Vertical variation in flight activity of the lesser short-tailed bat in podocarp and beech forests, Central North Island, New Zealand

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Abstract: Designing robust monitoring programmes for cryptic species is particularly difficult. Not detecting a species does not necessarily mean that it is absent from the sampling area. A conclusion of absence made in error can lead to misguided inferences about distribution, colonisation and local extinction estimates, which in turn affects where and how conservation actions are undertaken. It is therefore important to investigate monitoring techniques that reduce the non-detection rate of cryptic species. As habitat complexity plays an important role in the activity of bats within a forest, it was hypothesised that the amount of vegetative 'clutter' present at different heights within two different forest types affected the flight activity of lesser short-tailed bats (*Mystacina tuberculata*). This could affect detection of the species within different forest structures. To compare bat activity at three heights – top (22.0–25.0 m), middle (10.0–12.0 m) and bottom (1.5–2.0 m) – within a podocarp and a beech forest we used automatic bat monitors during January to March 2005. The number of bat passes was recorded at each height at two study areas within each forest and compared between forest types. The forest structure was described using the Recce method and vegetative cover estimated within the three height tiers sampled for bat activity. Within both forest types, the middle-level bat detectors logged the greatest amount of activity. However, differences between the forest types were most pronounced closer to the ground, where a high amount of activity was detected within the beech forest, and very little within the podocarp forest. This suggests that flight activity of lesser short-tailed bats may be affected by the level of vegetative clutter found at different heights within a forest. When designing monitoring programmes for lesser short-tailed bats, it is recommended that consideration be given to the forest structure and how this may affect detection of bat activity.

Keywords: automatic bat monitors; bat activity; bat flight; clutter; forest structure; monitoring; *Mystacina tuberculata*; vertical stratification

Introduction

For any conservation management programme to be successful, accurate and reliable information on the species in question is required, so that increased understanding of their ecology, behaviour and population dynamics can be used to optimise management decisions. Designing robust monitoring programmes for a cryptic taxonomic group such as bats is particularly difficult, since only a small portion of the population present may be detected in a survey due to their nocturnal behaviour, scarcity, patchy distribution and limitations in current bat monitoring techniques (Kalko 1995; Kuenzi & Morrison 1998). Not detecting a species does not necessarily mean that it is absent from the sampling area (Wintle et al. 2004; MacKenzie 2005). A conclusion of absence made in error can lead to misguided inferences about distribution, colonisation and local extinction estimates (MacKenzie 2005), that in turn affects where and how conservation actions are undertaken. It is therefore important to investigate monitoring techniques that reduce the non-detection rate of cryptic species.

The lesser short-tailed bat (*Mystacina tuberculata*) is one of only two extant species of bat in New Zealand. Populations are found in large stands of old-growth forest, and occur in both podocarp and beech forests (Lloyd 2001). Evaluating the status of lesser short-tailed bats through surveying and monitoring is listed as a high priority for the management of

the species (Molloy 1995). Typically, distribution surveys have involved the use of automatic bat monitors (ABMs), placed on the ground and directed towards potential flight paths. Most studies on bat activity globally have focused solely on sampling at ground level (e.g. Francis 1990; Fenton et al. 1998; Cosson et al. 1999; Estrada & Coates-Estrada 2002). Until recently, technical constraints have limited our ability to study how bats use vertical space (Kalcounis et al. 1999). Studies that have incorporated canopy sampling have found that there is a significant difference in activity between ground and canopy levels for some species (Francis 1994; Bernard 2001). It is now commonly recognised that there can be a strong vertical stratification in activity not only within bat communities where certain species are found at specific heights within the forest (Francis 1994; Kalcounis et al. 1999; Bernard 2001; Kalko & Handley 2001), but also within species (Hecker & Brigham 1999).

Habitat characteristics, such as degree of openness in the forest storey and canopy, and the size and number of forest gaps, can greatly affect where bats forage and fly (Fullard et al. 1991; McKenzie et al. 1995; Carmel & Safriel 1998; Sleep & Brigham 2003). The specialised use of different forest levels from ground to canopy by various species of bats suggests that the structural complexity of the forest is an important factor influencing bat activity. O'Neill and Taylor (1986) observed a vertical stratification in flight activity between five different

bat species in Tasmania, and suggested that this may have been related to a change in the density of vegetation with height above ground. Thus, the two slowest, most manoeuvrable species spent a large proportion of time in the lower, denser layer of the forest, whereas the two fastest flyers spent most of their time in the more open zones of the upper layer. Similarly, Law and Chidel (2002) found that activity of several bat species was negatively related to clutter. Clutter is broadly defined here as objects including leaves, branches, tree trunks and rocks that impede flight and echolocation.

Bats have to manage the physical challenge of spatial clutter, avoiding collisions with obstacles, while minimising energy-demanding manoeuvres (Schnitzler & Kalko 2001). The vegetation within cluttered environments provides not only physical obstacles, but also acoustic attenuation (Fullard et al. 1991). Within clutter, there tends to be multidirectional reflections of echolocation calls, which may complicate discrimination of prey echoes from background echoes (Brigham et al. 1997). It is, therefore, not unexpected that bat activity decreases with an increase in forest structural complexity.

We hypothesised that detection of the lesser short-tailed bat was likely to be influenced by the structural complexity of the forest type being sampled. For instance, descriptions of flight activity of lesser short-tail bats within a beech forest in the central North Island suggested that they fly in the relatively clear layer below the canopy but above the understorey, in this instance 2–5 m above the ground (Lloyd 2001). It is likely that ground-based detectors would successfully detect bats flying at that level. However, where the forest structure differs, bats may have to fly at different heights to access uncluttered flight paths, reducing our ability to detect them with ground-based detectors. This can be important when bats are found in low densities within the sampling area, increasing the likelihood of non-detection.

The aim of our study was to examine the flight activity of lesser short-tailed bats in two different forest types, to determine whether bats fly at different heights in response to different forest structure. Because habitat complexity plays an important role in the activity of bats within a forest (Fullard et al. 1991; McKenzie et al. 1995; Carmel & Safriel 1998; Sleep & Brigham 2003), it was hypothesised that fewer bats would be detected at heights where clutter was prominent. Understanding the flight activity of lesser short-tailed bats in response to vegetative clutter can aid in refining monitoring techniques.

Method

Study site

The study took place in the North Island within two types of New Zealand native forest – a podocarp forest at Pureora Forest Park (38°30' S, 175°30' E) and a beech forest in Rangataua Conservation Area, on the slopes of Mount Ruapehu, Ohakune (39°23' S, 175°30' E).

Pureora Forest Park (78 000 ha) straddles the Hauhungaroa Range west of Lake Taupo and east of Te Kuiti. It is one of the last remnants of the Central North Island mixed podocarp forest. Rimu (*Dacrydium cypressinum*), tōtara (*Podocarpus totara*) and miro (*Prumnopitys ferruginea*) frequently emerge over broadleaved trees or form the canopy themselves. Within Pureora, the Pikiariki Ecological Area (457 ha) was selected for sampling on the basis of the known presence of bats within the area.

The beech forest study areas were located within old-growth *Nothofagus* spp. forest that extended from Ohakune Mountain Road in the west to the Karioi pine plantation in the east; a large population of bats is known to exist here (Lloyd 2001). The forest encompassed Rangataua Forest Conservation Area (10 000 ha) and part of the Tongariro National Park. The forest is dominated by red (*Nothofagus fusca*) and silver beech (*N. menziesii*) throughout most of the area, with other species such as mountain beech (*N. solandri* var. *cliffortioides*) occasionally found.

Procedure

Two sites within each forest type were selected for bat sampling. In Pureora, due to the small size of the reserve area, the sampling sites were approximately 1 km apart. In Rangataua, the two sampling sites were separated by about 4 km. ABMs were placed in the branches of two trees (at least 200 m apart) at each site.

Seven ABMs were provided by the Department of Conservation, Wellington, and were rotated systematically across heights, trees, sites and forest types. Each ABM consisted of one bat detector (Batbox III, Stag Electronics, UK) linked to a Voice Activated Recorder (VAR) (Sanyo TRC 1196, Japan), in addition to a timer (Grasslin 24Hours Time Switch, Grasslin Controls Corporation, USA) and a talking clock (Voicer Talking Key Chain, Dick Smith Electronics, NZ). These were packed within a waterproof screw-top box (27.0 × 19.0 × 13.5 cm high) along with a 12 V, 7 Ah lead acid battery. Prior to deployment, the ABMs were calibrated using a 28 kHz sound source to standardise sensitivity.

A slingshot was used to shoot a line over a branch on each of the designated trees, to which a pulley (Zenith 20-mm Awning Pulley, ITW Proline, Australia) system was attached for hoisting the ABMs to three different levels: top (22.0–25.0 m above ground), middle (10.0–12.0 m above ground) and bottom (1.5–2.0 m above ground). Bat detectors were sensitised to 28 kHz, which corresponds to the peak amplitude of echolocation pulses in the lesser short-tailed bat (Parsons 1997); the timer was set to begin recording at c. 30 min before sunset and end at c. 30 min before dawn.

To maximise detection of bats ABMs were orientated toward the direction with the fewest obstructions (Weller & Zabel 2002). Once orientated, side ropes anchored the line in that position. At each forest type, four nights of recordings were obtained before the boxes were collected and moved to the next study area. Data included in analyses were collected between 7 January and 14 March 2005, and included only those nights when all three ABMs were operational. Owing to inclement weather and equipment failure, the number of nights per cycle and the number of cycles varied between forest types (Table 1).

A single listener analysed all recordings. A bat pass was considered to have occurred when a series of two or more clicks was heard from the recording (separated by a one-second silence). The number of bat passes was recorded for each hour of the night corresponding to each height level. The results were taken as an index of bat activity, rather than an absolute number of bats; a series of passes in an hour may have been produced by one or many bats.

The Reconnaissance (Recce) method was used to describe the vegetation structure of each forest type (Allen 1992). Recce descriptions have been widely used throughout New Zealand and are stored in the National Vegetation Survey Databank (NVS) at Landcare Research, Lincoln. Four plots

Table 1. Schedule of successful recordings from three automatic bat monitors at each site in Rangataua Conservation Area (beech forest) and Pureora Forest Park (podocarp forest) between January and March 2005.

Forest	Site	Tree	Nights
Beech	1	1	4
	1	2	4
	2	1	3
	2	2	4
Podocarp	1	1	5
	1	2	7
	2	1	4
	2	2	5

were established in podocarp forest where bat activity had been detected; two plots at two different sites were averaged to provide one set of cover values per area. Recce plots had been completed within the beech forest in the past and these were obtained from NVS to compare against plots completed within the podocarp sites. The NVS plots were completed in 1996 and therefore considered recent enough to be comparable. Four plots in the same areas as sites used for sampling bat activity were selected for comparison with the podocarp sites. Within each 20 × 20 m plot, the height range (in metres) and the foliage cover of each species (as a percentage of the sky above the plot blocked by foliage) within each height tier were estimated. The percentage cover for each species was summed to obtain an indication of total foliage cover for each height tier. Note that the sum of the estimates when added resulted in more than 100% cover in some instances, and these figures were used as an indicative comparison of cover. To correspond with heights at which bat monitoring occurred, cover was estimated in three tiers: 0.30–2 m (bottom), 5–12 m (middle) and 13–25 m (top). Data collected for the 2–5 m height tier were not analysed as they did not correspond with the placement of an ABM.

Statistical analysis

The package lme4 (Bates et al. 2011) in the statistical program R (R Development Core Team 2011) was used for all analyses. We used generalised linear mixed models to examine whether (1) the number of recorded bat passes and (2) vegetation cover varied with forest type and height tier. For the bat pass model, data for only three cycles, matched as closely as possible by date, were used from each site. This model initially included forest type (podocarp or beech), detector height (top, middle or bottom), cycle, and two- and three-way interactions of these three variables as fixed effects; individual ABM, tree within site, and cycle for given tree (to account for repeated measures from specific trees) were included as random effects. Number of bat passes was square-root transformed prior to analysis (infrequent observations with high numbers of passes skewed the raw data). The initial model for vegetation cover included forest type, height and their interaction as fixed effects, with forest type as a random effect to account for non-independence of measures from three height levels.

Because cover data were not related to specific bat sampling sites, we could not use sites as replicates to analyse the effects of vegetative cover on bat activity. Instead, we calculated the mean percentage cover and mean number of bat passes at the top, middle and bottom height tiers in each of the two forest types to investigate the relationship between cover and bat activity; data from all cycles (3–7 per site) were included in this analysis. This model for bat passes included forest type, cover and height as fixed effects, with forest type as a random effect to account for non-independence of data from the three height levels. All models were fitted using maximum likelihood parameter estimation and progressively simplified by removing fixed effects with $P > 0.1$ until no further variables could be removed without significantly affecting model fit (as determined by likelihood ratio tests). Significance of effects remaining in final models was also determined by likelihood ratio tests; significant increases in deviance when effects are removed indicate the effects' predictive value. All tests were two-tailed with $P \leq 0.05$ considered significant. Data are presented as mean ± SE.

Results

Forest type and detector height significantly affected bat activity (forest type: $\chi^2 = 112.56$, d.f. = 1, $P < 0.0001$; detector height: $\chi^2 = 25.57$, d.f. = 2, $P < 0.0001$; means for combinations of forest type and height are shown in Fig. 1). More bat passes were detected at beech (65.0 ± 7.7 per night) than at podocarp sites (22.6 ± 3.4 per night) with a particularly pronounced difference at the bottom tier (Fig. 1). No other effects remained
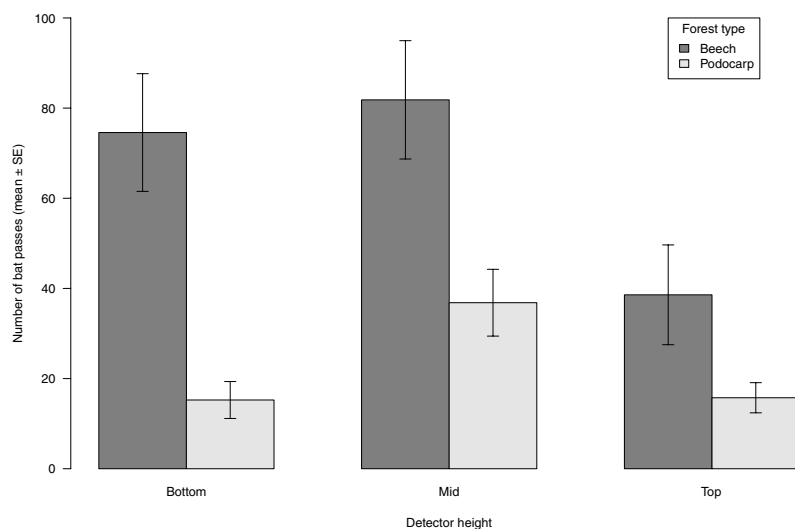

Figure 1. Mean number (±SE) of passes by lesser short-tailed bats (*Mystacina tuberculata*) recorded at three detector heights (bottom, middle and top) within a beech forest (dark grey bars) and podocarp forest site (light grey bars). Untransformed data are shown.

in the final model.

Vegetation cover was also significantly affected by the interaction of forest type and height level (χ^2 = 15.70, d.f. = 2, P = 0.0039) along with the two components of the interaction (forest type: χ^2 = 28.97, d.f. = 1, P < 0.0001; height level: χ^2 = 9.61, d.f. = 2, P = 0.0082). Within the podocarp forest the bottom height had notably more vegetative cover compared with the other two levels, and compared with the bottom level of the beech forest. Conversely, within the beech forest, the top level had most vegetative clutter compared with the other two levels, although there was no significant difference between the podocarp and beech forest types at that height.

The final model, analysing whether bat passes were affected by vegetative cover (incorporating forest-type average values), included only cover; bat activity was negatively correlated with amount of cover (χ^2 = 18.88, d.f. = 1, P < 0.0001, Fig. 2).

Discussion

It was hypothesised that flight activity in lesser-short-tailed bats would be influenced by variation in forest structure, which could affect the probability of detecting bats from ground-based recorders. We found (using recorders) that height had a significant influence on detection rate of bats within each forest type. Recorded bat activity was greatest at the middle height tier of both the beech and podocarp forest sites. Of most interest, however, was the large difference in detection rate at the bottom level of each forest type (the position bat detectors are normally placed), where the beech forest site had high levels of activity, while the podocarp site in comparison

Figure 2. Mean number of passes by lesser short-tailed bats (*Mystacina tuberculata*) recorded at three different detector heights (B = bottom, M = middle, T = top) versus the mean level of vegetative cover at those heights for beech forest (open circles) and podocarp forest sites (closed circles). Note that cover estimates for individual plant species within each tier were summed, which in some instances resulted in an indicative comparison of foliage cover of more than 100% at some sites. Untransformed data are shown.

had little activity (Fig. 1). As hypothesised, flight activity was negatively correlated with vegetative clutter (Fig. 2).

Sleep and Brigham (2003) showed that small bats exploited clutter only when insect density increased, supporting their hypothesis that the use of spatially complex habitat depends on opportunities for prey capture. In other words, the bats would use an energetically costly foraging mode when the energy intake outweighed the additional cost of foraging. Insect densities are generally higher in cluttered than in open environments (Kalcounis & Brigham 1995; Hanula et al. 2000). If insect densities followed predictions based on forest clutter, the results from this study paradoxically suggest flight activity was lowest in areas with the greatest insect densities. Christie (2006) found that lesser short-tailed bats concentrated their activity in one or several relatively small areas, dispersed widely in the study area. Activity was considered to be related to foraging behaviour, which comprised active searching for prey within these small areas, alternating with commuting between foraging areas. This suggests that the bats in our study were likely to be using the flight paths for commuting between such foraging patches.

When Brigham et al. (1997) experimentally increased structural clutter while keeping insect densities the same, they found that artificial clutter negatively affected the foraging activity of small bats (*Myotis* spp.). According to optimal foraging theory, animals should seek to maximise their net energy intake (Stephens & Krebs 1986), which would in this case be accomplished by taking the path of least resistance as the bats commuted from one foraging area to another. Menzel et al. (2005) found significantly higher bat activity above the canopy than below the canopy, although several of the species found above the canopy were classified as clutter tolerant. This indicates that even though the bats were well adapted to navigate through cluttered environments, it was energetically advantageous to travel above the canopy while commuting between sites.

The high level of clutter close to the ground in the podocarp site may prohibit the bats from moving effectively below the subcanopy, therefore the middle tier may provide an energetically more beneficial flight path as it is still close to the ground and highest clutter level where potential prey items would be located. Similarly, the middle level (and often the ground level) of the beech forest site provides individual bats with the most energetically efficient path of movement through the forest. The higher level of activity at middle height level may also be explained in part by the fact that the ground level presents additional acoustic clutter and ground attenuation, and therefore flight in close proximity to the ground may be avoided when commuting.

The possibility exists that even though the bats were present, the ABMs were not detecting them within vegetative clutter. Weller & Zabel (2002) found that more bats were detected when the detectors were orientated toward the area with the fewest trees, which supported previous recommendations to orient detectors towards areas with the least clutter (Larson & Hayes 2000). Clutter can obstruct or impede reception of echolocation pulses by bat detectors. Patriquin et al. (2003) found that sound transmission differed between different forest types. It was more difficult to detect 25 kHz sound in intact forest sites than in thinned forest sites, which suggests that a more cluttered forest type would inherently decrease the detectability of short-tailed bats by masking pulses.

Therefore, differences in clutter can violate the assumption that the number of bat passes recorded at a site reflects the
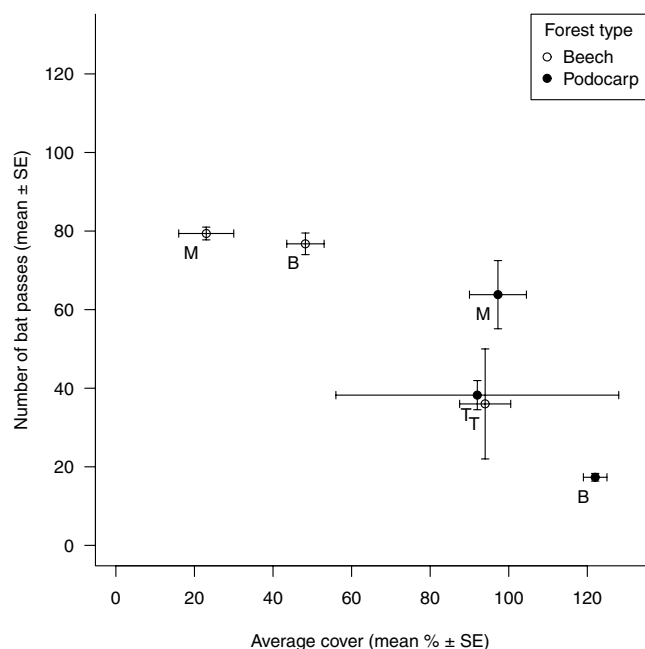
amount of bat activity (Hayes 2000). The lowest level within the podocarp site recorded a significantly lower amount of activity than the same level within the beech forest site; but this may simply reflect the higher level of obstruction rather than actual lack of activity. Accounting for the differences in detection due to clutter is complicated by the fact that the level of clutter may be affecting bat activity. However, regardless of whether the bats were present or not, detection was achieved most successfully at the bottom level within the beech forest site and the middle level of the podocarp forest site. This has implications for designing a robust monitoring programme for lesser short-tailed bats.

These results must be viewed in light of the limitations of this study. Vegetative clutter was estimated across broad height-range classes, rather than only within the narrow detection band of each ABM height. This was done to compensate for the lessening accuracy of estimates as height increased, and to follow a prescribed national methodology for measuring forest structure (Allen 1992). Future work could improve this study by specifically measuring clutter only within a height range of 2 m around each detector. In addition, it is likely that there was overlap between calls detected by each ABM. We acknowledge that the ABMs within a set were unlikely to be independent of each other, owing to the relatively small height differences separating them, and the calibration sensitivity of each ABM being set to detect most loud passes and miss most soft ones. The results from our study indicate that despite the overlap in detection by ABMs, there are differences in flight activity at different heights within these two forest sites, and that flight activity in lesser short-tailed bats is affected by vegetative clutter. However, only two forest sites were sampled representing two different habitat types, which provide only preliminary indications of site-specific variation in flight activity on a vertical axis.

We do not suggest that the activity patterns found in this study apply to all podocarp and beech forests, but do provide evidence that ground-based survey methods may not be equally effective in all forest types. When designing monitoring programmes for lesser short-tailed bats, we recommend that consideration be given to the forest structure and how this may affect detection of bat activity.

Acknowledgements

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