatures are cooler than our study site, O'Donnell (2000) recommended that surveys for long-tailed bats should focus on the first two hours after sunset to maximise the chance of detecting bats. Our research, using data collected in the Central North Island, found detections peaked later in the night than in Fiordland. We suggest, therefore, that to deal with this variability between locations, survey periods be extended to include the first four hours after sunset, although surveys for entire nights remain highly recommended.

The findings of this study support O'Donnell's (2000) caution that detectability of bats may vary between locations and situations. This study, therefore, contributes to developing national survey standards for long-tailed bats by determining patterns in bat detectability. However, a number of limitations should be kept in mind when interpreting these results. Firstly, these results are from one location over one year, and we stress caution extrapolating them to other regions of New Zealand. We encourage replication of this research to determine whether these trends are consistent across regions and years. Secondly, the data used in this analysis were collected using a protocol that specifically involved the avoidance of inclement weather. Further studies could explore the effects of high precipitation and wind on bat detectability. Thirdly, we did not test for interactions between environmental variables which may further explain peaks in bat detections. Finally, while this study shows that environmental variables can determine both whether, and how many, bat passes are

recorded, zeroes were nevertheless also recorded across the full range of environmental conditions. Long-tailed bats are not always detected, even when the weather appears suitable. Consequently, single-night surveys are not appropriate for determining the presence or absence of long-tailed bats.

So why does long-tailed bat detection data contain so many zeroes, even during seemingly favourable conditions? Although seasonal changes in behaviour account for some of the variation, it does not account for all of it. Borkin and Parsons (2009) suggested that it is necessary to survey sites with ABMs for a minimum of three nights to enable a reasonable chance of detecting long-tailed bats at a given site and it has been suggested that this may be because long-tailed bats use different parts of their range on different nights. We found high odds of not detecting bats even though we knew bats were really present in our survey area (false zeros). Our results support extending surveys over longer periods, or repeating these, to be more confident survey results are accurate. If bats do use different parts of their home range on different nights, then personnel undertaking long-tailed bat surveys designed to determine whether bats are present at a location should deploy arrays of ABMs over much larger areas than are generally currently surveyed. The spatial extent of an ABM array should reflect the extent of possible movements of long-tailed bat social groups. Research would be required to determine the size and density of an ABM array, but once it has been determined, detection of long-tailed bats on any one of the ABMs within the array would count as a detection for the entire array. This would reduce the likelihood of non-detection of bats at sites where they are both present and active. For example, in Fiordland *Nothofagus* forest, 50 long-tailed bats from three social groups, with overlapping collective foraging areas, ranged over 11 700 hectares (O'Donnell 2001). In Kinleith Forest, individual long-tailed bat home range spans were as large as 16 kilometres across (K Borkin, pers. obs). In this research, we placed ABMs over an area of approximately 16.5 × 14.0 km. Clearly, arrays of ABMs (if collectively viewed as one monitoring unit) should reflect these scales of movements, otherwise monitoring lacks independence and is therefore pseudo-replicative.

Future research could benefit from consideration of other statistical methods and survey equipment. For example, it is also necessary to determine how many nights of surveying is required at optimal temperatures to be confident that bats are unlikely to be present if they are not detected. An approach such as occupancy modelling (MacKenzie et al. 2006) could be useful for this but would require a study that used successive repeat surveys of sites to collect data that could then be used to estimate a probability of detection. This would allow the use of the following equation to estimate the survey effort required to provide a given level of confidence of detecting long-tailed bats if they are present (Tyre et al. 2003):

$$(1-p)^n \quad (5)$$

Where p is probability of detection and n is the number of surveys. It was not possible to use the data from Kinleith Forest in an occupancy analysis because data was collected once per month.

The use of passive acoustic recorders, which are relatively low cost, and easy-to-operate, has revolutionised bat surveys and monitoring in recent years (Klopper et al. 2016). Acoustic recorders have been used to determine species presence, composition, and activity for a wide range of fauna including bats (Law et al. 2015), birds (Williams et al. 2018a; Metcalf

et al. 2019), and marine mammals (Marques et al. 2012). Occupancy modelling of data collected using acoustic recorders has also been suggested as a tool for other threatened vocal, or detectable, species (Metcalf et al. 2019). Law et al. (2015) considered that, for bats, where the number of calls recorded is low then occupancy may be a more reliable indicator of change in population than activity rates. However, care is required when analysing data as Wright et al. (2016) caution that inappropriate modelling resulting in incorrect inferences can be costly for conservation efforts, suggesting it is essential to use model assessment tools when using this method. We suggest that the use, and appropriateness, of occupancy modelling for New Zealand bats and other threatened species should be investigated further.

We analysed detection data for long-tailed bats collected over one year within Kinleith Forest and found that the detectability of bats was determined by several environmental variables. Our results provide nuance to earlier analyses by O'Donnell (2000) and Griffiths (2007) which found temperature to be important. In addition, we found correlations between bat detection rates and wind speed, precipitation, and relative humidity. We suggest that bat surveys focus on the first four hours after sunset, on nights when the temperature at sunset is above 8°C, and preferably when the temperature stays in the 8 and 17°C range. Higher humidity and a light breeze may also be a desirable condition for surveying. A night that is similar to, or slightly warmer than, recent nights may be favourable. Survey periods should extend to at least the first four hours after sunset during nights when the weather is better than those previous, although surveying for entire nights remains highly recommended. Caution should be taken extrapolating these results to elsewhere because bats in other regions may respond differently to temperatures out of necessity. Long-tailed bat detection rates were highly variable even during apparently ideal conditions and we express caution in assuming bats are not present because they were not detected when using ABMs during a higher temperature or higher humidity night. In the central North Island and surrounding regions, several nights of surveying at these temperatures will be necessary to establish whether long-tailed bats are present. Given that the costs of sampling for longer periods using passive automated acoustic detectors do not increase substantially, apart from the costs of analyses (Skalak et al. 2012), provided no additional visits are required to replace batteries or download data, sampling over longer periods is recommended if populations are likely to be small or areas used infrequently. It would be useful to determine the number of survey nights needed to confirm bat presence or absence during suitable weather conditions. Such a study would require surveying to be undertaken over several nights in suitable conditions.

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Additional Information and Declarations

Conflicts of interest: The authors declare no conflicts of interest. Forestry companies, Waka Kotahi and the Steering Committee played no part in the collection, analysis, and interpretation of data, or in the writing of the report and in the decision to submit the paper for publication; however, permission has been given to do so.

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Data and code availability: Anonymised data and the R code used in the analyses are provided as supplementary files.

Author contributions: KMB conceived the idea, designed the study, and carried out data collection. KMB, DHVS, and JWM obtained funding. KMB, DHVS, and JG carried out analyses, and wrote the manuscript, with editorial contributions from JWM.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Sampling effort and bat passes at each survey location.

Appendix S2. Predictor selection—night model.

Appendix S3. Correlations among the predictor variables considered in this analysis for the night model.

Appendix S4. Predictor selection—hour model.

Appendix S5. Correlations among the predictor variables considered in this analysis for the hourly model.

Appendix S6. Model selection statistics.

Appendix S7. Parameters within each final model and supporting test statistics.

Appendix S8. Data and code (provided as *2n* .csv and *1n* .R files).

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